GRASPING COMPLEX MATTER

Large herbivore foraging in patches of heterogeneous resources

Promotor:	Prof. dr. H.H.T. Prins			
	Professor of Tropical Nature Conservation and Vertebrate			
	Ecology			
	Wageningen University			
Co-promotor:	Dr. ir. I.M.A. Heitkönig			
	Assistant Professor			
	Tropical Nature Conservation and Vertebrate Ecology Group			
	Wageningen University			

Examination committee:

Prof. dr. J.J.M. van Alphen Leiden University

Prof. dr. K.E. Giller Wageningen University

Dr. T. Piersma Netherlands Institute for Sea Research

Dr. S. de Bie Shell International

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Michael Drescher

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Abstract

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The functional response, defined as the relationship of forage intake with forage availability, is the principal link between a forager and a forage resource, and as such connects the trophic levels of consumers and producers. This thesis deals with the effects of forage resource structure on the shape of the functional response curve. Special attention was paid to the effects of the proportion of high quality forage within a heterogeneous forage resource, and of the spatial arrangement of high quality forage items within a matrix of low quality forage items. African Nguni cattle grazing stemmy, semi-arid grasslands were used as a model for large herbivores foraging in patches of heterogeneous forage resources. Decreasing the proportion of high quality forage decreased the asymptotic rate of forage intake and changed the shape of the functional response curve from a linear type I over an asymptotic type II to a dome-shaped type IV. Increased clustering of high quality forage items compensated for this decrease in forage intake to some extent. It is proposed that these effects result from the physical interference of low quality forage items with the cropping process in selective herbivores, thus connecting plant growth form with foraging behaviour. The generally negative relationship of forage availability with forage quality in natural grasslands suggests a dome-shaped functional response curve in the natural foraging situation, with low forage intake at high forage availability. However, because of pronounced spatial variation in forage availability and quality, foragers could utilise local foraging opportunities and achieved high forage intake and high diet quality even when on average forage availability was high and forage resource quality was low. Simulation models showed that such a system of a forager and a forage resource with variation in forage quality can reach different stable states, the major difference between these states being the exclusion or persistence of foragers in the system. It is further proposed that the spatial variation of forage availability and quality partially results from the local concentration of foraging efforts during times of plenty in a seasonally variable forage resource. This *de facto* resource partitioning can form the basis of species co-existence in herbivore assemblages, and can be useful in the management of species diversity in natural grasslands.

Key words: herbivory; functional response; grazing; food intake; food quality; selectivity; cattle; savanna.

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Chapter 1

General Introduction:

Large herbivore foraging and complex resources

The vast majority of large herbivores world-wide forage on grasslands. To the human eye a grassland at first glance might appear as a homogeneous and continuous forage resource. But to herbivores this is not so (e.g., O'Reagain, 1993; Heitkönig and Owen-Smith, 1998; Orians and Jones, 2001). Globally, most grasslands are extensively managed or are natural grasslands, with temporal and spatial variation in the forage resource on various scales. Especially, but certainly not exclusively, semi-arid grasslands are characterised by a high degree of complexity. The studies on which I report in this thesis were aimed at investigating the effects of forage resource structure, especially the effects of the proportion of high quality forage parts and of the spatial arrangement of forage parts, on foraging behaviour, with a focus on forage intake and diet quality.

Complexity in a natural forage resource

An important source of heterogeneity in natural grasslands is the nutritional inequality of different types of plant parts (e.g., Stobbs, 1973; Stockdale, 1999). The above ground part of a grass plant consists of leaves and stems, and, if the plant is in the reproductive state, of the inflorescence. Because of their larger availability, compared to inflorescences, leaves and stems are the more important plant parts to large herbivores, therefore we concentrate on the latter ones. Leaves and stems, when young, do not necessarily differ so much in their quality as forage. However, when matured, leaves generally are of much higher nutritional quality, require less force to be cropped, and are more easily digestible than stems, because of their comparatively higher tissue nutrient concentrations and lower fibre contents (e.g., Stobbs, 1975; Wales et al., 1990; Wright and Illius, 1995, Wilson and Kennedy, 1996). To herbivores, grasses are mosaics with within-plant resource heterogeneity, like variation in leaf density and tissue nutritive quality, determined by plant architecture and tissue development (Stobbs 1973, Orians and Jones, 2001). A herbivore-grassland system can be perceived more generally as a consumer-producer system with the producer population spilt into two classes: a high forage quality class, which are the leaves, and a low quality forage class, which are the stems.

Apart from the heterogeneity caused by the dichotomy of leaves and stems, there are other sources of heterogeneity in the grassland forage resource above the plant part level. Individual conspecific grass plants can differ in mass, plant part density and distribution, proportion of high quality plant parts, tissue nutrient concentrations and structural deterrents (e.g., O'Reagain, 1993; Laca *et al.*, 2001). Such differences between conspecific plants can be caused by variation in soil nutrient availability, as indicated by increased plant nitrogen

contents and digestibility after fertilisation (Stobbs, 1975; Day and Detling, 1990; Hassal *et al.*, 2001). Other causes of variation in plant structure and quality are defoliation and fire, which are generally beneficial for tissue quality and production (e.g., Douglas *et al.*, 1994; Milchunas *et al.*, 1995; Van de Vijver, 1999).

In multi-species grasslands, individual grass plants of different species are even more likely to differ from one other in the above mentioned characteristics, because of speciesspecific traits (e.g., Stobbs, 1973; Georgiadis and McNaughton; 1990; O'Reagain, 1993; Baruch and Bilbao, 1999). Grass species can differ widely in their growth form (tufted vs. cauline), height, tiller biomass and the proportion of high quality plant parts (e.g., O'Reagain 1993). On the one extreme we find mat-forming species, which are short, dense and leafy with thin stems. The other extreme are tall and stemmy, tuft-forming species with leaves concentrated at the base of the tufts or scattered along the stems.

Above the plant level, there may be variation in the forage resource structure and quality between patches, resulting from differences in soil nutrient levels, species composition, fire events and herbivore impact (e.g., Georgiadis and McNaughton; 1990; Ben-Sahar and Coe, 1992). Higher again, on the landscape level, the dominant source of heterogeneity in the forage resource are geomorphic features, like slope, rockiness and soil nutrients, and micro-climatic features, like rainfall and exposure affecting the species composition of the vegetation units (O'Reagain and Schwartz, 1995). To herbivores these forms of heterogeneity in grasslands mean that there is variation in the availability, accessibility and quality of forage on a number of spatial scales.

Seasonal variation in forage resource structure

The extensive utilisation of such grasslands is often related to the strong seasonal variation in the productivity of the grass swards. In resident foragers, population density is limited to a large extent by the forage availability during the periods of scarcity. During the growing season, forage productivity often temporary exceeds forage intake by the herbivores and the following accumulation of forage mass usually is accompanied by a decrease in forage resource quality (Fryxell, 1991; Hassal *et al.*, 2001; Bos, 2002). To cope with this decrease in forage quality, foragers may focus their foraging efforts spatially or temporally creating localities where forage availability and quality are intermediate, enabling high forage intake and diet quality (Fryxell, 1991; Bos, 2002). At the same time the forage production in other localities may go on without much forage consumption and these localities may proceed from the juvenile to the mature state.



Figure 1.1. In natural grasslands commonly a negative relationship is found of forage quality, here shown as the proportion of high quality forage, with forage availability.

In these matured localities, tissue differentiation between plant parts and resulting nutritional variation can be high, as can be the accumulation of moribund material (O'Reagain and Owen-Smith, 1996). This results in a mosaic of forage patches differing in mass, nutritional quality and architecture, which may shift through time and which may be reset by the seasonal decay of the forage resource during the dry season and by large-scale disturbances like floods or fires. Consequently, the dynamics of this consumer-producer system are seasonally changing.

Trading-off forage intake and diet quality

Most herbivores shrive to acquire a diet, which is of higher quality in terms of nutrient and energy content, and digestibility, than the average quality of the available forage (Hamilton *et al.*, 1973; Stobbs, 1975, Heitkönig and Owen-Smith, 1998; Prins, 1996). In grazing herbivores, such a high quality diet usually is characterised by a high proportion of high quality forage (e.g., Hamilton *et al.*, 1973; Stobbs, 1973). However, herbivores also show a preference for forage resources, which provide them with the highest short-term forage intake rate (e.g., Black and Kenney, 1984; Illius *et al.*, 1999). Herbivores usually can achieve a high short-term forage intake rate in resources with high forage availability, often defined as the mass of high and low quality forage parts per unit area. However, in natural grasslands, forage availability usually is inversely related to resource quality in terms of digestibility, nitrogen content or proportion of high quality forage parts (Fryxell, 1991; Prins and Olff, 1998; Hassall

et al., 2001; Bos, 2002; Figure 1.1). Acquiring a high quality diet requires searching for high quality forage parts and actively excluding low quality forage parts from the diet, possibly causing bite mass and bite rate to decline and depressing the rate of forage intake, compared to an indiscriminate diet. In grasslands with high forage availability herbivores therefore might face a trade-off between diet quality and forage intake. Herbivores might adjust to these constraints by choosing forage resource patches of intermediate quality and availability, in that way possibly finding an optimal solution to the quality-quantity trade-off, and maximising the net rate of nutrient and energy intake (e.g., Fryxell, 1991; Hassal *et al.*, 2001).

Effects of foraging on forage resource structure

Through foraging, herbivores alter the structure of the forage resource, the most obvious effect being the depletion of the forage resource (Laca et al., 1994a; Ginnet et al., 1999). On the other hand, selective foraging on high quality forage parts might result in only a minor decrease in overall forage availability, but in a decline in the availability of high quality forage, showing in a decrease of the proportion of high quality forage parts. These aspects of resource depletion can show on a number of spatial and temporal scales, starting at the level of the individual plant or feeding station up to camp or even landscape level, and they often lead to a decrease in diet quality (Kohlmann and Risenhoover, 1994; Ginnet et al., 1999; Ferguson *et al.*, 2001). However, when forage productivity is high and foraging intensity moderate, over somewhat larger scales foraging can have a positive effect on resource quality. For example, without foraging a productive grasslands accumulates mass, which normally is accompanied by an increase in the proportion of low quality support tissue, while at the same time high and low quality forage parts age and decrease in tissue quality, thus leading to a general decrease in resource quality. Foragers may tolerate a modest decrease in tissue nutrient levels or a decrease in the proportion of high quality forage parts to a certain level, but may be excluded from the resource if quality decreases further. Foragers might prevent that decrease in forage quality by removing forage from the resource before total forage mass and low quality support tissue accumulate and forage parts lose quality, in that way temporarily arresting a resource patch in the intermediate forage quantity - quality state (Fryxell, 1991; Bos, 2002). It is likely that there is an optimal foraging intensity for a given resource productivity, being high enough to maintain high resource quality, and at the same time being low enough prevent resource depletion.



Figure 1.2. Generally, three types of functional response curves are distinguished: (i) a linear type I curve, (ii) an asymptotic type II curve and (iii) a sigmoid type III curve. More recently a (iv) dome-shaped type IV curve is described for a number of forager-resource interactions involving foraging on complex resources.

The functional response

The functional response (sensu Solomon, 1949) is the relationship of the rate of forage intake with forage availability and as such plays a central role in the interaction of a forager with its forage resource. Understanding the factors governing the functional response is of fundamental importance to our insight into animal ecology. In the earliest models it was assumed that the functional response was linear. However, since Holling (1959) presented his disc equation we are aware that forage intake has an asymptotic relationship with forage availability, due to handling and processing constraints. It has been shown that the shape of the functional response curve depends on the type of foraging process. Commonly we distinguish three types of functional response curves (Figure 1.2). In a linear type I functional response curve, the rate of forage intake is a direct function of the density of food items. There is no real handling of food items involved in the harvest process or, compared to other processes like e.g., searching, handling takes negligible amounts of time. In the asymptotic type II functional response curve, the rate of forage intake first increases linearly with the density of food items, but then approaches an asymptotic value. The deceleration of the increase in the rate of intake is caused by a finite amount of time being necessary for the handling of food items, which thus is limiting the rate of processing of forage at high forage availability. In the sigmoid type III functional response curve, the rate of forage intake

increases first slowly but then its increase is accelerating until the intake rate becomes limited by the time for handling or processing and approaches an asymptotic value. This type of response might be caused by handling or searching of food items being less effective at low food densities. Besides of these commonly recognised types of functional response curves, more recently there is increasing evidence for the existence of a fourth type. In the domeshaped type IV functional response curve, the rate of forage intake initially increases with food density until it reaches a peak after which it decreases again (Figure 1.2). It appears that this type of functional response especially applies to selective foraging on a heterogeneous forage resource, with food items rather continuously than discrete distributed throughout the resource. The mechanisms causing a decrease in the rate of forage intake likely involve (i) a decreasing mass of cropped forage units and (ii) increasing handling efforts per unit forage through selection against low quality forage parts, with increasing forage resource availability.

Elements of the forage intake process

To understand the mechanisms which determine the type and shape of the functional response curve, we must have thorough of the process of forage intake. The basic unit of forage intake is a single bite of forage (Ungar, 1996). The bite has a mass, which is the mass of the harvested plant material, and a volume, which is the space previously occupied by the plant material before harvest (Ungar, 1996). The bite has a quality, which can be derived from the average quality of the ingested plant material or other properties like the proportion of high quality forage parts. Because the reach of a herbivore's cropping apparatus is spatially limited, bite mass is a function of plant part density and plant part mass. When there is spatial variation in plant part density on or above the scale of a herbivore's cropping apparatus, e.g., within a grass plant, bite mass is rather determined by the local density of plant parts than by average plant part density (Black and Kenney, 1984). If the forage resource is made up by a number of different forage parts, like leaves and stems, and the herbivore forages selectively, then the herbivore might limit the reach of its foraging apparatus to below its potential maximum in an effort to exclude low quality forage parts (e.g., Ruyle et al., 1987; Hongo, 1998; Ginnet et al., 1999). Bite mass might then rather be limited by the density of low quality forage parts instead of the density of high quality forage parts or total forage density. When a number of bites are taken in a series over some period of time, the bite rate, *i.e.*, the number of bites cropped per unit time, can be determined. As long as the mass of bites is rather low, bite rate is determined by the frequency of encounter with potential bites and the efforts necessary to handle a bite prior and during ingestion. Encounter frequency mainly is a function of the density of potential bites, the herbivore's foraging velocity and the width of its search path (Spalinger and Hobbs, 1992). Handling effort mainly depends on the grade of selectivity and the accessibility of the high quality forage parts, which may be a function of the physical properties of the high quality forage parts and of the degree of mixing with low quality forage parts. When bite mass surpasses the amount a forager can process in its vocal cavity without obstructing further handling and cropping of bites, bite rate decreases with increasing mass of bites (Laca *et al.*, 1994b). The rate of forage intake, *i.e.*, the amount of forage ingested over some period of time, is thus is thus the product of bite mass and bite rate. As bite mass and bite rate depend on the local density, mass and physical properties of high quality forage parts as well as on the degree of mixing with low quality forage parts, so does the rate of forage intake.

Study area and species

This study was mainly aimed at investigating the effects of heterogeneity in the forage resource on forage intake. For obvious reasons the fieldwork and experiments had to be performed in an area with strong variation in the quantity and quality of the forage resource. The choice fell on the Republic of South Africa, a sub-tropical country, which is covered for two thirds by extensive grasslands and savannahs and where temporal and spatial variation in natural processes still plays an important role in regulating the availability of the forage resource for large domestic and wild herbivores. Most of the South African land surface of some 1,219,900 km² (between 22° S, 16° E to 35° S, 33° E) is covered by a vast central plateau, varying in altitude between 1,200 and 1,800 m. It is rimmed at its west, south and east by mountain ranges, rising up to some 3,400 m in the Drakensberg Mountains, and which are surrounded by narrow coastal plains. The climate is Mediterranean with winter-rain in the south-west of the country, humid and tropical in the east, and semi-arid with summer-rain and variable temperatures in the highlands. Mean annual precipitation is less than 100 mm in the north-western Kalahari, increasing eastwards and reaching more than 1,200 mm at the eastern coastal plains of the province KwaZulu-Natal. Daytime maximum temperatures vary during the course of the seasons between some 15 to 45 ° C, with occasional overnight frosts during the winter months of June through to August in the higher altitudes.

In all experiments and observational studies the herbivore species used was cattle, *Bos taurus*. We used this species as a model-forager, representative of a larger number of other wild and domestic herbivore species. The choice fell on this species, because of four main

reasons. Firstly, cattle are relatively docile and easy to handle. This point was especially important because the study made it necessary to observe the herbivores in detail at close range. Secondly, cattle are extensively used as domestic livestock world-wide and so experimental animals are readily available, even in remote areas. Thirdly, because cattle are so widely used there is an extensive body of knowledge on the general behaviour of the species, with which the results of this study can be compared. And fourth, of all large herbivores, cattle are the most numerous. There is an estimated 1.3 billion cattle world-wide, which is more than 40 % of all domestic ruminants, and almost 30 % of all Artiodactyla, wild and domesticated (Van Soest, 1982; Van Wieren, 1996). Therefore, the findings of a study involving cattle has great relevance to many grazing systems, where cattle comprise the majority of foragers.

It is widely accepted that cattle are the domesticated descendants of the wild aurochs (*Bos taurus primigenius*), which presumably became extinct in the 17th century (Van Vuure, 2003). Cattle belong to the tribe Bovini, which first appeared in the Pliocene, between 5.0 and 1.8 million years ago. The Bovini include six genera amongst which are yak (*Bos grunniens*), African buffalo (*Syncerus caffer*) and American and European bison (*Bison bison* and *B. bonasus*). All Bovini are large-bodied, oxlike bovids. They are frequently classified as bulk and roughage feeders and due to their ability to digest cell wall components they are well adapted to foraging in grasslands (Van Soest, 1982).

As cattle are domesticated animals, one might argue that they are ill adapted to the natural environment. That one therefore cannot draw any conclusions about the interactions of wild herbivores with their natural forage resource and that cattle therefore are unsuited as a model for wild ruminant foragers. However, the races of cattle used in this study (Afrikaaner and Nguni) are indigenous to Southern Africa. At least for a 1,000 years they were used by Khoikhoi and Bantu people south of the Limpopo, who used to let them range freely in the grasslands and savannahs. Supplemental feeding during unfavourable periods was unknown to these people and we can safely assume that natural selection will have favoured the animals which were performing best in the natural grazing situation.

Objectives

Nutrients and fibre are unevenly distributed amongst different types of forage parts. Generally, leaves are high in nutrients and low in fibre, while stems are low in nutrients and high in fibre (e.g., Stobbs, 1975; Wales *et al.*, 1990; Wright and Illius, 1995, Wilson and Kennedy, 1996). Most foragers aim to ingest a high quality diet and therefore try to crop as

little low quality forage parts as possible (Hamilton *et al.*, 1973; Stobbs, 1973; Heitkönig and Owen-Smith, 1998). Up to the present day, functional response models typically have been developed in the temperate zone, sometimes on managed production grasslands, offering high proportions of high quality forage and little nutritional differentiation between leaves and stems. Often, these studies make insufficient distinction between high and low quality forage parts and do not address the effects of this heterogeneity on forage intake (e.g., Laca *et al.*, 1992, 1994b; Bergman *et al.*, 2000). However, the dichotomy between high and low-quality forage parts has been recognised as a potentially important factor affecting foraging behaviour (Fryxell, 1991; Hongo, 1998; Hassal *et al.*, 2001; Bos, 2002). This might especially be so when the proportion of high quality forage parts in the resource is comparatively small and the difference in nutritional quality between forage parts is large, as is the case in many natural and tropical grasslands.

In this study I investigated the effects of resource structure on the foraging behaviour of large herbivores. I dedicated special attention to the effects of mass and to the proportion of high quality forage and to the spatial arrangement of high quality forage parts on the shape of the functional response and on diet quality. I did so on a number of spatial scales, from the bite up to the patch level, because foraging behaviour on the various scales is likely to be interdependent and affected by scale-specific characteristics of resource structure. Ultimately, I strive to explain foraging behaviour as a series of hierarchic decisions taken over a number of scales in a seasonally changing environment.

Outline of the thesis

A natural grazing resource is made up by a number of types of forage, of which leaves and stems are the most important. Generally, leaves are higher in nutrients and lower in fibre than are stems, and most herbivores try to acquire a diet with a comparatively high proportion of leaves. The selection for high quality leaves and the exclusion of low quality stems is likely to have a negative effect on the rate of forage intake in stem-rich grasslands.

The first two chapters of this thesis deal with grazing experiments on artificial microswards. In Chapter 1, the swards used differed in mass, in the proportion of high quality forage, and in the spatial arrangement of high quality forage parts. In these swards, the rate of forage intake was measured in detail at the scale of a single feeding station. It was hypothesised, that decreasing the proportion of high quality forage should have a negative effect on the rate of forage intake. Therefore the shape of the functional response curve should change depending on the proportion of high quality forage in the sward. Furthermore, it was hypothesised that an increasing aggregation of high quality forage parts should have a positive effect on the rate of forage intake. A general model of the functional response was derived, explicitly including the degree of spatial aggregation of high quality forage parts.

In Chapter 2, the experimental swards differed in mass and in the proportion of high quality forage in the sward. Forage parts were distributed uniformly through the swards. In this study, the causal mechanisms governing the rate of forage intake were investigated. It was hypothesised that an increasing proportion of low quality forage should have a negative effect on bite mass and on bite rate, thus depressing the rate of forage intake. Therefore, special attention was paid to the effects of forage resource structure on the basic elements of the cropping process itself, e.g., on bite mass, on handling time and on searching time. From these results a functional response model of selective grazing in stem-rich swards was developed, driven by bite mass.

Chapter 3 deals with forage intake at patch level in a natural grassland. One aim was to test whether the factors controlling forage intake at the level of the feeding station also affect forage intake and diet quality in free-ranging herbivores grazing on a natural grassland. The grassland, which I chose for this study comprised of different sward types, differing widely in architectural characteristics, morphology and chemical properties. Because, foraging at larger spatial scales is likely to be controlled by other factors than on smaller scales, I also investigated factors that I had not studied on the smaller scales e.g., the spatial variation in sward height.

In Chapter 4, the results from the foraging experiments and the observations in the field, are taken to a theoretical level. The effects of forage resource structure, *i.e.*, the proportion of high quality forage parts, on the shape of the functional response curve were explicitly included in a simple simulation model of herbivore foraging. The model consists of a forager part and a forage resource part, with the latter being split into high and low quality forage. In this model, the production of low quality forage depends on high quality forage and the rate of forage intake depends on the proportion of high quality forage in the resource. The model enabled us to investigate how forage intake changes the structure of the forage resource and how this feeds back on forager-resource interactions.

Chapter 5 is a synthesis of the results of this study. Here the findings of the study were integrated and enriched with previously unreported data and results of other studies. A conceptual model of foraging on a complex forage resource was developed and tentative conclusions were drawn about the relationships of the factors governing forage intake on the feeding station level with foraging decisions on larger spatial scales. Further, the effects of

season on foraging behaviour were explored. Finally, the findings of this study were discussed in the context of alternative foraging strategies and resource partitioning as a potential base for niche differentiation and species-coexistence.

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Chapter 2

Forage availability and accessibility determine the functional response of herbivores in complex resources

Abstract

Herbivores utilize only a preferred part of the totally available forage resource. The density of preferred plant parts and their spatial aggregation likely affect the rate of forage intake. We investigated the effects of the proportion of leaves in the grass sward, of leaf cluster size, and of season on the functional response of a model herbivore, cattle, making use of artificial micro-swards. Decreasing the proportion of leaves from leaf-only to 45 % changed the shape of the functional response curve from Holling type I (linear) to type II (asymptotic) within our range of biomass on offer (20 - 180 g DM m⁻²), and depressed the maximum rate of intake from 0.85 to 0.15 g DM s⁻¹. For a leaf proportion of 25 % the intake rate did not correlate with total forage mass. Our results suggest physical interference of avoided plant parts with the bite formation process as a previously not recognized mechanism generating a type II functional response curve. Decreasing leaf cluster size from 200 cm², which coincided with the maximum bite area of our experimental animals, to below 50 cm² reduced the rate of intake. Intake rate limiting factors changed here from total forage mass to the proportion of leaves. We suggest that contrary to current theory the intake rate in food-concentrated patches is not only driven by bite mass, but also by bite rate. A 20 % decrease in intake rate from the wet to the dry season in uniform swards was linked to reduced leaf dry matter content. Worldwide, grazing resources range from simple, leafy swards in temperate and production grasslands, to complex, stemmy swards in semi-arid rangelands and savannas. Previous grazing models dealt with simple, leaf-only swards. We present a graphical, general grazing model, involving the proportion of leaves and leaf cluster size. This generalizes the applicability of the grazing model to a broader spectrum of resource types, over a range of environmental gradients.

Key words: functional response; resource availability; resource accessibility; grazing models; herbivory; selectivity; forage intake; savanna; grassland.

Introduction

Typically a large diversity in ungulate herbivore species is utilizing the forage resource provided by semi-arid grasslands, like Africa's savannas (Ritchie and Olff, 1999) To these herbivores, semi-arid grasslands are characterized by a high degree of complexity of the grazing resource, in contrast to most temperate and production grasslands. Grass species in semi-arid grasslands differ widely in their growth form, leaf/stem-ratio, and tiller biomass (O'Reagain, 1993). The patchy distribution of grass species adds a further level of heterogeneity to this (O'Reagain and Schwartz, 1995). To grazers, heterogeneity on these levels means spatial variation in available forage mass, its quality and its accessibility on various spatial scales. As a result, selective utilization of preferred plant parts, plants or patches is promoted (O'Reagain and Schwartz, 1995; Ruyle *et al.*, 1987; Augustine and Frank, 2001). In turn, due to selective grazing, herbivore impact further enhances spatial variation in forage mass and forage quality to this (O'Reagain and Schwartz, 1995; Bradbury *et al.*, 1996). This complexity of the grazing resource is suggested to affect the intake rate of herbivores.

The functional response, *i.e.*, the relationship of forage intake rate with forage mass (Holling, 1959), plays a central role in the interaction of consumers with their forage resource. The basic element of the forage intake rate in grazers is the process of taking a single bite, which includes all pre-severing manipulative movements of herbage as well as all movements related to severing and bringing this herbage into the mouth (Ungar, 1996). The forage intake rate is determined by the mass of the bites and the rate with which they are taken. Bite rate and bite mass, and thus the shape of the functional response curve, depend on the abundance and spatial arrangement of individual plants and plant parts. Due to the direct consequences of the functional response for animal fitness and production, and for understanding niche separation among grazing species, understanding the causal relationships of the specific form of the functional response with sward structure is of great interest for grazing ecology, wildlife management and animal husbandry.

The importance of spatial variation in forage quality, availability and accessibility on the scale of the patch has been dealt with in various models of forage intake rate on larger spatial scales (Ungar and Noy-Meir, 1988; Spalinger and Hobbs, 1992; Parsons *et al.*, 1994; Farnsworth and Illius, 1996). The common theme of the results is that in patches where food items are scattered and thus bite density is low, intake rate is limited by bite mass and searching time. On the other hand, intake rate mainly depends on bite mass in foodconcentrated patches where bite density is high.

On smaller spatial scales, like food-concentrated patches of the size of a feeding station, defined as the area in which a consumer can forage without locomotion (Novellie, 1978), experimental studies on the functional response of large grazers were concentrated on simple, leaf-only swards (Black and Kenney, 1984; Ungar *et al.*, 1991; Laca *et al.*, 1992a) or on vertically structured grass swards (Ginnet *et al.*, 1999; Bergman *et al.*, 2000). These studies were important in furthering our insight into the mechanics of bite formation. Generally they showed that bite mass and intake rate increase with sward height and bulk density. Furthermore it was found that the presence of stems in lower horizons of the sward had a negative effect on bite dimensions and reduced intake rates.

However, most grasslands have a complex structure, with a mixture of preferred (leaves) and avoided (stems) plant parts even within a single feeding station. Leaves are often attached on and thus in very close contact to stems, likely decreasing the accessibility of leaves. Local densities and levels of aggregation of preferred and avoided plant parts vary throughout the grass sward. Leaves and stems are usually unevenly distributed within a grass plant (Orians and Jones, 2001) and within-plant distribution of these plant parts varies between species of different growth forms (O'Reagain 1993) and between plants of different grazing history (Ruyle et al., 1987). In tuft-forming grasses leaves are aggregated at the base of the plant, favoring larger bite masses compared to cauline grasses where leaves are scattered along stems. Sparse tufts of grasses in grasslands of low productivity give rise to a horizontally uneven distribution of plant parts compared with dense production grasslands and swards dominated by mat-forming species. Grazers therefore encounter horizontal variation in the availability and accessibility of preferred plant parts on small spatial scales, to which they react by altering their cropping behavior (Roguet et al., 1998). Quantifying the effects of altered proportions of preferred and avoided plant parts in the sward canopy on the functional response is still lacking. Neither did we find any studies addressing the effects of spatial aggregation of preferred and avoided forage parts on the rate of forage intake. Current grazing models are therefore not suitable to predict intake from food-concentrated, complex swards. We performed two experiments with cattle (Bos taurus) grazing on hand-constructed swards of the (sub-) tropical grass Panicum maximum, differing in total mass, the proportion of leaves and the size (surface area) of clusters of leaves at the level of the feeding station.



Figure 2.1. Initially expected, hypothetical family of functional response curves in the experiment on forage availability: as proportion of leaves decreases, the initial take-off of the functional response curve from the x-axis moves towards higher total masses (1, 2a, 3a). A possible decrease in the slope of the curves was anticipated (1, 2b, 3b). It was not expected that the maximum intake rate would be affected by a change in the proportion of leaves.

Our first experiment was designed to quantify changes in the functional response with changes in the forage availability. Utilizable forage mass, which was called forage availability in this study, was the proportion of preferred parts of forage (leaves) in this total mass of forage. As we reduced forage availability we expected to find a shift of the functional response curves towards higher values of total forage mass with the maximum intake rate not being affected much (Figure 2.1, sections 1, 2a, 3a). We anticipated that we might find a decrease in the slope of the curves with decreasing proportion of leaves (Figure 2.1, sections 1, 2b, 3b).

Our second experiment was designed to quantify the effects of forage accessibility on the functional response. For a constant forage mass and constant proportion of leaves, the availability of preferred parts of the forage remains the same. However, the ease of ingestion of preferred forage parts, which was called forage accessibility in this study, depends on the dilution of preferred by non-preferred forage parts or, in other words, on the degree of local clustering of preferred plant parts. Thus, we varied forage accessibility by altering the size of clusters of preferred forage parts within the grass sward, while keeping total mass and proportion of leaves constant. By increasing accessibility, we expected to find an increase in intake rate.

Methods

Experimental swards

The study was conducted at the Research Farm of the University of Fort Hare, at Alice, Eastern Cape, South Africa. All experimental work was performed using hand-constructed swards (Black and Kenney, 1984; Laca *et al.*, 1992b). Each morning between 7:30 and 9:30, tillers of *Panicum maximum* were clipped in the field. At all times, plant parts were kept in water, sprayed and, if necessary, covered with plastic to prevent wilting. Leaves and stems were separated and then threaded through holes in wooden blocks. Per hole we used either three leaves (subsequently we call this one leaf tiller) or one stem, or holes were left empty. In each block of 10 cm x 10 cm there were 16 holes in a square grid at equal distance. Per block a minimum of one hole and a maximum of 8 holes were filled with leaves or stems, the resuming holes were left empty. Plant parts were clamped to the wooden block by shifting a plastic plate underneath the block and screwing it tightly against it. We fastened between 40 to 50 blocks on a large plastic board, to produce one hand-constructed sward of between 0.4 m² to 0.5 m² in size. Always, leaf tillers and stems were trimmed to produce a uniform canopy height of 15 cm. Hand-constructed swards were offered to the animals in a stable between 11:00 and 15:00.

Experimental animals

We used four Nguni oxen (*Bos taurus*) of 1.5 to 2 years, weighing 250 to 320 kg. Two of the oxen were esophageally fistulated more than 4 months earlier for other experiments. All animals were duly cared for by a veterinarian. When not in experimental trials and between experimental series, the animals were kept on a rangeland, but had daily contact with the experimenters. During the period of the experiments the animals were not supplemented.

Experimental design

The experiments were performed from February to March 2000, during the late wet season, and from May to June, during the subsequent early dry season. Prior to each experimental series, the animals were trained for at least 3 weeks to accustom them to the experimental setup. Each day, before beginning with the experimental trial, the animals were collected from the rangeland and brought to a stable, where they were fasted for 2.5 to 5 hours.

Table 2.1. Combinations of total forage mass with proportion of leaves in hand-constructed swards of *Panicum maximum* offered to cattle in the experiment on forage availability. All leaf tillers and stems were arranged uniformly over the grass sward. All treatments were applied in the wet and in the dry season.

Total mass [g DM m ⁻²]		Proportion of leaves	s [%]
20	-	45	100
80	25	45	100
180	25	45	-

Subsequently, one animal was led to the hand-constructed sward and allowed to graze. The grazing process was video taped and the observation was ended only after a substantial part of the herbage was removed or the animal seemed to lose interest. We measured the period of active grazing [s] using the video recordings; periods when animals followed other activities were excluded from the measurements. Available pre-grazing forage mass [g dry matter (DM)] was estimated *via* randomly selected and removed blocks. Totally ingested forage mass [g DM] was calculated as the difference of pre-grazing forage mass minus the residual forage mass after grazing. Average intake rate [g DM s⁻¹] was removed forage mass divided by active grazing time. In the remainder of this paper, forage mass is expressed as g DM per area. Each of the four animals was exposed to each treatment; animals were treated as replicate measurements.

Swards differed in total mass (g DM leaf + g DM stem), proportion of leaves (g DM leaf / g DM total * 100 %), and spatial arrangement of leaves and stems. We varied total mass by changing the density of filled holes, *i.e.*, by changing the bulk density. Due to logistic constraints we used an incomplete factorial design. We offered swards of low (\pm 20 g DM m⁻²), medium (\pm 80 g DM m⁻²), and high (\pm 180 g DM m⁻²) total mass. The proportions of leaves were low (\pm 25 % leaf), medium (\pm 45 % leaf), and high (100 % leaf). The spatial arrangement of leaf tillers and stems was varied by using leaf clusters of varying surface area: very small (\pm 12.5 cm²), small (\pm 25 cm²), medium (\pm 100 cm²), large (\pm 200 cm²), and very large (\pm 400 cm²). A leaf cluster, in this study, is one leaf tiller or a number of leaf tillers directly adjacent to one another. The perimeter of a leaf cluster is spatially defined by the stems surrounding it.
Table 2.2. Combinations of total forage mass with proportion of leaves and leaf cluster size in handconstructed swards of *Panicum maximum* offered to cattle in the experiment on forage accessibility. The combination of 80 g DM m⁻² with 45 % leaf was used for a more detailed investigation of the relationship of intake rate with leaf cluster size. All treatments were applied in the wet and in the dry season.

Total mass [g DM m ⁻²]	Proportion of leaves [%]	Leaf cluster size [cm ²]		
80	25	25, 200		
80	45	25, 100, 200, 400		
180	25	12.5, 200		
180	45	12.5, 200		

In the first experiment on forage availability leaf tillers and stems always were arranged uniformly over the grass sward. There was no apparent clustering of leaf tillers or stems. The combinations of total forage mass and proportion of leaves used for this experiment are presented in Table 2.1.



Figure 2.2. Schematic representation of the spatial arrangement of leaf tillers and stems in the experiment on forage accessibility. Each hand-constructed sward was constructed by 5 x 10 blocks with exception of treatments f) (48 blocks) and h) (40 blocks). In treatments a) - d), all blocks of one HCS are identical and carry leaves (L) and stems (S). Leaf cluster sizes for a) and b) were 25 cm², and for c) and d) were 12.5 cm². In treatments e) – h) blocks carry only leaves (L) or only stems (S). Leaf cluster size for e) was 100 cm², for f) and g) was 200 cm², and for h) was 400 cm².

In the second experiment on forage accessibility we arranged tillers of leaves and stems in various degrees of clustering over the grass sward. The combinations of leaf cluster size, total forage mass and proportion of leaves utilized for this experiment are presented in Table 2.2 and Figure 2.2.

Data analysis

We analyzed the data of the experiment on forage availability by regressing intake rate [*I*, g DM s⁻¹] on total forage mass [*M*, g DM m⁻²] making use of a linear type I or an asymptotic type II model, as fitting best. For the type I model we made use of the standard linear equation I = a + b M with dimensions [a] = g DM s⁻¹ and $[b] = m^2$ s⁻¹. For the type II model we used a rectangular hyperbola with I = c M / (d + M) and dimensions [c] = g DM s⁻¹, [d] = g DM m⁻². Fitting was done using linear and non-linear least squares fitting functions. We investigated the best fitting models for an effect of season by comparing the slope and the elevation of the regression lines (Zar, 1999) between wet and dry season models. In the case of the type II models we first linearized the functions before performing further analyses. In the absence of a significant effect of season we pooled the data over both seasons and fitted a non-seasonal model. Additional analyses for an effect of season over all intake rate data was performed making use of a repeated-measures ANOVA with animals as subjects and season and proportion of leaves * total mass as within–subjects factors.

The data of the experiment on forage accessibility were analyzed by regressing intake rate [*I*, g DM s⁻¹] on leaf cluster size [*S*, cm²] while keeping total forage mass and the proportion of leaves constant. We fitted asymptotic type II response curves making use of the rectangular hyperbola model I = e S / (f + S) with the dimensions of the maximum rate of intake [*e*] = g DM s⁻¹, and of the half-saturation constant [*f*] = cm². Best fitting models were identified using a non-linear least square fitting function. One series of treatments (100 g DM m⁻², 45 % leaf) was used for a more detailed analysis of the relationship of intake rate with leaf cluster size (Table 2.2). These data were investigated for effects of season, total forage mass and proportion of leaves by comparing slope and elevation of the linearized functions. An additional analysis of all fitted functions was performed by comparing the maximum rate of intake (*e*) and the half-saturation constant (*f*) between treatments and seasons. For this we made use of the Mann-Whitney *U*-test. All analyses were performed using the statistical software package SPSS 8.0 (SPSS Inc.).



Figure 2.3. The functional response of cattle grazing hand-constructed swards of *Panicum maximum* in the experiment on forage availability. Best fitting curves for different proportions of leaves and different seasons (late wet and early dry season) are shown. Solid lines and filled symbols are wet season data; dashed lines and open symbols are dry season data.

Results

Forage availability

The relationship of intake rate with total mass varied with the proportion of leaves and with season (Fig. 2.3). In swards with 100% leaf, intake rate was positively correlated with total forage mass. Over the range from about 20 to 80 g DM m⁻², the maximum individual intake rate was found to be 0.85 g DM s⁻¹. The type I model fitted best to both the wet and dry season data. By comparison of the models it showed that neither the slope (t = 0.742, v = 12, P > 0.20), nor the elevation (t = 1.404, v = 13, P > 0.10) differed significantly between seasons. Therefore, the data were lumped over both seasons to produce a non-seasonal type I model of intake rate on total forage mass (I = -0.03 g DM s⁻¹ + 0.01 m² s⁻¹ M, $R^2 = 0.87$, P < 0.001).

In mixed swards with approximately 45% leaf, we found a positive relation of intake rate with total mass over the range from about 20 to 180 g DM m⁻² (Fig. 2.3). In these swards the maximum rate of intake was 0.23 g DM s⁻¹. In both the wet and the dry season a type II model gave the best fit to the data. When comparing the wet and dry season models, neither the slope (t = 0.675, v = 20, P > 0.20) nor the elevation (t = 0.519, v = 21, P > 0.20) were significantly different. Accordingly we lumped the intake rate data over both seasons and determined one non-seasonal type II model for intake rate on total forage mass with I = 0.17 g DM s⁻¹ M / (18.37 g DM m⁻² + M); $R^2 = 0.26$.

Table 2.3. Parameter values of the rectangular hyperbola model I = e S / (f + S) (see text) of intake rate curves as a function of leaf cluster size for cattle grazing hand-constructed swards of *Panicum maximum* in the experiment on forage accessibility. I_{50} and I_{200} are intake rates at leaf cluster sizes of 50 and 200 cm².

Total mass [g DM m ²]	Proportion of leaves [%]	Season	e [g DM s ⁻¹]	f [cm ²]	I_{50} [g DM s ⁻¹]	I_{200} [g DM s ⁻¹]
80	25	wet	0.34	52.46	0.17	0.27
		dry	0.18	39.02	0.10	0.15
80		wet	0.29	12.67	0.23	0.27
	45	dry	0.19	13.77	0.15	0.18
180	25	wet	0.33	32.04	0.20	0.29
		dry	0.21	32.26	0.13	0.19
180	45	wet	0.36	18.32	0.26	0.33
		dry	0.27	16.59	0.21	0.25

In mixed swards with approximately 25 % leaf, the maximum rate of intake was 0.15 g DM s⁻¹ (Fig. 2.3). Over the range of about 80 to 180 g DM m⁻², the rate of forage intake stayed constant, *i.e.*, there was no correlation of intake rate with total forage mass. Parallel to the 100 % and 50 % leaf treatments, we did not find a significant effect of season on the elevation of the models (t = 1.458, v = 12, P > 0.05). The data lumped over both seasons gave rise to a type I model, which reduced to I = 0.09 g DM s⁻¹.

Over all treatments there was an average decrease in dry matter intake rate of 19 % from the wet to the dry season for matched pairs of observations (animal, treatment). This drop in intake rate coincided with an average decrease in dry matter leaf mass of 22 % from the wet to the dry season, also for matched pairs of observations. Nevertheless, a repeated-measures ANOVA did not show a significant effect of season on the rate of forage intake (P = 0.138).

Forage accessibility

For swards of about 80 g DM m⁻² and 45 % leaf (Table 2.2) we found that leaf cluster size had a positive effect on intake rate, yet, this effect was limited to small leaf cluster sizes. We found that asymptotic type II models fit well to the seasonally split data: I = 0.289 g DM sec⁻¹ S / (12.670 g DM m⁻² + S), $R^2 = 0.19$, wet season and I = 0.191 g DM sec⁻¹ S / (13.766 g DM m⁻² + S), $R^2 = 0.15$, dry season (Figure 2.4). Comparison of the linearized models showed that there was no effect of season on the slope (t = 0.495, v = 14, P > 0.50), but on the elevation (t = 3.036, v = 15, P < 0.005) of the functions. Thus, intake rates from larger leaf clusters were higher in the wet season than in the dry season (Table 2.3).



Figure 2.4. The effects of leaf cluster size and season on the intake rate of cattle grazing handconstructed swards of *Panicum maximum* of about 45 % leaf and 80 g DM m⁻² total mass in the experiment on forage accessibility. Means of experimental data and best fitting curves are presented. Filled symbols and solid line are wet season data; open symbols and dashed line are dry season data. Error bars show the standard error of the mean.

Compared to the total range of leaf cluster sizes, the half-saturation constant was very low for both models (Table 2.3), indicating a very rapid approach to the maximum intake rate with increasing leaf cluster size (see I_{50} and I_{200} in Table 2.3). Above a cluster size of 200 cm² the fitted models hardly experienced any further increase in intake rate (Fig. 2.4).

Over all combinations of total forage mass, proportion of leaves and season, we found a significant effect of season on the maximum of the fitted type II intake rates (U = 16, $n_1 = 4$, $n_2 = 4$, P = 0.025, Figure 2.5, Table 2.3). For each curve the maximum intake rate was lower in the dry season than in the wet season (53 – 75 % of the wet season value, see Table 2.3). This effect was mirrored by a decrease of the rate of forage intake from the wet season to the dry season over all treatments of 25 % and a decrease of the dry matter leaf mass, also by 25 %. Contrary to the effect of season on the maximum rate of intake, there was no effect of season on the half-saturation constant (U = 8, $n_1 = 4$, $n_2 = 4$, P > 0.10). There was no effect of the proportion of leaves on the maximum rate of intake of the fitted models (U = 7, $n_1 = 4$, $n_2 = 4$, P > 0.20), but there was a significant effect on the half-saturation constant (U = 16, $n_1 = 4$, $n_2 = 4$, P = 0.025). For the 25 % leaf treatments the half-saturation constant was consistently larger than for the 50 % leaf treatments (Table 2.3). There was no effect of total forage mass on either the maximum intake rate nor the half-saturation constant.



Figure 2.5. The effects of leaf cluster size, proportion of leaves and season on the intake rate of cattle grazing hand-constructed swards of *Panicum maximum* in the experiment on forage accessibility. Best fitting curves are presented. Filled symbols and solid lines are wet season data; open symbols and dashed lines are dry season data.

Discussion

Our results show the importance of the proportion of preferred forage parts and of the spatial distribution of these forage parts in the grazing resource for the rate of forage intake of herbivores. We quantified how selective grazing on the grazing resource and the spatial arrangement of plant parts affect the shape of the functional response curve and how they cause a change between the mechanisms generating a type II functional response curve in food-concentrated patches.

We found that the shape of the functional response curve changed with forage availability, *i.e.*, with the proportion of preferred parts in the total forage mass. This change took place in such a way that both the slope and the maximum value of the intake rate curves were depressed, which was different from our expectations (Figures 2.1 and 2.3). For leaf-only swards we found that a linear type I model with a rather steep slope fitted our data well. In other studies (Black and Kenney, 1984; Gross *et al.*, 1992; Bergman *et al.*, 2000) it was found that the functional response curve asymptotically approached some maximum value as total forage mass per unit area was increased and the herbivore's intake rate became limited by the capacity of its ingestive apparatus. We were aware that also in this study a deceleration of the intake rate curve, giving rise to an asymptotic type II model, would have been likely if we increased total forage mass further. When we decreased forage availability (45 % leaf), we found that an asymptotic type II model had the best fit with our data. Compared to leaf-only swards intake rates were depressed and the rate of forage intake approached the asymptotic

maximum already at rather low values of total forage mass. Similar negative effects of the dilution of preferred forage parts by avoided forage parts are found in other studies for herbivores (Ginnet *et al.*, 1999; Bergman *et al.*, 2000) and for predatory fish (Czesny *et al.*, 2001). When decreasing forage availability even further (25 % leaf), intake rates were constant and very low over the range of total forage mass we offered. We do not expect intake rates to rise when total forage mass offered would be increased further.

In simple, leafy swards intake rates were closely related to total forage mass. This complies with other studies (Allden and Whittaker, 1970; Black and Kenney, 1984; Wickstrom et al., 1984; Hudson and Frank, 1987; Wilmshurst et al., 1999). In such swards all parts of the offered forage are preferred forage parts, and the mechanical explanation for the tight link of intake rate with total forage mass is that intake rates are mainly driven by the bulk density of the preferred forage parts in the cropped bite volume and thus by bite mass (e.g., Spalinger and Hobbs, 1992). However, in complex, stemmy grass swards intake rates were limited by the proportion of preferred forage parts (leaves) instead of the total forage mass, and even a major increase in total forage mass was not likely to raise intake rates. We propose that in such swards bite volume and thus bite mass, became depressed with increasing proportion of avoided plant parts, due to their physical interference with elements of the bite formation process, like the tongue sweep. Further we propose that because of selective grazing, handling times were increased, as suggested by Stobbs (1973). These combined effects limited the rate of intake and increasing bulk density only served to intensify the interference with the bite formation process, thus keeping intake rates depressed. We propose a threshold in the proportion of preferred plant parts where a change in limiting factors could be expected (this threshold could not be determined in our study, but is expected to lie above 45 % leaf for cattle-like animals). Above this threshold intake rate is driven by bulk density and a type II functional response curve is expected to arise caused by the competition between cropping and chewing as suggested in other studies (Spalinger and Hobbs, 1992; Gross et al., 1992; Laca et al., 1994a). However, below this threshold intake rate is depressed by the limitation of bite mass and handling time caused by the interference with avoided plant parts, which therefore constitutes an alternative mechanism generating a type II functional response curve in food-concentrated patches.

As predicted, intake rates increased with forage accessibility, *i.e.*, leaf cluster size. Contradictory to our expectations, this effect was restricted to rather small leaf cluster sizes. From a leaf cluster size of about 200 cm² onwards, leaf cluster size did not seem to have any further effect on intake rate. Even in the largest leaf clusters (*ca.* 400 cm²) intake rates stayed comparatively low and never exceeded 50 % of the intake rates from leaf-only swards (0.38 g DM s⁻¹ vs. 0.85 g DM s⁻¹). Interestingly, the threshold-value of 200 cm² was very similar to the maximum bite area in leaf-only swards (185 cm²) and thus was about the same as the maximum potential bite area. We propose that for a given total forage mass in stemmy swards with small leaf clusters, intake rates were depressed due to the before mentioned mechanism of the physical interference of avoided plant parts with the bite formation process. Increasing aggregation of preferred plant parts then enables the herbivore to crop bites interference-free from within the cluster of preferred plant parts.

Forage accessibility in stemmy swards was high when preferred plant parts were arranged in large leaf clusters (400 cm²) and was thus permitting grazers interference-free cropping of bites with maximum bite size. In such a situation the rate of intake should be driven by bite mass and thus by leaf density in leaf clusters, comparable to the situation of leaf-only swards. However, intake rates stayed well below the maximum in leaf-only swards. We conclude that besides the interference with avoided plant parts, there must be other factors involved in the depression of intake rates in swards with leaf clusters. Intake depression due to resource depletion has been investigated before (Laca et al., 1994b; Ginnet et al., 1999). It was found that intake rates declined mainly as a consequence of increasing overlap of bites as the grazing horizon became depleted. In the present study, in grass swards of low forage availability (45 % leaf) obviously there was less leaf area available for bites to be placed compared to leaf-only swards. We propose that this caused increased bite overlap as can also be seen in the work of Ungar et al.(2001). Furthermore, we propose that edge effects were involved in the depression of intake rates. A conceptual model of bite formation put forward by Laca et al. (1993) implies that residual leaf material is left behind after cropping a bite. Attempts to crop residual material near a leaf cluster edge presumably result in smaller bite mass compared to leaf-only swards. Also, taking bites from spatially separated leaf clusters might decrease bite rates compared to leaf-only swards where herbivores can take bites directly next to each other. It might be expected that if leaf cluster sizes were to be increased towards the size of a whole feeding station (about 0.5 m^2), the strength of the intake depression should slowly subside. We suggest that the increasing aggregation of preferred plant parts has the potential to change the mechanism generating a type II functional response curve from interference with the bite formation to competition between cropping and chewing. However, due to the involvement of edge effects this change is expected to take place only gradually.



Figure 2.6. Conceptual model of the relationship of intake rate on feeding station level with total mass, proportion of leaves and leaf cluster size. For very small to small leaf cluster sizes (a) intake rates are a function of proportion of leaves, besides of total mass and leaf cluster size, indicating a limitation of intake by bite mass and bite rate. For large leaf cluster sizes (b) intake rates are mainly a function of total mass, showing intake regulation mainly by bite mass. As leaf clusters get even larger (c) intake depression by resource depletion and edge effects gradually becomes weaker and intake rates are regulated by cluster size and total mass, again showing the effect of bite mass on intake rates. Finally, as leaf cluster sizes approach the size of a whole feeding station (d), intake rates get released from intake depression by edge effects and are only a function of total mass or bite mass, thus reaching the values of leaf-only swards.

In Figure 2.6 we present a conceptual, graphic model of the effects of increasing aggregation of preferred plant parts on forage intake, following the postulated mechanisms as described in the previous sections.

In stemmy swards of a given leaf cluster size, the proportion of preferred plant parts (leaves) in the sward essentially regulates the density of leaf clusters throughout the sward. Leaf cluster density relates negatively to the distance between leaf clusters. Therefore, decreasing the proportion of leaves in the sward means increasing the distance between leaf clusters. We suggest that taking bites from increasingly distant leaf clusters causes bite rates to decrease and has a negative effect on the rate of forage intake. We put this forward as a probable mechanism causing the rate of forage intake to decrease with decreasing proportion of preferred plant parts at a moderate level of aggregation of preferred plant parts in food-concentrated patches (see I_{200} in Table 2.3). This is contradictory to the general assumption in many foraging models that the rate of forage intake in food-concentrated patches is solely driven by bite mass (e.g., Spalinger and Hobbs, 1992; Farnsworth and Illius, 1996).

Conclusion

Preferred (leaves) and avoided (stems) plant parts are intricately mixed in natural grasslands, thus decreasing the accessibility of preferred plant parts. Leaves and stems usually are unevenly distributed within a grass plant and within-plant distribution varies between species of different growth forms and between plants of different grazing history. This causes the spatial distribution of preferred and avoided plant parts to show small-scale variation throughout the grass sward. Hence, natural grasslands show much local variability in (i) the proportion of preferred plant parts, (ii) the density of plant parts and (iii) the size of aggregations of plant parts. Since the functional response of our herbivores was strongly affected by local variation in the spatial distribution of preferred and avoided plant parts in our hand-constructed swards, we suggest that herbivores also respond to the non-uniform distribution of plant parts in natural grasslands. Present forage intake models (Black and Kenney, 1984; Ungar et al., 1991; Laca et al., 1992a) are constrained to uniform, leafy swards as usually found in temperate and production grasslands, and likely overestimate forage intake rates in complex, stemmy swards. More general models of forage intake, also applicable to the more complex, stemmy swards in many semi-arid and natural grasslands, should differentiate between preferred and avoided plant tissues (leaves vs. stems). In particular, they should include variables describing the availability and accessibility of preferred plant parts. We propose that the factors (i) proportion of leaves and (ii) local leaf aggregation fulfil this function. This set of variables widens the applicability of our forage model from leaf-only (Figure 2.6 section d) to complex swards (Figure 2.6 sections a, b, c) thus enabling a more realistic estimation of forage intake rates from complex, natural resources.

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Chapter 3

Depressed intake rates with increasing forage availability in complex resources

Abstract

Forage intake rates from complex resources depend on the density and accessibility of preferred forage parts. Depending on the quality of the forage resource, different mechanisms can control the functional response. We investigated the effects of the density of preferred and avoided forage parts and of season on the forage intake of a model herbivore, cattle, grazing artificial micro-swards. As expected, bite mass was found to control the rate of forage intake in food-concentrated patches. However, opposite to conventional theory, we found that it was not the competition between forage acquisition and forage processing, which was generating a Holling's type II (asymptotic) functional response curve. Instead, intake rates were depressed because of a decrease in bite mass without saturating the processing capacity. The decrease in bite mass was caused by decreased accessibility of preferred forage parts, due to the physical interference of avoided forage parts with the harvesting process. In extreme cases, this mechanism is likely to generate a Holling's type IV (domed) functional response curve in complex forage resources. A foraging model based on the described interference-mechanism is generating functional response curves, which correspond qualitatively with field observations. The model can be applied over a range of forage resource qualities and is likely to predict forage intake rates from complex resources more accurately than previous models.

Key words: functional response; resource accessibility; grazing models; herbivory; selectivity; forage intake; savanna; grassland.

Introduction

The functional response, *i.e.*, the relationship between the rate of forage intake and the available forage mass, is the central process in the trophic interaction of a forager with its forage resource. It has been argued that in large grazers foraging in food-saturated patches, owing to the competition between forage acquisition and forage processing, the rate of forage intake is saturating with increasing forage abundance and is therefore approaching an asymptotic maximum generating a so called type II functional response curve (e.g., Holling, 1959; Spalinger and Hobbs, 1992).

Experimental evidence for this view has been found for many predator-prey systems, including grazing herbivores foraging in simple, leafy grasslands. In such uniform grasslands, forage quantity, typically measured as sward mass per unit area, drives bite mass, which in food-concentrated patches can be used to predict the rate of forage intake (Black and Kenney, 1984; Bergman *et al.*, 2000; Iason *et al.*, 2002). The finite capacity of the herbivores' forage processing apparatus limits forage ingestion at high bite masses and therefore gives rise to the asymptotic functional response curve.

However, the situation appears different in natural grasslands, which are complex forage resources with strong variation in the quality of parts of the forage resource and with local variation in the quantity and accessibility of preferred forage parts (e.g., Georgiadis and McNaughton, 1990; Ben-Sahar and Coe, 1992; Hendrickson *et al.*, 1997). This variation has consequences for the foraging behaviour of herbivores on various scales (Stobbs, 1973, 1975; Ben-Sahar and Coe, 1992; Chapter 2).

Most free-ranging herbivores select for preferred plant parts to some degree (Stobbs, 1975; Hongo, 1998; Bergman *et al.*, 2000). To them, a grassland is a complex mosaic of preferred (leaves) and avoided (stems) plant parts (e.g., Heitkönig and Owen-Smith, 1998), because of the uneven distribution of these plant parts within the plant (Orians and Jones, 2001) and because of the differences in growth form of grass species (O'Reagain, 1993). It has been proposed that avoided plant parts in intimate mixture with preferred plant parts interfere with the cropping process, resulting in a decrease of bite mass and bite rate. In such a situation bite mass does not reach levels where the capacity of the processing apparatus becomes saturated. Consequently, it is unlikely that the previously proposed competition between forage acquisition and forage processing causes the asymptotic shape of the functional response curve in complex swards (Chapter 2).

Because sward mass does not account for the differences in quality between plant parts, nor incorporates aspects of the accessibility of preferred forage parts, sward mass in itself is not sufficient as an accurate predictor for the rate of forage intake (Hongo, 1998; Van der Wal *et al.*, 1998; Iason *et al.*, 2002; Chapter 2). Instead, in complex grasslands it is rather the density of preferred plant parts, being a function of the proportion of preferred plant parts in the sward and of sward mass, and the density of avoided plant parts, which determine the rate of forage intake (Chapter 2).

Various experimental studies addressed the effects of density of plant parts (Black and Kenney, 1984; Laca *et al.*, 1992a) and of vertical variation in the density of plant parts (e.g., Ginnet *et al.*, 1999) on the rate of forage intake in leaf-only swards, *i.e.*, swards consisting only of preferred plant parts. A number of studies investigated the effects of the presence of avoided plant parts in sub-canopy layers of the sward (Ginnet *et al.*, 1999; Bergman *et al.*, 2000). However, only very few studies addressed the effects of avoided plant parts in the canopy layer of the sward (but see Ruyle *et al.*, 1987, Hongo, 1998). As a consequence, up to now it still it remains unclear by which mechanisms the distribution of preferred and avoided plant parts throughout the sward, including the sward canopy, affects bite mass and bite rate, and how these ultimately affect forage intake and the shape of the functional response curve.



Figure 3.1. A conceptual model of forage intake over short time scales. The model is hierarchically organised with the rate of forage intake on the top, being the product of bite mass with bite rate. Bite mass is a function of the number of tufts of leaves cropped per bite and of bite depth, which is the depth at which the cropped leaf tufts are severed. Time per bite is the inverse of bite rate. Time per bite is the sum of handling time plus searching time.

This is an impediment to our understanding of forage intake in natural grazing systems, because an important characteristic of natural grasslands is the intimate association of preferred and avoided plant parts throughout the whole grass sward, including its canopy layer.

In this study we investigated the mechanisms by which the densities of preferred and avoided forage parts affect the rate of forage intake and the shape of the functional response curve in large herbivores. To do so, we used a conceptual model of forage intake over short time scales (Figure 3.1). This model is hierarchically organised and at its top we find the rate of forage intake. Intake rate is defined as the product of bite mass and bite rate, which form the second layer of the model. Bite mass here is perceived as a function of the number of tufts of leaves cropped per bite and of bite depth. Bite depth being the average depth at which cropped leaf tufts are severed. The number of tufts of leaves cropped per bite and bite depth therefore comprise part of the third and most basic model layer. Bite rate, and its reciprocal, time per bite, are functions of handling time and of searching time, which also form part of the third model layer. We investigated the effects of sward quality and forage accessibility on each element of the grazing model. Working our way downwards through the hierarchy we aimed to reveal progressively more fundamental effects on the grazing process and to identify the major source of variation in the rate of forage intake.

Forage quantity, sward quality and forage accessibility are closely related attributes of a grass sward. Forage quantity is determined by the density of all forage parts in the sward. In this study it is defined as the density of tufts of leaves and of stems in the sward, where each tuft of leaves is a tight group of three leaves. Sward quality is determined by the proportion of preferred plant parts in the sward and is defined here as the proportion of leaf tufts in the sward. Forage accessibility is determined by the density of avoided plant parts, here stems, because they interfere with the cropping process and deter forage intake.

The main objectives of this study were: (1) To investigate whether the density of preferred plant parts in food-concentrated patches, has a positive effect on the rate of forage intake, and whether this is the result of increasing bite mass as the number of plant parts cropped per bite increases. Bite rate on the other hand, was not expected to be affected much, because processing efforts have no effect on handling time for the low bite mass achieved in complex swards. (2) To study whether forage accessibility, as the inverse of the density of avoided plant parts, has a negative effect on the rate of forage intake, as they interfere with the process of cropping of preferred plant parts. It was expected that this interference with the cropping process leads to a decrease in bite mass as the number of cropped plant parts per bite

decreases, and to a decrease in bite rate as handling and searching efforts increase. (3) To construct a functional response model, based on the mechanics of the cropping process in complex swards of varying quality, consisting of preferred and avoided plant parts. This model describes a mechanism alternative to the previously proposed competition between forage acquisition and forage processing, causing the deflection of the functional response curve with increasing forage quantity.

We performed our experiments using Nguni cattle (*Bos taurus*), a breed of cattle which is indigenous to Southern Africa. Nguni cattle are easily handled animals and were trained to graze artificial micro-swards of the (sub-) tropical grass *Panicum maximum*.

Methods

Experimental swards

The experiments were conducted at the Research Farm of the University of Fort Hare, Alice, Eastern Cape, South Africa. All experimental work was performed using artificial microswards (Black and Kenney, 1984; Laca *et al.*, 1992b) made up by plant parts of *P. maximum*, which were clipped every morning. Plant parts were separated and either three leaves (subsequently we call this one tuft of leaves) or one stem were threaded through holes in wooden blocks, or holes were left empty. Per block a minimum of one hole and a maximum of eight holes were filled with leaves or stems. Micro-sward of 0.5 m² area were made up by 50 blocks fastened on a large plastic board. Tufts of leaves and stems were trimmed to produce a uniform canopy height of 15 cm. Micro-swards were offered to the experimental animals in a stable between 11:00 and 15:00. A more detailed description of the method is presented in Chapter 2.

Experimental animals

We used four Nguni oxen weighing 250 to 320 kg. More than four months earlier, two of the oxen were esophageally fistulated for other experiments. All animals were cared for by a veterinarian as necessary. When not in an experimental trial and between experimental series, the animals were kept in a rangeland, but had daily contact with the experimentators. During the experimental series the animals were not food-supplemented. Each of the four animals was exposed to each treatment, animals were treated as replicate measurements.

Experimental design

The experiment was performed from February to March 2000, during the late wet season, and from May to June, during the subsequent early dry season. Prior to each experimental series, the animals were trained for at least 3 weeks to accustom them to the experimental set-up. Each day, before starting the experimental trial, the animals were collected from the rangeland and brought to a stable, where they were fasted for 2.5 to 5 hours. Subsequently, one animal was led to a micro-sward and allowed to graze until a substantial part of the herbage was removed and / or the animal seemed to lose interest. Animal behaviour was measured from video recordings of the grazing process.

Treatments differed in the densities of preferred and avoided plant parts in the microswards. The densities of preferred plant parts (tufts of leaves) used were 50, 100, 200 and 400 m^{-2} , which corresponds to about 10, 20, 40 and 80 g DM leaf m^{-2} (subsequently leaf tuft density will be called leaf density). The densities of avoided plant parts (stems) were 0, 50, 200, 300, 400 and 600 m^{-2} . In all treatments tufts of leaves and stems were arranged uniformly throughout the micro-swards. Because of logistic constraints, we combined leaf densities with stem densities in an incomplete factorial design: 50 leaf tufts m^{-2} was combined with 50 stems m^{-2} , 100 leaf tufts m^{-2} was combined with 0 and 300 stems m^{-2} , 200 leaf tufts m^{-2} was combined with 0 and 400 stems m^{-2} .

Experimental measurements

We measured the period of active grazing [s]. Periods when animals followed other activities were excluded from the observations. Active grazing was divided into two mutually exclusive activities: 1) locating a bite and 2) handling a bite. Locating a bite starts when the severing of the last bite has been finished and ends as soon as the handling of the next bite begins. Locating includes perceiving potential bites, deciding about the next target bite and locomotion of the head to the target bite. Subsequently, we will call the period during which location of bites takes place searching time [s]. Handling includes all manipulative and cropping activities on the plant parts to be ingested, like gathering and severing of leaves, as well as all manipulative activities on the plant parts to be excluded, like pushing away of stems. Subsequently, we will call the period during which handling of bites takes place handling time [s]. The time the animals allocated to searching and handling was measured by counting individual video frames in sub-samples of the video sessions. Video-fragments were chosen as sub-samples only if they fulfilled the conditions of visibility of the animal's muzzle

and the continuity of the grazing process. If possible, always two video-fragments were chosen, one at the beginning and one at the end of the grazing session, and the results averaged. This was done to compensate for possible depletion effects, though no obvious differences between the beginning and the end of the sessions were noticed by us. The period of sub-sampling was chosen as long as possible, constrained by the above mentioned conditions, and varied between 4 and 40 seconds with an average of 11 seconds. One second of video recording corresponds to an average of 25 video frames. From the video recordings also the number of bites during active grazing was determined on the basis of acoustic clues indicating the severing of leaves. Bite rate $[s^{-1}]$ was calculated as the number of bites during active grazing divided by active grazing time. Available pre-grazing forage mass was estimated by randomly selected blocks and expressed as dry matter [g DM] per unit area. Totally ingested forage mass [g DM] was calculated as the difference of pre-grazing forage mass minus the residual forage mass after grazing. Forage intake rate [g DM s^{-1}] was calculated as the product of bite mass with bite rate. Bite mass [g DM] was calculated as ingested forage mass divided by number of bites. Number of tufts of leaves harvested per bite was the number of grazed tufts of leaves (totally or in part removed) divided by the number of bites. Bite depth was calculated as pre-grazing forage height less the average residual height of all grazed plant parts. Season was wet season or dry season.

Data analysis

We tested the factors leaf tuft density, stem density and season for their effects on 1) the rate of forage intake, 2) bite mass, 3) bite rate, 4) the number of leaf tufts cropped per bite, 5) bite depth, 6) handling time, and 7) searching time. We did this by using multiple linear regression analysis. Besides the main factors, we investigated for possible effects of interaction terms. We calculated the product factors 1) leaf density * stem density, 2) leaf density * season, 3) stem density * season, and 4) leaf density * stem density * season and included them in the regression analyses. We used a forced entry procedure to include all independent factors into the regression model.

We used a regression model of the number of leaf tufts cropped per bite on stem density and the product factor leaf density * stem density to investigate in more detail the relationship of the number of leaf tufts cropped per bite and of intake rate with leaf tuft density and stem density. We investigated the relationship of the rate of forage intake with bite mass, bite rate and the number of tufts of leaves cropped per bite by 1) using simple linear regression of intake rate on bite mass, on bite rate, and on the number of cropped leaf tufts, 2) using multiple linear regression of intake rate on bite mass and bite rate. Possible collinearity between bite mass and bite rate in the latter regression was not expected to be a problem because the purpose of the analysis was retrieving the standardised partial correlation coefficients of both independent variables. As forage intake rate is the product of bite mass and bite rate, all variables were log-transformed before proceeding with the analysis.

Furthermore, we investigated the relationship of bite mass with the number of tufts of leaves cropped per bite and bite depth, for each variable separately. The relationship of time per bite with handling time and searching time was investigated by 1) simple linear regression of time per bite on each variable, 2) using multiple linear regression of time per bite on handling time and searching time.

All analyses were performed making use of the statistical software package SPSS (10.0).

Results

Bite mass and bite rate as sources of variation in the rate of forage intake

We found that the rate of forage intake increased with increasing leaf density, and decreased with increasing stem density. The relative effects of leaf density and of stem density on intake rate were of the same order of magnitude, as indicated by the standardised partial regression coefficients ($\beta_{LD} = 0.52$ and $\beta_{SD} = -0.45$, respectively). The negative effect of stem density on the rate of intake was stronger for high leaf densities. The change of season from wet to dry had a negative effect on the rate of forage intake (Figure 3.2a, Table 3.1).

The pattern of variation in bite mass was very similar to the one observed for the rate of intake. As with intake rate, increasing leaf density had a positive effect on bite mass, while increasing stem density had a negative effect. The relative effect of leaf density ($\beta_{LD} = 0.57$) was greater then the effect of stem density ($\beta_{SD} = -0.36$). The negative effect of stem density was stronger when leaf density was high. In the dry season, bites were lighter than in the wet season (Figure 3.2b, Table 3.1). A simple regression model of forage intake rate on bite mass explained 97 % of the variation in the rate of intake (IR = -0.08 g DM s⁻¹ + 1.01 s⁻¹ BM, $R^2 = 0.97$, P < 0.001).



Figure 3.2. The effects of leaf tuft density, stem density and season on a) the rate of DM intake, b) bite mass, and c) bite rate of cattle grazing hand-constructed swards of *Panicum maximum*. Filled symbols and solid lines are wet season data, open symbols and dashed lines are dry season data. Error bars are standard error of the mean. Lines connect data points of equal leaf density in order to facilitate comparison, these are no regression lines.

Bite rate increased with increasing leaf density, and decreased with increasing stem density. The relative effect of stem density on bite rate ($\beta_{SD} = -0.59$) was stronger than the effect of leaf density ($\beta_{LD} = 0.27$). There was no apparent interaction-effect of leaf density with stem density. Bite rates were lower in the dry season than in the wet season (Figure 3.2c, Table 3.1). A simple regression model of forage intake rate on bite rate explained 46 % of the variation in the rate of intake (IR = -0.18 g DM s⁻¹ + 0.56 g DM BR, $R^2 = 0.46$, P < 0.001).

Table 3.1. Results of the multiple regression analyses for the effects of the independent factors leaf density (*LD*), stem density (*SD*), and season and their product factors on various elements of the grazing behaviour of cattle grazing artificial micro-swards of *Panicum maximum* as dependent variables. Top figures in cells give the unstantardized partial regression coefficients. Bottom symbols give the probability values for the indicated *t*-tests as n.s. is P > 0.05, * is $P \le 0.05$, ** is $P \le 0.01$, and *** is $P \le 0.001$. *IR* = intake rate, *BM* = bite mass, *BR* = bite rate, *LT* = leaf tufts cropped per bite, *BD* = bite depth, *TH* = handling time, *TS* = searching time.

Independent Factor	Dependent variable						
	IR	BM	BR	LT	BD	TH	TS
Constant	0.24	0.27	0.86	1.03	7.16	0.75	0.50
	***	***	***	**	***	***	***
LD	6.68 E-04	7.10 E-04	4.21 E-04	6.78 E-03	-3.42 E-04	-5.72 E-04	-5.26 E-05
	***	***	*	***	n.s.	n.s.	n.s.
SD	-3.76 E-04	-2.88 E-04	-5.96 E-04	-2.37 E-03	-3.82 E-05	1.44 E-03	9.45 E-04
	***	***	***	***	n.s.	***	***
Season	-7.48 E-02	-6.07 E-02	-0.13	-2.85 E-02	2.21	0.29	-0.12
	***	**	**	n.s.	***	*	*
LD * SD	-3.07 E-06	-3.02 E-06	-1.14 E-06	-1.83 E-05	9.15 E-06	8.11 E-07	1.09 E-06
	***	***	n.s.	***	n.s.	n.s.	n.s.
LD * season	-2.01 E-04	-1.36 E-04	1.95 E-04	-2.96 E-04	-2.47 E-03	-1.00 E-03	-5.99 E-04
	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
SD * season	1.75 E-04	8.52 E-05	2.62 E-04	5.26 E-04	1.34 E-03	7.39 E-04	-1.18 E-03
	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***
LD * SD * season	1.34 E-06	3.90 E-07	1.18 E-06	-2.71 E-06	-4.22 E-06	-3.56 E-06	-1.21 E-06
	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
R^2	0.85	0.83	0.55	0.82	0.55	0.50	0.65

A multiple regression model of log intake rate on log bite mass and on log bite rate, as expected, explained 99 % of the variation in intake rate. Bite mass and bite rate did not show collinearity (tolerance = 0.85). The important point here is that the relative effect of bite mass was greater ($\beta_{logBM} = 0.71$) than the effect of bite rate ($\beta_{logBR} = 0.48$).

The number of tufts of leaves cropped per bite and bite depth as sources of variation in bite mass

As with bite mass, we found that the number of leaf tufts cropped per bite is showing a very similar pattern of variation as the one observed for the rate of forage intake. The number of leaf tufts cropped per bite increased with the density of leaves, and decreased with the density of stems.



Figure 3.3. The effects of leaf tuft density, stem density and season on a) the number of tufts of leaves cropped per bite and, b) bite depth of cattle grazing hand-constructed swards of *Panicum maximum*. Filled symbols and solid lines are wet season data, open symbols and dashed lines are dry season data. Error bars are standard error of the mean. Lines connect data points of equal leaf density in order to facilitate comparison, these are no regression lines.

As with bite mass, the relative effect of leaf density on the number of leaf tufts cropped per bite was greater ($\beta_{LD} = 0.69$) than the one of stem density ($\beta_{SD} = -0.37$). Again, the negative effect of stem density was strong when leaf density was high but virtually absent when leaf density was medium or low. There was no effect of season on the number of cropped leaf tufts (Figure 3.3a, Table 3.1).

After exclusion of non-significant terms from the multiple regression model of the number of cropped leaf tillers per bite (Table 3.1), we arrived at a rather simple model of the number of tufts per bite on leaf density and the product factor of leaf density * stem density, $LT = 0.38 + 9.995 * 10^{-3} \text{ m}^2 LD - 1.33 10^{-5} \text{ m}^4 LD SD$, $R^2 = 0.81$, P < 0.001. The explained 81 % of the variation in the number of cropped leaf tufts are still large compared to the full, original regression model (Table 3.1), which explained 85 % of the variation.



Figure 3.4. Behaviour of a multiple linear regression model describing the number of leaf tufts cropped per bite as a function of leaf tuft density and stem density in cattle grazing hand-constructed swards of *Panicum maximum*. The model is based on the experimental data presented in Figure 3.3. The contour diagram shows isolines of the number of leaf tufts cropped per bite (1 - 8) and isolines of the proportion of leaf tufts of all plant parts (leaf tufts and stems) in the sward (25 % – 75 %). The 0 % and 100 % isolines are located on the y- and on the x-axis, respectively.

A diagram of this model (Figure 3.4) shows that in swards with a high proportion of leaf tufts (100 % and 75 %), the number of cropped leaf tufts per bite steadily increased with increasing sward density (follow the isolines of the proportion of leaf tufts from the origin of the diagram to the right and see how they are intersecting the isolines of the number of leaf tufts cropped per bite). However, in swards with a medium or low proportion of leaf tufts (50 % and 25 %), the number of cropped leaf tufts per bite, after having increased initially, decreased again with increasing sward density.

A simple regression model of bite mass on the number of leaf tufts cropped per bite explained 75 % of the variation in bite mass (BM = 0.06 g DM + 0.11 g DM LT, $R^2 = 0.75$, P < 0.001). A linear regression model of forage intake rate on the number of leaf tufts cropped per bite was very similar to the previous model of bite mass. It explained 75 % of the variation in the rate of forage intake (IR = -0.03 g DM s⁻¹ + 0.11 g DM s⁻¹ LT, $R^2 = 0.75$, P < 0.001).

Bite depth was not affected by leaf density nor by stem density. However, bite depth was affected by season, with bites being less deep in the wet season compared to the dry season (Figure 3.3b, Table 3.1). A regression model of bite mass on bite depth was not significant, nor did we find a significant model of intake rate on bite mass.

Handling time and searching time as sources of variation in bite rate and in time per bite

Handling time per bite was not affected by leaf density. However, handling time increased with elevated stem density. Season had an effect on handling time, with cattle taking longer to crop bites in the dry season compared to the wet season (Figure 3.5a, Table 3.1). A simple linear regression model of time per bite on handling time explained 58 % of the variation in time per bite (TB = 0.25 s + 1.15 TH, $R^2 = 0.58$, P < 0.001).



Figure 3.5. The effects of leaf tuft density, stem density and season on a) searching time per bite and, b) handling time per bite of cattle grazing hand-constructed swards of *Panicum maximum*. Filled symbols and solid lines are wet season data, open symbols and dashed lines are dry season data. Error bars are standard error of the mean. Lines connect data points of equal leaf tuft density in order to facilitate comparison, these are no regression lines.

As in the case of handling time, searching time was not affected by leaf density, yet it increased with elevated stem density. There was a strong interaction effect of stem density with season on searching time. For lower stem densities (up to 300 m⁻²) searching times in the wet season were equal to or lower than the dry season values. For higher stem densities searching times were much longer in the wet season than in the dry season. Generally, searching times increase stronger with elevated stem density in the wet season than in the dry season than in the dry season (Figure 3.5b, Table 3.1). A simple linear regression model of time per bite on searching time explained only 14 % of the variation in time per bite (TB = 1.37 s + 0.92 TS, $R^2 = 0.14$, P = 0.005).

A multiple linear regression model of time per bite on handling time and searching time explained 58 % of the variation in time per bite (TB = 0.23 s + 1.10 TH + 0.16 TS, $R^2 = 0.58$, P < 0.001). There was no sign of collinearity between handling time and searching time (tolerance = 0.82). As expected, the standardised partial regression coefficient of handling time was much higher ($\beta_{TH} = 0.73$) than the one of searching time ($\beta_{TS} = 0.07$). In fact, searching time did not contribute significantly to the explanation of the variation of time per bite ($P_{ST} = 0.243$).

Discussion

We suggest that the rate of forage intake in consumers foraging on a complex resource, *i.e.*, made up by preferred and avoided forage parts, does not necessarily approach an asymptotic maximum with increasing forage mass (Holling's types II and III), as conventionally implied. Instead, after having reached an initial maximum, the intake rate may decrease again, giving rise to a domed functional response curve (Holling's type IV). The initial increase in the rate of forage intake is caused by an increasing density of preferred forage parts within the harvested bite volume, thus increasing bite mass. The following decrease in the rate of forage intake is the result of a decreasing accessibility of preferred forage parts. It is caused by the increasing density of avoided forage parts interfering ever stronger with the harvesting process and depressing the volume of bites. The decreasing accessibility of preferred forage parts and enhancing the negative effect on handling times, too, thus decreasing bite rates and enhancing the negative effect of decreasing accessibility on the forage intake rate. Ignoring the deflection of the functional response curve at high forage mass in complex forage resources may lead to an overestimation of the rate of forage intake. This applies especially to foraging in natural

systems (opposite to simple production systems), where the quality of the forage resource, made up by preferred and avoided forage parts, usually is lower.

Sources of variation in the rate of forage intake

The pattern of variation shown by bite mass under the effects of leaf density and stem density was strikingly similar to the one observed for the rate of intake. Contrary to this, bite rate showed a very different pattern. In line with these results, we found that in simple and multiple regression equations bite mass explained much more of the variation in intake rate than did bite rate. Therefore we conclude that of the two variables bite mass and bite rate, it is bite mass, which is the most important variable in determining the rate of forage intake. This result is in line with previous work (e.g., Spalinger and Hobbs, 1992; Farnsworth and Illius, 1996) in which it was concluded that in food-concentrated patches, mainly bite mass controls the rate of forage intake.

Because of the importance of bite mass in controlling intake rate, we were interested in further investigating the sources of variation in bite mass. Bite mass is proportional to the product of the number of leaf tufts cropped per bite times the average depth at which leaf tufts were severed. Thus the number of leaf tufts per bite and bite depth have a direct effect on bite mass. However, while the regression models of bite mass and intake rate on the number of cropped leaf tufts per bite were highly significant, this was not the case for bite depth. Apparently, changes in plant part densities did not affect bite depth, which therefore caused the lack of correlation with bite mass. We conclude that in the situation of constant canopy height, the number of leaf tufts cropped per bite is the most important factor in determining bite mass and the rate of forage intake.

Our results show that leaf density has a strong positive effect on the number of cropped leaf tillers per bite and on bite mass. This finding is in line with a great body of previous work (e.g., Black and Kenney, 1984; Ungar *et al.*, 1991; Laca *et al.*, 1992a). Generally it is agreed upon that this effect is caused by the increasing number of leaves within the bite area, *i.e.*, within the reach of the animal's tongue sweep, when leaf density is increased. However, besides of the positive effect of leaf density, the results also showed a negative effect of stem density on the number of cropped leaf tillers per bite and on bite mass. The video recordings showed that the effect of stem density was caused by a change in cropping style by the herbivores. In leaf-only swards the herbivores applied typical circular tongue movements to gather groups of leaf tufts in each bite. However, as our herbivores selected strongly against stems, in stemmy swards, stems physically interfered with the gathering tongue sweep.

Consequently the animals reduced the reach of their tongue sweep to avoid including stems into the bite. In the more extreme cases the cattle changed their cropping style all together. They abandoned the tongue sweep and instead sought out individual tufts of leaves in between the stems, clamping them between their lips. We estimated the reach of an animal's lips (muzzle) as one and a half of the width of the incisor arcade (in our study animals on average 67 mm), thus being 10 cm at the most. This is considerably smaller than the reach of the tongue, 14 cm, judging from the occasionally successful cropping of two tufts of leaves per bite at the lowest leaf density. The reduction in the number of leaf tufts cropped per bite and in bite mass with increasing stem density, therefore can be explained mechanically as the result of the physical interference of the stems with the cropping process. This interference results in a reduction of the reach of the animal's cropping apparatus and leads to a change in cropping style, from sweeping to clamping. The decreased bite area apparently is not compensated for by the increased leaf density and thus causes the number of cropped plant parts per bite to decline.

Though bite mass is of greatest importance in determining the rate of forage intake, variation in bite rate is amplifying the effects of bite mass, thus resulting in the observed pattern of variation in intake rate. Multiple regression analysis showed that, though searching time varied more than did handling time ($CV_{ST} = 60$ % and $CV_{HT} = 36$ %), searching time did not significantly effect time per bite. We suggest, that handling times were so much longer than searching times, that the effect of handling time completely masked the possible effects of searching time. Handling time mainly varied under the negative effect of stem density. An increasing investment of time into handling was related to the previously mentioned change in cropping style. The video recordings showed that with increasing stem density, our herbivores gradually increased the use of their muzzles for pushing aside stems, before sweeping their tongues around groups of leaf tufts or clamping individual leaf tufts between their lips. In swards with high stem density even the bulk of all movements was dedicated to excluding stems from the bite. Because of the low bite masss in our study, bite rate was not limited by mastication and therefore increasing numbers of manipulative movements had a direct negative effect on bite rate. This conclusion is supported by the results of Laca et al. (1994) who found that intake rate was negatively related to the number of gathering jaw movements per bite.

The shape of the functional response curve in complex swards

In Chapter 2 it was shown that the shape of the functional response curve of large herbivores changed from Holling's type I (linear) to type II (asymptotic) when the quality of the forage resource was decreased, *i.e.*, when the proportion of avoided plant parts (stems) was increased. For the highest proportions of avoided plant parts, intake rate was lowest and did not show a correlation with forage quantity. The findings presented here, illustrate a likely mechanism causing the observed change in the shape of the functional response curves and enable us to infer some conclusions over the consequences for the general grazing situation.

In high quality, leaf-only swards, bite mass, which is the principal driving factor of intake rate, increases with forage density, as this increases the density of forage parts within the harvestable bite volume. Only when bite mass increases above a critical level determined by the capacity of the herbivore's processing apparatus, we can expect competition between forage acquisition and forage processing leading to a deflection in the rate of forage intake (e.g., Spalinger and Hobbs, 1992; Laca *et al.*, 1994). Thus, depending on the scale of forage masses offered to the herbivore, we will observe a linear type I or an asymptotic type II functional response curve.

However, the situation is different in medium to low quality, complex swards, *i.e.*, in swards made up by preferred (leaves) and avoided (stems) forage parts. While increasing forage density leads to an increase in the density of preferred parts in a harvestable bite volume, it also leads to an increased interference of avoided parts with the cropping process and to a limitation of the reach of the herbivore's cropping apparatus. For medium proportions of avoided forage parts, increasing forage density initially only causes an increase in bite mass as the density of preferred forage parts in the harvestable bite volume increases. However, when forage density surpasses a critical value, the increasing density of preferred parts in the bite volume cannot make up anymore for the decrease in bite volume itself, and bite mass declines. As handling times will rather increase with increasing density of avoided parts, it is unlikely that herbivores can compensate for declining bite mass by increasing bite rate. Consequently, increasing the forage mass by increasing bulk density can have the counter-intuitive effect of decreasing bite mass and depressing the rate of forage intake, in the extreme case causing a type IV (domed) functional response curve.

We illustrate this point by re-working the plot of the regression model of the rate of forage intake on the densities of leaves and stems (Figure 3.5). Because of the close correlation of intake rate with the number of leaf tufts cropped per bite, we were able to use the latter as an index of intake rate.



Figure 3.6. Functional response curves of cattle grazing hand-constructed swards of *Panicum maximum*, differing in the proportion of leaf tufts in the sward (25 % - 100 %). The curves are based on the multiple linear regression model presented in Figure 3.4.

Further, we defined the sum of the densities of leaves and of stems as an index of forage mass. We investigated the effect of changes in the quality of the forage resource, defined as the proportion of preferred forage parts, on the shape of the functional response curve (Figures 3.6). The plot shows that decreasing resource quality from 100 % to 25 % changes the shape of the functional response curve from type I (linear) to type II (asymptotic) and then type IV (domed). Our results suggest that only in simple, leafy swards the shape of the functional response curve of grazers is following type I or type II (Black and Kenney, 1984; Spalinger and Hobbs, 1992; Prins and Olff, 1998, Prache *et al*, 1998). In complex, stemmy grass swards the shape of the functional response curve can rather be expected to follow type IV.

We were interested in the consequences of our findings for forage intake in a more natural situation, where we usually find a negative correlation of forage resource quality with forage mass (e.g., Stobbs, 1973; Georgiadis and McNaughton, 1990; Ben-Sahar and Coe, 1992; Prins and Olff, 1998; Hendrickson *et al.*, 1997, Orians and Jones, 2001). Therefore we examined the shape of the functional response curve for three different hypothetical grasslands, dominated to varying degrees by stemmy or leafy grasses. We assumed that in leafy grasses (e.g., creeping grasses) leaf production involves less production of stems, therefore forage resource quality decreases slowly with increasing forage mass.



Figure 3.7. Functional response curves of cattle grazing swards of *Panicum maximum*, differing in the slope of the negative correlation of forage quality with forage mass (*i.e.*, forage quality is decreasing strongest with forage mass for the steepest quality/mass slope). The model is derived from the multiple linear regression model presented in Figure 3.4 and is built on the assumption that in natural grasslands forage quality, here defined as the proportion of leaf tufts in the sward, and forage mass are negatively correlated.

However, in stemmy grasses (e.g., cauline or tuft-forming grasses) leaf production involves a relatively stronger increase in stems, mainly as support tissue, therefore resource quality decreases relatively faster with increasing forage mass. Accordingly, the slope of the negative quality/mass correlation can be interpreted as an indicator distinguishing between grasslands dominated by leafy or stemmy grasses. We made use of the same indices of intake rate, forage mass and forage resource quality as in the previous section. As slopes of the quality/ mass correlation we used – 0.04, - 0.06 and - 0.13 % m⁻² to cover a range from leafy to stemmy grasslands (Figure 3.7). The plot shows that in all cases the shape of the functional response curve is type IV. However, depending on the stemminess of the grassland and the region of forage mass under investigation, the curve can appear as if being a linear type I or an asymptotic type II. The plot also shows that, with increasing stemminess, the maximum rate of forage intake decreases and the forage mass at which the maximum intake rate is reached, progressively shifts to higher forage masses.

Conclusions

As intended, we demonstrated the positive effect of preferred forage parts and the negative effect of avoided forage parts in the resource canopy on forage intake. Our results showed that

the number of preferred forage parts cropped per bite is the most important element of forage intake determining the rate of forage intake in complex, food-concentrated patches. Above that, we were able to show that the decrease in the number of cropped forage parts per bite is the result of increased physical interference of avoided forage parts with the harvesting process. A model of the relationship of the rate of forage intake with the densities of preferred and avoided forage parts was able to create a spectrum of functional response curves (Holling's type I, II and IV), which are in qualitative agreement with field observations. The model was used to illustrate how the delayed negative effect of avoided forage parts on bite mass depresses intake rates for high forage quantities and gives rise to a Holling's type IV (domed) functional response curve in complex forage resources. As this model incorporates the forager's selectivity for parts of the resource, it is a more accurate description of foraging by free-ranging herbivores in complex resources, compared to previous models.

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Chapter 4

Forage intake and diet quality at patch level in relation to scale-dependent foraging strategies

Abstract

Factors governing forage intake in large herbivores are differing between scales. Forage intake at small scales is affected by resource complexity, but it remains unclear which factors control foraging behaviour at larger scales. We observed the foraging behaviour of a freeranging model herbivore, cattle, foraging in natural grassland and investigated which factors control forage intake and dietary quality at patch level. As expected, forage intake was a positive function of forage availability, but appeared to be otherwise unrelated to forage resource structure and complexity. We suggest that due to the negative correlation of forage availability with resource quality, opportunities for the selection of high-quality forage parts were present over a range of forage types, resulting in dietary quality being consistently higher than average forage quality. The pattern of utilisation of forage resource types through the foragers diverted from expectations based on a short-term energy intake maximisation rule. Instead foragers likely were making decisions regarding forage type acceptability based on a daily energy requirement maximising or satisficing rule. Our results suggest a change of intake controlling factors between temporal and spatial scales, which should be taken into account when extrapolating forage intake between scales. Further we illustrate potential relationships of foraging behaviour at one scale with foraging decisions on lower and larger scales.

Key words: Forage intake; diet quality; spatial scale; temporal scale; resource complexity; metabolisable energy; rate maximising; satisficing rule.

Introduction

The functional response, as the relationship of forage intake rate with forage availability, is a key processes in the interaction between a forager and its forage resource and therefore a central topic in animal ecology. For large vertebrate herbivores, forage intake rate and diet quality, which determine the rate of energy and nutrient intake, depend on the composition and structure of the forage resource. As the condition and fitness of a forager in a given habitat to a large extent depend on the rate of energy and nutrient intake, an understanding of the mechanisms by which forage resource structure determines the rate of forage intake and diet quality, is of great importance to our insight into animal ecology.

Commonly it is assumed that forage intake by large herbivores is a function of bite mass, bite rate and foraging time. Bite mass, which is the most difficult to measure, is usually modelled as a positive function of total forage mass, forage height or forage bulk density. This approach is based on data gathered from grazing experiments involving rather uniform, high-quality forage resources, like temperate production grasslands (e.g., Wallis de Vries *et al.*, 1998) or homogeneous, high-quality micro-patches (e.g., Laca *et al.*, 1992; Illius and Gordon, 1999). Bite rate normally is modelled as a negative function of bite mass and as a positive function of forage density (Spalinger and Hobbs, 1992). However, these traditional approaches may not be valid for foraging in rather complex resources, where bite mass and bite rate might be determined by forage accessibility instead of by forage availability (Chapter 3).

The complexity of a forage resource structure can manifest itself in a number of ways and can evoke a variety of herbivore responses: i) The forage resource can consist of parts of different quality and the herbivore is foraging selectively for high-quality parts. Limitation of bite dimensions, of bite mass and of bite rate by low-quality forage parts and structural plant defence has been shown in a number of studies (Stobbs, 1973; Ruyle *et al.*, 1987; Haschick and Kerley, 1997; Ginnet *et al.*, 1999; Bergman *et al.*, 2000; Chapter 3). ii) The forage resource mass may not be distributed uniformly in space, but may show small-scale variation brought about by changes in forage height or bulk density. Positive effects of local variation in the height and density of forage (Allden and Whittaker, 1970; Black and Kenney, 1984; Ungar and Noy-Meir; 1988) and effects of distance between forage patches (Laca *et al.*, 1993; Shipley and Spalinger, 1995) on bite mass and on forage intake rate have been found. iii) Forage parts of high and low quality may be spatially arranged in a non-uniform pattern. It has been shown that the increasing accessibility of high-quality forage parts brought about by the increasing clustering of plant parts is affecting foraging site choice (Heitkönig and OwenSmith, 1998) and has a positive effect on the rate of forage intake in selectively foraging herbivores (Chapter 2). iv) The forage resource may consist of a number of forage species, each with species-specific morphology and physical characteristics of forage parts. Effects of forage morphology on forage intake and diet choice have been found in a number of studies (Stobbs, 1973; O'Reagain, 1993; O'Reagain *et al.*, 1996; Hjalten *et al.*, 1996; Shipley *et al.*, 1998). It appears that except for high-quality production resources various forms of resource structure introduce a high degree of complexity to most forage resources. Considering these aspects of resource complexity is essential for our understanding of foraging behaviour.

Predictions of forage intake by free-ranging herbivores in the field, mainly with the purpose of predicting animal production, can be done on the basis of larger-scale foraging experiments (e.g., Stobbs, 1973; 't Mannetje and Ebersohn, 1980; Van der Grinten *et al.*, 1992). However, by their very nature, these studies cannot be detailed enough to reveal the underlying processes controlling forage intake and diet selection. Therefore, the results of such studies apply to a rather limited set of range conditions, *i.e.*, a certain forage species and narrow ranges of available forage mass and forage quality.

Accurate predictions of forage intake and diet quality over a wider set of environmental conditions require a thorough knowledge of the controlling processes. Small-scale experiments, e.g., involving micro-forage patches (Black and Kenney, 1984; Ungar et al., 1991; Laca et al., 1992; Bergman et al., 2000) are suitable to acquire a detailed understanding of the mechanics and processes involved at these scales. In many cases, implicitly it is assumed that the results obtained at the small scale can be linearly extrapolated to describe forage intake on larger scales and over wider ranges of environmental conditions. However, only in very few instances were these predictions verified by experiments on larger scales (Laca et al., 1993; Wallis de Vries et al., 1998; Wilmshurst et al., 1999) and studies of forage intake and diet quality usually are restricted to a single temporal or spatial scale. This is quite remarkable, as it differs from the common perspective on forage intake, which is approached as a hierarchic process with different factors controlling foraging decisions on the various scales (e.g., O'Reagain and Schwartz, 1995; Bailey, 1996). The interdependence of foraging decisions taken at various scales can be illustrated by the limitation of the range of possible foraging decisions on smaller scales originating from larger scale foraging decisions, while on the other hand foraging decisions taken at smaller scales form the basis for foraging decisions at larger scales (Bailey, 1996; Prins, 1996). Thus, it appears that a thorough knowledge of the factors controlling foraging decisions on all scales involved is essential to our complete understanding of foraging behaviour.

The conditions encountered by free-ranging herbivores in the field differ from the conditions during foraging experiments involving micro-swards. Notable differences are (i) the residence time and number of bites per feeding station typically are much lower in the field than in foraging experiments at micro-sward level (personal observation), possibly giving rise to differential effects of local forage depletion; (ii) so far foraging experiments on micro-sward level were restricted to forage resources structured vertically (one dimension) or horizontally (two dimensions), in the field however forage resources are simultaneously structured vertically and horizontally (three dimensions), which may have effects on foraging behaviour (e.g., Ruyle *et al.*, 1987); (iii) the effects of morphological, physical and nutritional properties of forage types are seldomly investigated at the micro-sward level, though in the field foragers often encounter multi-species forage resources and a variety of forage tissues, differing widely in the before mentioned properties, probably affecting foraging behaviour (e.g., O'Reagain *et al.*, 1996).

The purpose of this study was to identify characteristics of foraging behaviour and of forage resource structure which are controlling forage intake and diet quality in free-ranging herbivores at patch level. To do so, we investigated two groups of characteristics. First, characteristics relating to forage intake (i - vii), which were chosen to be investigated because in previous experiments (Chapters 2 and 3) they were found to affect forage intake at the level of a micro-sward, *i.e.*, at the scale of a single feeding station. Second, characteristics relating to diet quality (viii – xii), which were chosen because in other studies of the foraging behaviour of free-ranging herbivores (e.g., Stobbs, 1973; Prins and Beekman, 1989; De Boer and Prins, 1990; Prins, 1996; Heitkönig and Owen-Smith, 1998; Drescher, personal observation), these characteristics appeared to affect diet quality at the feeding site or camp level.

We expected to find the following effects of characteristics of foraging behaviour and forage resource structure: (i) forage intake rate is mainly driven by bite mass instead of bite rate; (ii) bite mass is increasing with increasing forage availability, which was measured in a number of ways, *i.e.*, grass mass, live mass and leaf mass per unit area and unit volume and as grass height; (iii) bite mass is increasing with resource quality, which in this study was defined in two ways, first, as the proportion of high-quality forage parts, *i.e.*, leafiness, and second, as the proportion of live forage parts, *i.e.*, greenness; (iv) bite mass is increasing with increasing accessibility of high-quality forage parts, *where* accessibility is inversely related to the density of low-quality forage parts, *i.e.*, the number of stems, stem mass, dead mass and the mass of forbs plus woody species, all per unit area; (v) bite mass is increasing with

increasing local aggregation of forage, which in this study was measured as sward roughness, *i.e.*, the deviation of the sward surface from a level surface; (vi) bite mass increases with the size of high-quality forage parts, *i.e.*, length and width of leaves; (vii) bite mass decreases with the size of intake deterring low-quality forage parts, *i.e.*, diameter and length of stems.

For diet quality, we expected to find the following effects of characteristics of foraging behaviour and of forage resource structure (making use of the same definitions as mentioned above): (viii) diet quality, measured as the organic matter digestibility of bites, relates inversely to bite mass; (ix) diet quality decreases with increasing forage availability; (x) diet quality increases with resource quality; (xi) diet quality increases with the accessibility of high-quality forage parts; (xii) diet quality correlates positively with forage tissue quality, measured as the grass tissue concentrations of nitrogen, phosphor, calcium and sodium and as grass digestibility, and correlates negatively with the concentration of neutral detergent fibre. Other factors like morphological properties were not expected to be involved in the control of diet quality.

Material and Methods

Study area

The study was conducted on the Kwanare Game Ranch located 10 km north of Stoffberg, Mpumalanga, South Africa, at 25 ° 20 ' S and 29 ° 42 ' E. The area is situated in Transvaal sour bushveld (Tainton, 1999) in a transitional zone from the drier Highveld in the west and the more humid Lowveld in the east. The average annual rainfall in the region is 649 mm. A rainy season can be distinguished lasting from October to April during which an average of 599 mm rainfall is received. The experimental site of 28 ha was on deep, sandy and well-drained soil and was fenced as protection against surrounding wild game species. The site has been utilised since more than 20 years by cattle (*Bos taurus*) and goats (*Capra hircus*). The tree layer was dominated by *Acacia karoo*. The species composition of the grass layer was variable. In open grassland patches often were dominated by *Hyparrhenia hirta*, *Hyperthelia dissoluta*, *Cynodon dactylon*, *Eragrostis* spec. or *Aristida* spec., while under denser tree cover *Panicum maximum* dominated patches could be found.

Study animals

The study animals were cattle (*Bos taurus*) of mixed breed and made part of a free-ranging herd of nine adults and five calves. Out of this herd five adult cattle of varying but moderate size were chosen as focal animals, because they were docile enough to allow the

experimentators in their vicinity. During a period of four weeks preceding the actual observations, the focal animals were made familiar with the presence of the experimentators.

Data collection

Within the study site, sward types were distinguished based on sward architecture and floral composition. To be suitable for this study, patches of these sward types had to fulfil the following criteria: 1) being quickly identifiable by distant vision; 2) having rather clear boundaries; 3) having a large enough total area over all patches of this sward type to ensure a high likelihood to encounter cattle in them; 4) having a large enough area per patch to observe cattle during grazing for a period of at least 30 s; 5) being sufficiently different in forage availability, forage quality and morphological properties between sward types to show their potential effects. Seven sward types fulfilled these criteria. In open grassland these were three short sward types (sward height < 15 cm) and two tall sward types (sward height > 20 cm). The three short sward types were *C. dactylon*-dominated, *E. barbinodis* dominated, and of mixed species composition. The two tall sward types were *H. dissoluta*-dominated and again of mixed species composition. Under dense tree cover, we distinguished two more sward types, being short *P. maximum* (sward height < 15 cm) and tall *P. maximum* (sward height ca. 20 cm).

The five focal animals were followed during daytime over a period of 46 days from the mid to the end of the rainy season (February to April 2001). We aimed to observe each animal once in a patch of each of the seven chosen sward types, resulting into 35 observations. When an animal entered a patch of the chosen sward types and the patch was large enough to allow observation, the animal was video-recorded. From these video recordings, we determined the bite rate. Bite weight was estimated by bite simulation on the grazing site following Wallis de Vries (1995). Bite samples were air dried in the field and later oven dried in the lab at 70 ° C for at least 8 hours to determine their dry mass. Bite samples were analysed for *in vitro* digestibility according to Tilley and Terry (1963) expressed as proportion of dry matter mass (DM) as found for samples being dried for at least 8 hours at 105 ° C. Forage intake rate was calculated as the product of bite rate and bite mass.

Within a week of the video recording, close to each feeding site, we identified ungrazed vegetation similar to the grazed vegetation. In this vegetation we placed randomly two frames of 0.5 m x 0.5 m. Within these frames grass was distinguished from herbs and woody species. Grass species were identified and their cover estimated as the part of the surface projection containing 90 % of all plant parts. (Co)-dominant grass species were defined as covering at

least 25 % of the total area covered by all vegetation in at least one of the two frames. For each feeding site, we determined the following average values over all (co-)dominant grass species: leaf width and leaf length, stem length, stem diameter and stem density. We harvested the vegetation in the frames to stubble height and hand-sorted it into grass and the remaining vegetation. All (co-)dominant grass species were sorted into leaf, stem and dead tissue. All plant material was air dried in the field and later in the lab oven dried at 70 ° C for a period of at least 8 hours and dry matter mass (DM) was determined. In the remainder of the paper, all masses are expressed as mass per m². For each feeding site we calculated grass mass, live mass, leaf mass, stem mass, dead mass as average values over all (co-)dominant grass species. We also calculated the mass of all woody species plus forbs.

Plant samples were destroyed following the procedure of Novazamsky *et al.* (1983) and analysed for the contents of nitrogen and phosphorous using a Skalar San-plus autoanalyzer. The samples were analysed for sodium and calcium contents using a flame photometer. Neutral detergent fibre (NDF) was measured according to Goering and Van Soest (1970) and *in vitro* digestibility according to Tilley and Terry (1963), both expressed as proportion of dry matter mass (DM) as found for samples being dried for at least 8 hours at 105 ° C. From these measurements we calculated the average for each feeding site over all plant parts of all (co)-dominant grass species.

Close to each feeding site, two transacts of 5 m were placed randomly in ungrazed vegetation similar to the grazed vegetation. Along these transacts the height of the sward was measured by lowering a small polystyrene foam disc (10 cm diameter) along a beam onto the vegetation. The measuring interval was 10 cm and the unit of height measurements was 2.5 cm. The sward height was calculated as the average height of the resulting height profiles. From the height profiles, the sward roughness, being the divergence of the profile from a straight line, was calculated as the fractal dimension of the profile (Farina, 1998).

Data analysis

Multivariate techniques were used for dimension reduction, *i.e.*, to reduce the complex sample by vegetation characteristics data set into a two-dimensional ordination diagram, providing an overview of differences in vegetation characteristics between sward types on the one hand and their relation with forage intake characteristics on the other hand. As ordination techniques, we used Redundancy Analysis (RDA) to analyse the relationship between vegetation characteristics and sward types and Principal Component Analysis (PCA) to analyse the relationship between vegetation characteristics and forage intake characteristics. In the RDA,

we used vegetation characteristics as "species data" and sward type as explanatory variables. In this way, within-sward type variation in the observations on vegetation characteristics is disregarded and an optimal summary of the differences between the sward types is obtained. In the PCA, we entered the vegetation characteristics as "species data" and the forage intake characteristics as passive explanatory variables. Since we were not interested in an animal effect, animal was entered as a nominal co-variable, *i.e.*, a variable which explained variance is excluded from the analysis. Monte Carlo permutation tests were used for testing of the significance of the relationships (Ter Braak, 1995; Ter Braak and Smilauer, 2002).

In all ordination analyses, variables related to density, weight, length, width and area were base-e log-transformed to down-weight high values. When a zero was present, log-transformations was done by log (ax+1), in which a was determined according to Van den Brink et al. (2000). When a missing value was present, the mean of all other observations was used instead. Next, the transformed values were centred and standardised to make them mathematically equally important.

We interpreted the results of the PCA biplot as indications of the correlations between vegetation characteristics and forage intake characteristics. In PCA, variables are represented as vectors and the positions of these vectors are indicative of their correlation (Makarenkov and Legendre, 2002). Vectors representing variables which are perfectly positively correlated, lie on top of each other, vectors which are perfectly negatively correlated, lie at 180° of each other, and vectors of variables which are uncorrelated, lie at 90°. Therefore, we reasoned that in our analysis a sward characteristic and an intake characteristic were likely to be correlated positively, if the angle between the two vectors was 45 $^{\circ}$ at the most. Following the same argument, a sward characteristic and an intake characteristic were likely to be correlated negatively, if the angle between one vector and the mirror image of the other vector was 45 $^{\circ}$ at the most. If the enclosed angle was larger than 45°, we reasoned that characteristics were likely to be uncorrelated. All sward characteristics identified as likely correlated with a forage intake characteristic, were used as independent main factors in a multiple linear regressions analysis. Following the principle of parsimony, we excluded interaction terms from the analyses, as these would involve a prohibitively large amount of additional assumptions. Significant factors were identified by a stepwise forward selection procedure.

Multivariate analyses were performed using the computer program Canoco for Windows 4.5 (Ter Braak and Smilauer, 2002). Multiple linear regression analyses were performed making use of the statistical software package SPSS for Windows 10.0.

Sward	Architectural attributes				Chemical attributes		Morphological attributes	
type	Grass mass [g DM m ⁻²]	Proportion leaf [%]	Sward height [cm]	Sward roughness [-]	OMD [%]	Nitrogen content [%]	Leaf width [mm]	Stem diameter [mm]
short P. maximum	103	43	11.1	1.04	39	1.3	7.9	1.1
tall P. maximum	± 20 149	± 2.7 40	± 1.1 20.1	± 0.01	± 5.2	± 0.2	± 0.6 9.0	± 0.2
	± 24	± 5.5	± 1.9	± 0.01	± 7.0	± 0.5	± 0.5	± 0.1
H. dissoluta	434	24	53.1	1.28	28	0.4	3.4	1.7
	± 110	± 1.5	± 5.3	± 0.01	± 3.9	± 0.0	± 0.2	± 0.1
C. dactylon	71	52	9.4	1.01	29	1.3	2.5	0.5
	± 13	± 4.9	± 0.6	± 0.00	± 7.2	± 0.2	± 0.4	± 0.1
E. barbinodis	80	32	9.1	1.02	42	1.1	3.2	0.7
	±11	± 1.8	± 0.5	± 0.01	± 4.9	± 0.1	± 0.2	± 0.1
tall-mixed	319	36	26.2	1.13	30	0.7	3.2	1.2
	±75	±1.3	± 1.1	± 0.01	± 2.0	± 0.1	± 0.2	± 0.1
short-mixed	94	54	9.3	1.02	41	1.2	3.7	0.6
	±12	±1.6	0.9	± 0.01	± 6.9	± 0.2	± 0.1	± 0.2

Table 4.1. Vegetation characteristics of seven sward types (indicated by dominant species), which were identified as distinct vegetation units in a natural, semi-arid grassland. Shown are average values with standard errors.

Results

Differences in vegetation characteristics between sward types

In Table 4.1 we present typical vegetation characteristics of the seven chosen sward types, varying over a range of factor two to six. The RDA showed that sward types explain 67 % of the total variance of the vegetation characteristics (Figure 4.1). The remaining 33 % of the total variance can be attributed to within sward type variation.



Figure 4.1. RDA biplot showing the relation between vegetation characteristics and sward types in a natural, semi-arid grassland. Of all variance 67% could be attributed to sward type. Of this explained variance, 63% is displayed on axis 1 (horizontal), another 22% on axis 2 (vertical).

The first (horizontal) axis of the RDA represents 63 % of the explained variance. It reflects the separation of sward types due to resource quality, *i.e.*, leafiness, on the left side, and forage availability, *i.e.*, measures of plant (part) mass and height, on the right side. The positioning of measures of resource quality and of forage availability on opposite sides of the origin of the diagram indicates that they are negatively correlated. This axis mainly separates the short sward types (short-mixed, *C. dactylon* dominated and *E. barbinodis* dominated), which appear to be of low forage availability, but high resource quality, from the tall sward types (tall-mixed and *H. dissoluta* dominated). Tall sward types appear to be high in forage availability and low in resource quality.

of sward types owing to size of high-quality forage parts, *i.e.*, leaf width, and forage tissue quality, *i.e.*, forage tissue concentration of nutrients, on top of the diagram, and forage availability, *i.e.*, leaf density, and forage accessibility, *i.e.*, stem density, on the down-side of the diagram. This is indicative of a negative correlation between forage tissue quality and forage availability on the one hand, but a positive correlation between forage tissue quality and forage accessibility on the other hand. This axis separates the *P. maximum* dominated swards (short and tall *P. maximum*), which appear to offer high forage tissue quality and

forage accessibility but low forage availability, from all other sward types. The third axis (not shown) accounts for only 8 % of the explained variance.

The Monte Carlo permutation tests showed that all sward types differed significantly from one another (P < 0.05), except for the short-mixed and the *C. dactylon* dominated swards. It could not be shown that the tall *P. maximum* swards differed significantly from the short *P. maximum* swards and the tall-mixed swards, because their lumped sample sizes were to small to allow sufficient permutation possibilities to yield a *P*-value < 0.05.

Relationships among vegetation characteristics and forage intake characteristics

In Table 4.2, we present the forage intake characteristics in the chosen sward types. The variability of intake characteristics decreased from intake rate over bite weight, bite rate to bite digestibility (*c.v.* 56 % - 18 %).

The PCA revealed that forage intake characteristics could explain 42 % of the total variance in vegetation characteristics (Figure 4.2). The nominal co-variable "animal" explained just 7 % of this variance. However, in a separate general factorial analysis of the rate of forage intake with fixed factor sward type, the co-variate animal had a significant effect (F = 6.826, v = 1, P = 0.016).

	Forage intake characteristics						
Sward type	Intake rate [g DM s ⁻¹]	Bite mass [g DM]	Bite rate $[s^{-1}]$	Bite digestibility [%]			
short P. maximum	0.16 ± 0.01	0.23 ± 0.02	0.73 ± 0.08	60.1 ± 1.9			
tall P. maximum	0.15 ± 0.03	0.24 ± 0.05	0.61 ± 0.00	59.8 ± 9.4			
H. dissoluta	0.33 ± 0.08	0.38 ± 0.06	0.83 ± 0.09	43.2 ± 0.8			
C. dactylon	0.15 ± 0.04	0.20 ± 0.03	0.76 ± 0.11	43.6 ± 1.1			
E. barbinodis	0.21 ± 0.05	0.25 ± 0.03	0.83 ± 0.13	44.2 ± 3.1			
tall-mixed	0.20 ± 0.07	0.31 ± 0.10	0.67 ± 0.10	39.1 ± 1.1			
short-mixed	0.19 ± 0.03	0.25 ± 0.01	0.74 ± 0.07	50.4 ± 2.5			
<i>C.V.</i>	56 %	40 %	27 %	18 %			

Table 4.2. Forage intake characteristics of free-ranging cattle of mixed breed grazing in seven distinct sward types (indicated by dominant species) of a natural, semi-arid grassland, from the mid to the end of the rainy season. Shown are average values with standard errors and coefficient of variation (c.v.).



Figure 4.2. PCA biplot showing the relation between vegetation characteristics and forage intake characteristics for five cattle of mixed breed foraging in a natural, semi-arid grassland. Of the total variance, 7 % could be attributed to differences between animals. Of the remaining variance, 42 % could be explained by intake characteristics. Of this variance, 63 % is explained by axis 1 (horizontal), and another 20 % on axis 2 (vertical).

Of the explained variance, 63 % can be accounted to the first (horizontal) axis of the PCA, while the second (vertical) axis represents 20 %. Similar to the RDA, the first axis of the PCA mainly reflects the separation of resource quality measures, *i.e.*, leafiness, on the left, and forage availability measures, *i.e.*, plant (part) mass, on the right. The second axis reflects the separation between measures of the size of high-quality forage parts, *i.e.*, leaf width, and forage tissue quality, on top, and forage availability, *i.e.*, leaf density, and forage accessibility, *i.e.*, stem density, on the bottom of the diagram

The Monte Carlo Permutation test showed that forage intake rate (P = 0.003), bite mass (P = 0.001) and bite digestibility (P = 0.019) were significantly correlated with vegetation characteristics. However, though bite rate showed considerable variability (c.v. = 27 %), this intake characteristic was not correlated to vegetation characteristics. There was no significant effect of grazing day.

The vectors representing forage intake rate and bite mass were almost identical, indicating a close positive correlation (Figure 4.2). Neither of these vectors showed

resemblance to the vector representing bite rate. In a multiple regression model of forage intake rate on log bite mass and log bite rate, the relative effect of bite mass on intake rate was larger than the one of bite rate, as indicated by their standardised partial regression coefficients ($\beta_{logBM} = 0.77$ and $\beta_{logBM} = 0.45$). In a simple linear regression bite mass alone explained 79 % of the variation in intake rate. Under the assumption that bite mass explained most of the variation in intake rate, we concentrated our subsequent analyses of forage intake on bite mass.

The multiple linear regression analysis of bite mass on the vegetation characteristics, likely correlated with bite mass as indicated by the PCA (Table 4.3), delivered a regression model of bite mass (*BM*) on grass mass (*GM*) explaining 69 % of the variation in bite mass (*BM* = 0.18 g + 5.09 10⁻⁴ m² *GM*, $R^2 = 0.69$, P < 0.001). All other vegetation characteristics were excluded from the model by the stepwise forward selection procedure.

Table 4.3. List of vegetation characteristics likely to be correlated with bite mass and with bite digestibility as indicated by the PCA (Figure 4.2) and direction of the indicated correlation. These characteristics were used as independent factors in a multiple linear regression analyses on bite mass and on bite digestibility. Stepwise forward regression was used to identify significant factors.

Bite mass		Bite digestibility	
Vegetation characteristic	Direction of correlation	Vegetation characteristic	Direction of correlation
Grass mass	+	No-grass mass	+
Live mass	+	Greenness	+
Leaf mass	+	Leaf width	+
Stem mass	+	Grass digestibility	+
Dead mass	+	% N	+
Height	+	% P	+
Roughness	+	% Ca	+
Leaf length	+	% Na	+
Stem density	+	Stem density	-
Stem length	+		
% NFD	+		
Greenness	-		
Leafiness	-		
Grass digestibility	-		
% N	-		
% P	-		

The vectors representing bite digestibility and bite mass point to opposite quadrants of the PCA, indicating a negative correlation (Figure 4.2), but a simple linear regression model of bite digestibility on bite mass was not significant. Further analysis of bite digestibility and grass digestibility showed that bite digestibility was not correlated with grass digestibility (P = 0.445). However, we found that bite digestibility on average was 12 % higher than grass digestibility (t = 4.804, v = 28, P < 0.001).

The multiple regression model of bite digestibility on the vegetation characteristics, likely correlated with bite mass as indicated by the PCA (Table 4.3), delivered a regression model of bite digestibility on leaf width explaining 64 % of the variation in bite digestibility. All other vegetation characteristics were excluded by the stepwise selection procedure. However, in a general factorial analysis with sward as fixed factor and covariate animal, sward type had a highly significant effect on bite digestibility (F = 8.661, v = 6, P < 0.001).

Discussion

The results of this study suggest that the short-term rate of forage intake on patch level is primarily related to forage availability. Contrary to our expectations, our data do not consistently indicate an effect of forage resource structure on forage intake, even if forage resource quality is low (25 % leaves). We propose that this might be the result of locally increased accessibility of high quality forage, caused by the spatially uneven distribution of high quality forage in the grass sward, thus masking other effects of forage resource structure. Further, in this study the negative relationship of forage resource quality, resulted into constant selection opportunities for high quality forage parts. This enabled foragers to acquire a diet which was constantly higher than the average forage quality, but which was otherwise unrelated to forage quality (Prins, 1996). Further, our results do not support the notion that large herbivorous foragers follow a short-term energy intake rate maximisation rule. Instead it seems more likely that foragers take decisions on forage type choice according to a long-term energy intake maximising or satisficing rule (De Boer and Prins, 1989; Prins 1996).

Forage intake

The standardised partial regression coefficients showed that the relative effect of bite mass on intake rate was larger than the one of bite rate. This finding supports our expectation (i), namely that intake rate in free-ranging herbivores is mainly driven by bite mass rather than by bite rate.

Further, forage intake on patch level was positively related to forage availability as found in the multiple regression analysis, supporting expectation (ii). As all other vegetation characteristics were excluded by the forward selection procedure, effects of resource quality (iii), accessibility of high-quality forage parts (iv), local aggregation of forage mass (v), size of high-quality forage parts (vi), and of the size of intake deterring low-quality forage parts (vii) on forage intake could not be indicated.

These results differ from previous studies at feeding station level (Chapters 2 and 3). In these previous studies it was found that forage accessibility and resource quality have strong limiting effects on forage intake, even at high forage availability. However, we want to caution not to draw premature conclusions concerning the absence of effects of resource structure on forage intake. It is important to note that the above mentioned discrepancy between the results concerning the controlling factors at the levels of the patch and feeding station could be an artefact caused by one of the following factors:

First, in the present study we could be confronted with a methodological problem. Due to logistic constraints, the sample size was small (n = 31). This could mean that possibly the power of our statistical tests was to small to indicate really existing, but not as strong, effects of forage resource structure on forage intake.

Second, the vegetation characteristics used as explanatory variables in the multiple regression model showed manifold correlations between each other, as can be deducted from the biplots of the ordination analyses already. Consequently, we found that the regression model delivered by the forward selection procedure was not stable. An additionally performed backward selection procedure in fact excluded total forage availability (grass mass, expectation ii) because of collinearity, and instead delivered a multiple regression model based on the availability of high quality forage parts (leaf mass, expectation ii) and on the local aggregation of forage mass (sward roughness, expectation v).

Third, the foragers could have seized foraging opportunities opened up by small-scale variation in the distribution of high quality forage parts, below the resolution of our measurements at patch level in the present study. We observed that the foragers did not utilise the forage patches uniformly. Instead, in tall patches they exploited the existing within-patch variation by concentrating their foraging efforts on gaps in the vegetation. We found that, while the vegetation in tall patches frequently reached heights of more than 180 cm, 70 - 100 % of all bites in tall patches were taken from below 50 cm high. In a simple linear regression model the proportion of bites taken from below 50 cm high was correlated positively with the rate of forage intake and explained 81 % of the variation in forage intake. Foragers utilised

vegetation gaps directly by foraging on the forage within them, which typically was of higher accessibility and quality than the surrounding tall vegetation. But they also used these gaps as a starting point from where to approach neighbouring forage items sideways, thereby avoiding confrontation with foraging deterring low-quality support tissue, a strategy already mentioned in an earlier paper by Ruyle *et al.* (1987).

We attempted to account for the positive effects of sward gaps, by measuring the roughness of the swards with high resolution (*i.e.*, 10 cm). However, we were not able to consistently link sward roughness to forage intake (expectation v), which perhaps can be attributed to a strong positive effect of even small vegetation gaps. In a previous study, we showed that cattle-sized foragers responded positively to little increments in the surface area of small-scale aggregations of high-quality forage parts. However, this effect was absent for larger aggregations (Chapter 2). Parallel to this, it might be that in the current study foragers may have been able to effectively utilise even small sward gaps, and that increasing sward gap surface might not have had additional positive effects on foraging efficiency, thereby making the positive effects of small gaps statistically difficult to detect.

The positive effect of vegetation gaps described here appears complementary to a mechanism suggested by Ungar and Noy-Meir (1988). In their study, increased forage intake is the result of larger bite mass when foragers crop local forage aggregations, *i.e.*, increased sward height. However, this study ignored that these local forage aggregations most likely will have a different structure than the surrounding forage resource. Especially, these aggregations likely will have higher contents of low-quality support tissue, *i.e.*, the accessibility of high-quality forage parts within the aggregations might be lower.

As expected forage intake rate was related to bite mass rather than to bite rate (expectation i). This finding is consistent with the general theory on forage intake (e.g., Spalinger and Hobbs, 1992; Farnsworth and Illius, 1996). However, the total lack of a relationship of bite rate with vegetation characteristics is conspicuous. Though we did not *a priori* focus on this aspect, we expected bite rate to decrease with stem density, caused by increased handling efforts of bites, or to decrease with sward roughness, due to increasing demands to the visual identification of potential bites. We offer two hypotheses explaining this lack of correlation. Firstly, foragers might be able to compensate for negative effects of vegetation characteristics by adjusting their foraging behaviour, e.g., by adapting foraging velocity or by decreasing handling times (Newman *et al.*, 1994), which would imply that foragers are not resource limited. Secondly, conflicting effects of sward structure may compensate each other, e.g., the negative correlation of forage availability with forage

accessibility, *i.e.*, the inverse of stem density, might lead to decreasing searching times being compensated by increasing handling times.

Diet quality

Diet quality was consistently higher than forage resource quality, but otherwise unrelated to vegetation characteristics or intake characteristics, therefore not supporting our expectations (viii – xii). Instead, contrary to our expectations our results suggest that average leaf width of the grasses is an important variable in determining diet quality. Again the vegetation characteristics used as explanatory variables in the multiple regression model showed some degree of collinearity. But, differently from the analysis of forage intake, in the case of diet quality the regression model delivered by the forward selection procedure was stable, as indicated by an additionally performed backward selection procedure. Nevertheless, there is no scientifically valid reason as to what kind of causal link could exist between leaf width as such and diet quality. Instead, we suggest that leaf width is a kind of indicator variable correlated with other vegetation characteristics which are linked with diet quality. However, which vegetation characteristics this might be remained unclear, and could neither be revealed by an additional path analysis (results not shown).

We propose that the lack of a correlation between diet quality and vegetation characteristics might be the result of forage availability being negatively correlated with resource quality leading to omnipresent selection opportunities for high-quality forage parts. At high forage availability the proportion of high-quality forage parts is rather low, but as forage mass is high, there is ample opportunity to select high-quality forage. As low forage availability was in part caused by high foraging pressure, low-quality forage parts, *i.e.*, moribund material or support tissue, could not accumulate, again providing easy access to high-quality forage parts. These findings differ from an earlier study by Hamilton *et al.* (1973) who suggested that decreasing forage availability forces foragers to include low-quality forage parts into their diet above their proportion in the forage resource. However, we acknowledge that the mechanism we described for our study depends on the abundance of high-quality forage parts and that this might not be so during the dry season, when the production of high-quality forage parts ceases and their availability decreases.

Energy gain

We used our results of forage intake rate and diet quality to calculate the short-term rate of intake of metabolisable energy in our foragers. The metabolisable energy content of organic

digestible matter is 15.06 kJ g⁻¹ (Centraal Veevoederbureau in Nederland, 1999). For our observations, this results in intake rates of metabolisable energy ranging between 18 - 221 kJ min⁻¹. Taking into account differences in mass, gender and breed we estimated the requirements of our foragers for metabolisable energy at maintenance (zero growth and no change in condition) to range between 38 - 78 MJ day⁻¹ (Agricultural Research Council, 1980). We investigated the short-term energy intake rates and daily energy requirements for maintenance for a relationship, but were unable to detect any.

Furthermore, we investigated whether the short-term rates of energy intake per forage resource type would be sufficient to cover the daily energy requirements for maintenance. We took maximum daily foraging time to be 650 minutes (Chacon, 1976). Further, we assumed that foragers spent the total daily foraging time in one forage resource type only and that forage resources are not depleted during foraging. We found that daily energy intake on the basis of the short-term energy intake rates in one forage type only, would have resulted in frequent daily energy deficiencies in all individuals, with shortfalls of up to 85 %, especially in lactating animals.

However, if we assumed that foragers allocated the total daily foraging time equally over all measured forage resource types and also assuming that forage resources are not depleted during foraging, we found that daily energy intake rates would have resulted in reduced energy deficiencies in one individual (56 %) and satisfaction of daily energy requirements for maintenance in all other individuals.

If our foragers were to maximise daily energy intake rates, they should have concentrated their foraging efforts on the resource types where they could achieve maximum short-term energy intake rates, assuming no depletion of forage resources during foraging. However, we frequently encountered individuals foraging on resources where they achieved very low short-term energy intake rates. This is not necessarily a proof that foragers were not following a maximisation rule. Foraging on resources offering low energy intake rates might be the result of the foragers' sampling of potential forage resources or of foraging while in transit from one high-quality resource patch to the next (Van Wieren, 1996). Nevertheless, as none of our foragers lost condition during the observational period (personal observation), we conclude that they were at least fulfilling their daily energy requirements for maintenance. Interestingly, an equal distribution of daily foraging time over all resource types already would result in the satisfaction of their daily energy requirements. In this context it is important to note, that such an equal distribution of foraging time could serve the dual purpose of satisficing energy requirements and achieving a balanced diet at the same time

(Prins and Beekman, 1989). We conclude that our foragers were probably not following a short-term energy intake rate maximising rule. Instead, they likely followed a long-term (perhaps day) average-rate maximising rule or satisficing rule, though our data are not sufficient to conclude which one of these alternative rules should be given preference.

Conclusion

Though forage resource complexity is important in determining forage intake at feeding station level, our data gave no indication that this is also the case at patch level. Forage intake at patch level seemed to be determined mainly by forage availability. On the basis of our results, we suggest that the factors governing forage intake may differ between these spatial and temporal scales, which should be taken into account when scaling up forage intake measurements. Further, the negative correlation of forage availability with resource quality in natural grasslands may provide foragers with ample opportunity for the selection of a high quality diet. Nevertheless, this situation may change when average forage availability and resource quality are decreasing due to reduced forage production in the dry season. Additionally we found, that foragers likely follow a daily energy intake maximising or satisficing rule, resulting in a rather indiscriminate utilisation of a number forage types offering a wide range of short-term energy intake rates. Taking decisions over the acceptability of forage types on basis of a long-term energy requirement satisfaction criterion, therefore would give the foragers considerable flexibility in deciding over the short-term utilisation of forage resource patches.

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Chapter 5

The functional response as a function of prey quality and its consequences for predator-prey interaction

Abstract

The functional response as the link between the predator and its prey is a central issue in ecology. Although the prev population often consists of low and high quality parts due to *e.g.* nutritional or structural differences, differences in the quality of the prey parts, are not explicitly considered so far. In this paper, we derive a model for the functional response that depends on prey quality, *i.e.*, the proportion of high quality parts in the prey population. A downward deflection of the functional response is due to a depression of the maximum consumption rate at high densities of low quality prey parts. This intake depression is caused by increased efforts of gathering and processing prey parts, as indicated in recent experiments. Hence, our model of the functional response gives a more mechanistic explanation for decreasing consumption rates with decreasing prey quality at high prey densities than has been given so far. Compared to a functional response with constant maximum consumption rate, our model with variable consumption rate shows discontinuous changes in both the low and high quality prey parts and in the predator density. The effects critically hinge on the positive feedback between the predator density and the proportion of high quality prev parts. A decrease in the proportion of high quality prey parts leads to a decrease in the consumption rate that consequently decreases the predator population. A decreased predator population is not able to maintain a relatively high proportion of high quality parts and prey quality decreases further. On the other hand, a decrease in low quality prey parts causes an increase in the consumption rate and can lead to a relatively high predator population. High consumption rates depress the growth of low quality prey parts stronger than of high quality prey parts leading to an increase in the proportion of high quality prey parts. We argue that our approach is applicable to many predator-prey interactions where the predator is not receiving a direct feedback to enable diet choice while foraging.

Key words: alternative stable states; predator-prey model; grazing, food intake; food quality; Allee effect.

Introduction

The functional response as the relationship between the consumption rate and the abundance of prey items is the link between the predator and its prey (Holling, 1959). The dynamics of interacting predator and prey populations is one of the most thoroughly studied problems in ecology. Many theoretical studies explore the consequences of different types of the functional response on predator and prey populations, such as the shape of the functional response (Van de Koppel *et al.*, 1996) and a prey-dependent versus a ratio-dependent predator functional response (Akçakaya *et al.*, 1995; Blaine and De Angelis, 1997; Abrams and Ginzburg, 2000). Others derive models for the functional response based on different mechanisms of searching and handling by the predator (Spalinger and Hobbs, 1992; Gross *et al.*, 1993). In all these studies, however, differences in the quality of the prey, such as nutritional or structural differences, are not explicitly considered. In reality, the prey population often consists of low and high quality parts, where high quality parts are preferred over low quality parts since the profitability is higher (Hamilton *et al.*, 1973; Sarma *et al.*, 1997; Czesny *et al.*, 2001). These quality differences should thus be considered in the functional response (Fryxell, 1991).

In this paper, we concentrate on the functional response in one type of predator-prey interaction, namely the interaction between mammalian herbivores and the vegetation, though the wider applicability of our findings to other trophic interactions will be discussed. Originally, functional response models were thought to represent the predator consumption rate of discrete, homogeneous food items (Holling, 1959). For mammalian herbivores, however, the prey is often a complex sward where food items are difficult to distinguish. We assume here that one bite is one food item (cf. Spalinger and Hobbs, 1992). A sequence of bites during a certain period can be described by the functional response.

It has been shown that, as vegetation biomass increases, its average quality as forage for herbivores decreases (Fryxell, 1991; Wilmshurst *et al.*, 1995, 1999; Prins and Olff, 1998; Van der Wal *et al.*, 1998; Hassall *et al.*, 2001). We illustrate this by the decrease of the proportion of leaves (as high quality food) and the average nitrogen content in the plants with increasing accumulation of biomass in a natural grassland in a South African savanna (Figure 5.1). Food quality is in this paper defined as the proportion of high quality parts, where high quality parts contain high protein content or few structural components. The decrease of food quality with increasing grass biomass can be caused by, for example, higher structural investments in plants due to competition for light when the vegetation becomes more dense (Stobbs, 1973).



Figure 5.1. Decreasing (a) proportion of leaves and (b) average nitrogen content in a natural grassland dominated by different species of grass in a South African savanna in the late wet season.

The actual mechanism by which this decrease in forage quality affects the functional response received little attention so far.

Hamilton *et al.* (1973) and Stobbs (1973) studied the effects of changes in the quality and composition of the prey population on forage intake in mammalian herbivores. They found that increasing proportion of high quality prey led to increase in quality of the ingested food and an increase in forage intake. A recent study on forage intake in large herbivores demonstrates that the consumption rate depends on the density and on the proportion of low and high quality parts in the vegetation, stems and leaves respectively (Drescher *et al.*, Chapter 2; Figure 2.2). Density and proportion had several effects on the functional response. Drescher *et al.* (Chapter 3) show that the effort to gather a certain amount of high quality food depends on the density of low quality parts. An effect of this is that for given total forage mass on offer, a decrease in the proportion of high quality parts depresses the maximum per capita consumption rate. A decrease in consumption rate with decreasing proportion of high quality food on offer has also been observed in a number of other predator-prey interactions. The causes appear to depend on the size of the forager relative to the size of the prey items, the degree of selectivity, and the spatial density and distribution of prey items: 1) increased efforts involved in the identification of offered prey types and decision about the acceptance of prey items (Czesny *et al.*, 2001); 2) decreased encounter rate with the offered high quality prey type without diet switching (Sarma *et al.*, 1997); 3) increased handling efforts per prey item as selection demands increase (Ruyle *et al.*, 1987; Engelmayer, 1992); 4) decreasing volume of ingested high quality food items (Hongo, 1998; Drescher *et al.*, Chapter 3); 5) increased processing efforts as the proportion of the less profitable parts in the ingested food increases (Wales *et al.*, 1990; Wilson and Kennedy, 1996). These factors can explain the decrease in maximum consumption rate with decreasing quality of the food on offer.

In this paper, we derive a function for the predator functional response that depends on the proportion of preferred, high quality parts in the prey on offer. We study the effects of this functional response on predator and prey populations by including it in a simple predator-prey model.

The model

Often used functional response and predator-prey model

The rate of prey consumption by the predator is often described as a monotonically saturating function (type II curve; Holling, 1959), denoted as

$$c(P) = c_m \frac{P}{P + k_1} \tag{1}$$

where *P* is the prey density, c_m is the maximum per capita consumption rate and k_1 is the half saturation constant where the consumption rate is the half of the maximum consumption rate. In Appendix 5.1, the used symbols, their interpretation and units are enumerated. Though a finite processing capacity is the ultimate cause of the asymptotic shape of the relationship, the search and handling time that largely determine the functional response of the predators are not explicitly considered in eq. 1. Patterns that fit eq. 1 have been found in many experiments, particular in simple environments with only a single type of prey (Gross *et al.*, 1993; McCoull *et al.*, 1998; Koski and Johnson, 2002).

Figure 5.2. (Opposite page) The maximum consumption rate $c_m(H,L)$ (eq. 4) as function of (a) the proportion of high quality prey p_H and (b) the density of high and low quality prey. Parameter values are: $c_{Hm} = 1.0$, $c_{Lm} = 0.1$, $k_2 = 0.2$.



In simple predator-prey models, the rate of change of the prey and predator populations can be generally represented by the differential equations

$$\frac{\mathrm{d}P}{\mathrm{d}t} = f(P) - c(P)N \tag{2a}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = g(P)N \tag{2b}$$

where f(P) describes prey growth as a function of prey density, c(P) is the consumption rate of the predator (eq. 1), N is the predator density, and g(P) is the per capita net growth rate of the predator population, *i.e.*, the numerical response. The numerical response of the predator population is usually represented as

$$g(P) = ec(P) - d \tag{3}$$

where e is the consumption-to-growth conversion coefficient and d the specific loss rate of the predator. Although this model contains several assumptions about prey and predator growth, it is often used to describe predator-prey interactions (see e.g., Yodzis, 1989).

Model for the functional response as function of food quality

Based on the findings of Drescher *et al.* (Chapter 2), we formulated the effect of the proportion of high quality parts of the prey on offer (p_H) on the maximum consumption rate as

$$c_m(H,L) = c_{Hm} \frac{1+k_2}{1+k_2 c_{Lm}} \frac{p_H + k_2 c_{Lm}}{p_H + k_2}$$
(4)

where c_{Hm} is the maximum consumption rate when the prey consists of only high quality parts, *i.e.*, $p_H = 1$; c_{Lm} is the maximum consumption rate when the proportion of high quality prey is zero, *i.e.*, $p_H = 0$, expressed as a fraction of c_{Hm} ; and k_2 is the half saturation constant where the consumption rate is the half of the maximum consumption rate. The maximum consumption rate as function of the proportion of high quality prey (eq. 4) is illustrated in Figure 5.2a.

The prey density is P = H + L, where *H* is the density of high quality prey and *L* is the density of low quality prey. The proportion of high quality prey is calculated as

$$p_H = \frac{H}{H+L} \tag{5}$$

The effects of the densities of high and low quality prey on the maximum consumption rate are illustrated in Figure 5.2b. This figure shows several properties of eq. 4. First, the maximum consumption rate is at its highest when the density of low quality prey on offer is zero. Note that the model cannot produce the maximum consumption rate when both the

density of offered low and high quality prey is zero. Second, the maximum consumption rate increases with an increasing proportion of high quality prey on offer, while the prey density *P* remains constant, following a saturating function (see Figure. 5.3a). Third, the maximum consumption rate decreases when the constant prey density on offer has an increasing proportion of low quality prey (Engelmayer, 1992; Drescher *et al.*, Chapter 2, Figure 2.3).

Based on eq. 4, the rate of prey consumption by the predator can then be denoted as

$$c(H,L) = c_m(H,L)\frac{P}{P+k_1} = c_{Hm}\frac{1+k_2}{1+k_2c_{Lm}}\frac{p_H+k_2c_{Lm}}{p_H+k_2}\frac{H+L}{H+L+k_1}$$
(6)

The effect of the offered density of low and high quality prey on the functional response of eq. 6 is illustrated in Figure 5.3a. This figure shows that at high density of high quality prey, the consumption rate decreases with increasing density of low quality prey. When the density of high quality prey is low, the consumption rate shows a unimodal curve with the density of low quality prey (Figure 5.3b). This agrees with findings that, in herbivores, forage intake decreases with decreasing forage quality when the vegetation biomass increases (Fryxell, 1991; Van de Koppel *et al.*, 1996; Wilmshurst *et al.*, 1995, 1999; Van der Wal *et al.*, 1998). Figure 5.3 further shows that at all densities of low quality prey, the consumption rate increases with increasing high quality prey density, following a saturating function.

Functional response as function of prey quality in predator-prey model

For our analysis of the effect of the functional response as formulated in eq. 6 on predatorprey dynamics, we use a simple prey model. Therefore, we consider a grass model where the low quality prey parts are the stems of the grass. The leaves form the high quality prey parts. The growth rate of the low quality parts depends on the density of the high quality parts, *i.e.*, there is hardly any photosynthetic material when the leave density is low and, therefore, the growth of the stems is low. The specific growth rate of the low quality food parts is modelled as

$$r_L(H) = r_{Lm} \frac{H}{H + k_3} \tag{7}$$

where r_{Lm} is the maximum specific growth rate of the low quality parts and k_3 is the half saturation constant where the specific growth rate is the half of the maximum specific growth rate. Without predation, the rate of change of the low quality prey density is formulated as

$$\frac{\mathrm{d}L}{\mathrm{d}t} = r_L(H) - m_L L \tag{8}$$



Figure 5.3. (Opposite page) The consumption rate of the predator or the functional response c(H,L) (eq. 6) as function of (a) the density of low and high quality prey parts, and (b) the density of low quality prey parts. For the solid line in (b), the density of high quality prey H is constant and the proportion high quality prey p_H decreases (see inset) as the low quality prey density L increases. The dashed line in (b) represents an increase in the proportion of high quality prey p_H (see inset) since with increasing low quality prey L, also the density of high quality prey H increases. Parameter values: (a and b) $k_1 = 0.5$, $k_2 = 0.2$, $c_{Lm} = 0.05$, $c_{Hm} = 0.1$, (b) solid line with H = 0.2 and dashed line with H = 0.2 L.

where m_L is the specific loss rate of the low quality prey, *i.e.*, a constant decay rate of ageing stem material. The rate of change of the high quality prey without predation is assumed to be

$$\frac{\mathrm{d}H}{\mathrm{d}t} = r_H - m_H H \tag{9}$$

where r_H is the specific growth rate of the high quality parts and m_H is the specific loss rate, *i.e.*, a constant decay rate of ageing leaves. Note that both the high and low quality prey follows logistic growth. The prey density in the absence of predation at equilibrium (thus where the change in the state variables is zero, *i.e.*, dL/dt = dH/dt = 0, is $P^* = H^* + L^*$, where

$$H^* = \frac{r_H}{m_H} \qquad L^* = \frac{r_H r_{Lm}}{m_L (k_3 m_H + r_H)}$$
(10)

These equilibria are stable for the parameter ranges we use.

The predator-prey model can now be formulated as

$$\frac{\mathrm{d}L}{\mathrm{d}t} = r_L(H) - m_L L - (1 - \rho_H)c(H, L)N \tag{11a}$$

$$\frac{\mathrm{d}H}{\mathrm{d}t} = r_H - m_H H - \rho_H c(H,L)N \tag{11b}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \left(e_H \ \rho_H + e_L \left(1 - \rho_H\right)\right) c(H, L) N - d N \tag{11c}$$

where ρ_H is the proportion of high quality prey in the diet of the predator and is based on the quality of the food on offer. It provides thus the selection possibilities of the predator; e_H and e_L are coefficients for the consumption-to-growth conversion for the ingested high and low quality prey parts, respectively. The proportion of high quality prey in the predator diet is calculated as

$$\rho_H = \left(1 + \beta\right) \frac{p_H}{p_H + \beta} \tag{12}$$

where β is the coefficient that represents the selection possibilities of the predator. When $\beta = 0$, the diet consists only of high quality prey parts since $\rho_H = 1$, and $\beta = \infty$ means that the diet

of the predator reflects the supply (Figure 5.4). Then, the fraction of high quality prey in the diet equals the proportion of high quality prey on offer since $\rho_H \approx p_H$ when $\beta \rightarrow \infty$.

Results

Analysis of the predator-prey model

We analyse two versions of the predator-prey model described by eq. 11. On the one hand, we consider the model with the often used functional response as formulated by eq. 1, where the rate of prey consumption is a function of the offered prey density P = H + L, and is independent of the proportion of high quality prey p_H . On the other hand, we include the functional response with the effect of food quality on the maximum consumption rate in the predator-prey model. Here, we use the functional response formulated in eq. 6 where the rate of prey consumption is a function of the density of both high and low quality food on offer. In our analyses, we first assume that the diet of the predator is equal to the offered prey ($\beta = \infty$ in eq. 12).



Figure 5.4. Proportion of high quality prey in the ingested food of the predator ρ_H as function of the proportion of high quality prey on offer p_H for different values of the parameter β (eq. 12): dashed line for $\beta = 0.5$ and solid line for $\beta = 100$.
One way to analyse the dynamics of the predator-prey model is by plotting the equilibria of the low and high quality food on offer and the predator density (dL/dt = dH/dt = dN/dt = 0) as a function of some parameters that are expected to significantly change the behaviour of the model. We separately analysed the effects of two parameters, namely the maximum specific growth rate of the low quality prey parts r_{Lm} and the consumption-to-growth conversion coefficient for ingested low quality food e_L . An increase in r_{Lm} means an increase in the density of low quality prey on offer and will have no effect on the density of high quality prey on offer (eq. 10). Therefore, it leads to a decrease in the proportion of high quality prey on offer p_H .

An increase in e_L , with constant e_H , means that the benefits of consuming low quality food for the predator become higher. The analysis of the effect of e_L is relevant since, for example, the magnitude of the difference between e_L and e_H can depend on the predator species, see Appendix 5.2 for examples of herbivores. A decrease of e_L can also occur during a certain period of time since the protein content or digestibility of the ingested low quality food may decrease. For example, the forage quality of leaves and stems for herbivores decreases drastically from the beginning until the end of the wet season, but stronger so for stems (Stobbs, 1973).

Allee effect in predator dynamics

Before analysing the equilibrium density of the low and high quality prey populations and of the predator population, however, we first investigate the properties of the predator dynamics (eq. 11c). The rate of change of the predator population dN/dt can be plotted as function of the predator density N (Figure 5.5). Here, the density of low and high quality prey are kept constant. When the proportion of high quality prey on offer has no effect on the consumption rate, *i.e.*, the consumption rate has a constant maximum (eq. 1), the rate of change in predator density shows a unimodal curve with predator density, according to logistic growth. At the points where the curve meets the *N*-axis, *i.e.*, where the rate of change in predator density is zero dN/dt = 0, the predator density is at equilibrium. This can be either a stable or unstable equilibrium as indicated in Figure 5.5. The arrows indicate the direction of development of the predator density. As can be expected for the predator-prey model with the conventional functional response, the equilibrium density of predators increases with increasing the maximum specific growth of the low quality food (r_{Lm}) since more food is available.



Figure 5.5. The rate of change in the predator population (dN/dt, eq. 11c) as function of predators density (*N*) for a constant density of low and high quality prey on offer. On the left hand side, the rate of change in the predator population is given for a constant maximum consumption rate (eq. 1), on the right hand side for a variable maximum consumption rate (eq. 6). Stable equilibria are indicated with solid dots, unstable with open dots. The arrows indicate the direction of development. Parameter values (a) $r_{Lm} = 0.5$, (b) $r_{Lm} = 0.8$ and (c) $r_{Lm} = 1.6$, other parameters: $c_m = 1.0$ (for left-hand side), $c_{Hm} = 1.0$ and $c_{Lm} = 0.1$ (for right-hand side), $k_1 = 0.5$, $k_2 = 0.2$, d = 0.06, $m_L = 0.1$, $k_3 = 5$, $r_H = 0.9$, $m_H = 0.5$, $e_H = 0.1$, $e_L = 0.05$, $\beta = 100$.

However, for the predator with the variable maximum consumption rate depending on the proportion of high quality prey on offer (eq. 6), a different pattern can be observed. At intermediate levels of the maximum specific growth of the low quality food (r_{Lm}), one unstable and two stable equilibria occur (Figure 5.5b). When the predator density is below the unstable equilibrium, then the predator density decreases due to the negative rate of change until the stable equilibrium N_1^* is reached. Above this threshold, the predator density will develop towards N_2^* . This can be explained by the positive feedback between the predator density and the proportion of high quality prey on offer: a high predator density can keep the proportion of high quality prey high, thus maintaining a high consumption rate. A low predator density, on the other hand, leads to an increase in the proportion of low quality prey and thus to a depression of the consumption rate. The result is an accumulation of low quality prey on offer, which consequently leads to a decrease in predator density since the consumption rate further declines. This can be seen as an Allee-type of effect where low predator density cannot keep the prey at high quality. For herbivores, for example, this means that high numbers of herbivores can keep the grass sward at a state with relatively low stem density and high leaf density, thus maintaining high average quality in so-called grazing lawns (Vesey-FitzGerald, 1969; MacNaughton, 1984).

When the specific growth rate of the low quality prey is high (Figure 5.5c), the predator cannot maintain the prey on offer at high proportion of high quality. Then, the consumption rate is low leading to the disappearance of the predator.

Effect of the maximum specific growth rate of the low quality food r_{Lm}

Now, we will investigate the behaviour of both predator-prey systems (with constant and variable maximum consumption rate) for changes in the maximum growth rate of the low quality prey r_{Lm} (Figure 5.6). The equilibria of low and high quality prey and of predator density are shown. Arrows indicate the direction of the development. As expected, the equilibrium proportion of high quality prey on offer, p_{H} , decreases with increasing r_{Lm} (Figure 5.6c). For the predator with constant maximum consumption rate, the increase in r_{Lm} results in a slight increase in predator density (Figure 5.6d). Due to the rising consumption rates with increasing total prey density as the density of low quality prey increases (Figure 5.6a). For the predators. Due to these two stable states, there are discontinuous changes in the density of low and high quality prey and in the predator density. When r_{Lm} is small and low quality prey is sparse, the per capita consumption rate is high and all newly grown low quality prey is readily consumed, thus keeping the density of high quality prey, the consumption rate and the density of predators all high.



Figure 5.6. Changes in the equilibria of low and high quality prey density and the predator density as function of the maximum growth rate of the low quality prey r_{Lm} . The graphs on the left-hand side show the equilibria when the functional response with constant maximum consumption rate (eq. 1) is included. The dot-dashed lines are the equilibria without predation, the solid lines with predation.

Figure 5.6. (Continued from opposite page) On the right-hand side, the equilibria are shown for the system with the functional response with a variable maximum consumption rate (eq. 6). Here, the solid lines represent stable equilibria and the dashed lines the unstable equilibria. The arrows indicate the direction of development. The effects of r_{Lm} are shown on respectively (a) the density of low quality prey, (b) the density of high quality prey, (c) the proportion high quality prey p_H , and (d) the density of predators. Parameter values: $c_m = 1.0$ (for left-hand side), $c_{Hm} = 1.0$ and $c_{Lm} = 0.1$ (for right-hand side), $k_1 = 0.5$, $k_2 = 0.2$, $k_3 = 5$, d = 0.06, $m_L = 0.1$, $m_H = 0.5$, $r_H = 0.9$, $e_H = 0.1$, $e_L = 0.05$, $\beta = 100$.

When the density of low quality prey increases as a result of an increase in r_{Lm} , the system can either contain a high or a low density of predators, depending on the initial value of the predator density. In contrast to low predator density, high predator density can keep the prey on offer at high quality. Note that both an increase and a decrease in r_{Lm} result in discontinuous changes in the densities of low and high quality prey and of the predator population. However, these changes occur at different values (*i.e.*, we find a hysteresis effect; Noy-Meir, 1975; May, 1977). As r_{Lm} increases even further, this leads to an ever-increasing density of low quality prey on offer (Figure 5.6a). However, because the proportion of high quality prey on offer is low (Figure 5.6c), the consumption rate of the predator is low. The predators are unable to control the accumulation of low quality prey on offer and will eventually disappear (Figure 5.6d).

Effect of the consumption-to-growth conversion coefficient of low quality food e_L

The changes in the equilibrium densities of low and high quality prey and predator density as a function of the consumption-to-growth conversion coefficient of ingested low quality food e_L are shown in Figure 5.7. For the predator with the constant maximum consumption rate, an increase in e_L leads to an increase in the predator density since the benefits of low quality food increase (Figure 5.7d). For the predator with the variable maximum consumption rate, the predator density shows again discontinuous changes with changing e_L . For low levels of e_L , the predator density is zero. Here, the proportion of high quality prey on offer is not sufficient to keep the predator present. For higher values of e_L , the ingested food provides sufficient benefits to the predators to sustain, and they manage to keep the low quality prey on offer at a low proportion. Increasing e_L then leads to a further increase in the predator population. As changes in e_L occur over time, for example, when herbivores experience a decrease of e_L because of a decrease in the forage quality of the stems, the herbivores cannot keep the vegetation in a short stage with a high proportion of leaves. Then, because of a decrease in consumption rate the herbivore population decreases and low quality stems dominate the vegetation (Van der Wal *et al.*, 1998).



Figure 5.7. Changes in the equilibria of low and high quality prey density and the predator density as function of the coefficient for the consumption-to-growth conversion for the low quality prey e_L . The graphs on the left-hand side show the equilibria when the functional response with constant maximum consumption rate (eq. 1) is included. On the right-hand side, the equilibria are shown for the system with the functional response with a variable maximum consumption rate (eq. 6).

Figure 5.7. (Continued from opposite page) Here, the solid lines represent stable equilibria and the dashed lines the unstable equilibria. The arrows indicate the direction of development. The effects of e_L are shown on respectively (a) the density of low quality prey, (b) the density of high quality prey, (c) the proportion high quality prey p_H , and (d) the density of predators. Parameter values: $c_m = 1.0$ (for left-hand side), $c_{Hm} = 1.0$ and $c_{Lm} = 0.1$ (for right-hand side), $k_1 = 0.5$, $k_2 = 0.2$, $k_3 = 5$, d = 0.06, $m_L = 0.1$, $m_H = 0.5$, $r_H = 0.9$, $r_{Lm} = 0.5$, $e_H = 0.1$, $\beta = 100$.

Effect of the coefficient for prey selection β

Finally, we changed the coefficient that represents prey selection β (Figure 5.8). An increase in β means that the ingested food of the predator is increasingly representative of the composition of the total prey on offer (eq. 12 and Figure 5.4). At $\beta = 0$, the diet consists of solely high quality prey parts, independent from the composition of the prey on offer. Low values of β represent small animals since their mouth morphology enables them to select high quality forage (Murray and Illius, 2000). As can be expected, an increase in β leads to a decrease in the density of low quality prey on offer since it is increasingly included in the diet (Figure 5.8a). The consumption rate increases then slightly since the proportion of high quality prey on offer increases. The predator density, however, decreases due to the low consumption-to-growth coefficient of the low quality prey that is increasingly included in the diet.

Discussion

In this paper, we derived a model for the functional response that depends on prey quality, *i.e.*, the proportion of high quality parts in the prey population. Different from previous studies (Fryxell, 1991; Van de Koppel *et al.*, 1996; Bos, 2002) we did not *a priori* assume a depressed consumption rate due to some undefined negative effect of increasing prey density. Instead, we explicitly state that the consumption rate depends on the proportion and density of both low and high quality prey on offer. A downward deflection of the functional response is caused by the maximum consumption rate being depressed at high densities of low quality prey on offer. As is argued, this intake depression is due to the increased efforts of gathering and processing prey parts, as has been indicated in a previous study (Drescher, Chapter 3). Therefore, this model gives a much more mechanistic explanation for decreasing consumption rates with increasing prey densities then has been given so far (Fryxell, 1991; Van de Koppel *et al.*, 1996; Bos, 2002).



Figure 5.8. Changes in the equilibria of low and high quality prey density and the predator density as function of the coefficient that represents the prey selection β . Low values of β means a highly selective predator (see Figure 5.4). The functional response of the predator has a variable maximum consumption rate (eq. 6). The arrows indicate the direction of development. The effects of β are shown on respectively (a) the density of low quality prey, (b) the density of high quality prey, (c) the proportion high quality prey p_H , and (d) the density of predators. Parameter values: $c_m = 1.0$ (for left-hand side), $c_{Hm} = 1.0$ and $c_{Lm} = 0.1$ (for right-hand side), $k_1 = 0.5$, $k_2 = 0.2$, $k_3 = 5$, d = 0.06, $m_L = 0.1$, $m_H = 0.5$, $r_H = 0.9$, $r_{Lm} = 0.5$, $e_H = 0.1$, $e_L = 0.05$.

Differences between our approach and diet choice models

Previous foraging models including variation in food quality introduced diet choice (e.g., Fryxell and Lundberg, 1994). In these models, one prey type is more attractive to the predator than another, possibly due to higher energy content or to differences in handling time. Both prey types can occur with different density and may have different probabilities of attack. A change in the density of one prey type can lead to sudden changes in the diet of the predator. In this paper, however, we discuss what kind of decisions predators are really likely to be able to make and under what conditions. Generally, assumptions for this decision-making are made about the perceptive and cognitive abilities of foragers.

In carnivorous predators, the quality of a prey item is positively related to prey size as the energy content per unit prey volume is rather independent of prey size. The quality of a prey item can therefore be assessed through the predator while handling or by judging its gut fill after handling. This offers the predator the opportunity for learning about prey quality by direct assessment of its own condition immediately after handling the prey and this may form the basis for diet choice.

Herbivorous predators, however, can take tens of thousands of prev items (bites) every day, typically covering a wide range of prey types. The energy content per unit prey item can differ depending on prey type, its age and environmental factors such as season. Information about the quality of the ingested prey items is available to the herbivore only with a timedelayed feedback after digestion and integrated over a large number of different prey items. Taking this into account, it seems unlikely that herbivorous predators have a detailed knowledge of the nutritional values of individual prey items, which they could use to make decisions on diet choice (Prins and Olff, 1998). This is not to say that herbivorous predators cannot use general, physical clues about the profitability of individual prey items, such as greenness or toughness. A herbivore can readily assess these clues while foraging and can link them directly with energy expenditure for handling and processing and thus prey profitability. As many physical properties are to some degree correlated to chemical properties of the prey type, in an indirect way a herbivore might choose a diet of high quality prey while selecting against these physical properties. Besides that, different from carnivorous predators, prey items for herbivorous predators come not as discrete units. In a complex sward, different prey types (high and low quality) are intimately mixed and cannot easily be separated. Hence, the opportunity for selection is limited for physical reasons and virtually every bite consists of both low and high quality parts, often closely resembling the composition of the prey population on offer. For herbivorous predators, our model of the functional response that depends on the proportion of high quality prey better reflects reality than a diet choice model.

Without including the consumed mass of high quality food in relation to the body mass of the herbivorous predator, however, we still cannot completely grasp the process of consumption. For herbivores, it is hypothesised that animals with large body mass are able to digest low quality food (Belovsky, 1997; Prins and Olff, 1998). For these animals, the benefits of consuming low quality food are higher than for smaller sized animals. In a complex sward with a mix of low and high quality parts, heavy animals might thus tolerate a certain percentage of low quality food in each prey item (say 10% of each bite contains low quality parts). Smaller animals that are able to select and take time to search and crop high quality parts might also tolerate one bite of low quality food next to numerous bites of high quality parts (say 1 out of 10 bites contains low quality parts). The problem arises, however, when this animal has to take many bites of low quality followed by many more bites of high quality (say 1,000 out of 10,000 bites contain low quality parts). In the first two situations, our model predicts an increase in predator body mass given that the predator growth rate based on the consumed food is greater than the predator loss rate. In the latter situation, the predator drastically decreases in body mass that may ultimately lead to the death of the predator. The effect of the sequence of bites of low and high quality prey is an intriguing subject for further investigation.

Functional response as function of food quality in predator-prey model

Based on the functional response with variable maximum consumption rate, we developed a predator-prey model and studied its dynamics under the effects of changes in the proportion of high quality prey. Few other model studies consider the effect of prey quality on the predator-prey dynamics, *i.e.*, herbivore-vegetation dynamics (Van de Koppel et al., 1996; Bos, 2002). As is found in this paper, these studies also found two stable states, where in one state, the herbivores maintain a low standing crop, the other state being dominated by a dense vegetation unsuitable for herbivore grazing. As is mentioned above, our model for the functional response contains a mechanism that explains the decrease in consumption rate with decreasing proportion of high quality parts with increasing prey density. This enables us to make predictions about the effect of body mass of the predator since the maximum consumption rate shows a relationship with body mass: higher body mass corresponds to higher maximum consumption rate (Gross et al., 1993; Prins and Olff, 1998). Animals with higher body mass have higher tolerance for low quality food. Their maximum consumption rate would not decrease as fast with decreasing prey quality than for smaller animals. This means that their consumption rate would remain relatively high in low quality swards (*i.e.*, with high biomass). This agrees with general observations that large herbivores can be found grazing in swards of high biomass with a relatively low proportion of high quality parts.

Our study illustrates the effects of the quality of the offered prey population on the consumption rate of the predator and its numerical response, and on the subsequent predatorprey relationship. The effects critically hinge on the positive feedback between the predator density and the proportion of high quality prey on offer. The results suggest that small changes in the density of high or low quality prey may trigger this positive feedback, since both result in changes in the proportion of high quality prey, and thus in changes in the consumption rate. At a low density of high quality prey, an increase in the density of either low or high quality prey leads to an increase in the consumption rate, but a further increase in low quality prey density results in a decrease of the consumption rate (Figure 5.3b). This decrease in the consumption rate consequently decreases the predator population, which is not able to keep a high proportion of high quality parts in the prey on offer. On the other hand, a decrease in low quality prey and thus an increase in the consumption rate may lead to a relatively high predator population. This high predator population reduces the growth of low quality prey parts by consuming high quality prey so that the proportion of high quality prey remains high. A high tolerance of the predator for low quality prey could keep a high proportion of high quality parts in the prey on offer.

Applicability of our findings to other trophic interactions

We present a model for the functional response of a predator that explicitly depends on the quality of the offered prey. Experiments (Drescher et al., Chapters 2 and 3) show that decreasing food quality depresses, among others, the maximum consumption rate. This gives us an explanation for the decrease of the consumption rate of predators with decreasing food quality, which is not necessarily linked to prey density. There are several examples of predator-prey relationships where the prey population consists of at least two prey types differing in their quality for the predator. In all these examples, we advocate the relevance of our functional response since the predator (or pathogen as a type of predator) is not able to receive a feedback for diet choice while foraging. For example, Reason et al. (1998) reported on the variation in susceptibility to a pathogen by larvae of the African armyworm. This system has been theoretically investigated as a host-pathogen system with the host population consisting of a susceptible and a resistant type, thus varying in quality as a resource to the pathogen (White and Wilson, 1999). It was found that the existence of a resistant host type could stabilise an unstable host-pathogen interaction. Engelmayer (1992) and Czesny et al. (2001) studied the behaviour of piscoid predators and found them foraging less effectively when the proportion of a low quality prey type increased on the cost of the proportion of a high quality prey type. Sarma et al. (1997) found that increasing the proportion of high quality prey in a prey population of low and high quality prey led to an increased numerical response of a rotifoid predator. Dicke et al. (1990) and Micky and Denno (2000) investigated predator-prey relationships in aracoid predators and found that the numerical response of the predators depended on the type of prey, though prey preference was often related to other characteristics. We conclude that our approach of the functional response that depends on the proportion of high quality prey parts is necessary to study dynamics and discontinuous

changes in many predator-prey relationships, from infectious diseases over carnivorous predators to herbivores.

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Р	prey density [g m ⁻²]
L	density of low quality prey [g m ⁻²]
Н	density of high quality prey [g m ⁻²]
Ν	predator density [g m ⁻²]
c_m	maximum per capita consumption rate [g $g^{-1} d^{-1}$]
k_1	half saturation constant [g m ⁻²]
е	consumption-to-growth conversion coefficient [g g ⁻¹]
d	specific loss rate of the predator [d ⁻¹]
c_{Hm}	maximum consumption rate when the prey consists of only high quality parts, <i>i.e.</i> ,
	$p_H = 1 \text{ [g g}^{-1} \text{ d}^{-1}\text{]}$
c_{Lm}	maximum consumption rate when the proportion of high quality prey is zero, <i>i.e.</i> ,
	$p_H = 0 [-]$
k_2	half saturation constant [-]
p_H	proportion of high quality parts in the prey on offer [-]
m_L	specific loss rate of the low quality prey $[d^{-1}]$
<i>r_{Lm}</i>	maximum specific growth rate of low quality prey [g m ⁻² d ⁻¹]
<i>k</i> ₃	half saturation constant [g m ⁻²]
r_H	specific growth rate of the high quality prey $[g m^{-2} d^{-1}]$
m_H	specific loss rate of the high quality prey $[d^{-1}]$
e_H	coefficient for the consumption-to-growth conversion for the high quality prey [g
	g ⁻¹]
e_L	coefficient for the consumption-to-growth conversion for the low quality prey [g
	g ⁻¹]
β	coefficient that represents the diet choice [-]

Appendix 5.1. List of the used parameters and variables, their interpretation and units.

Appendix 5.2. The consumption-to-growth conversion coefficient for several herbivorous predators (Prins, 1989).

Grasshoppers	0.166
Grazing termites	0.140
Other termites	0.090
Domestic cattle	0.026
Voles and mice	0.024
Impala	0.022
White-tailed deer	0.012
Uganda kob	0.011
African elephant	0.005

Chapter 6

Synthesis:

Towards an understanding of the interactions of a forager with a complex, seasonal forage resource In this chapter I develop a general concept of the dynamic interactions of a forager with a complex forage resource. These dynamic interactions comprise the responses in foraging behaviour to multi-scale spatial and temporal variation in the quality and structure of a forage resource, as well as the feed-back of the impact of foraging on the forage resource.

To do so, first, I review the results of the previous chapters and provide additional findings in support of that general concept of forager-resource interaction. I link the results of the separate chapters in order to sketch a comprehensive picture of the processes involved on the scales that I studied. Then, drawing on additional information gathered in the course of the study and from other sources, I extend the concept beyond the scope of the results presented so far, into higher order temporal and spatial scales and processes.

Forage accessibility and functional response

In the previous chapters I reported on the effects of resource structure on forage intake and diet choice from the level of the bite, over the feeding station and patch up to the camp level. On the smallest scale I investigated the effects of changes in the density and proportion of high quality forage (leaves) on the shape of the functional response (Chapter 2). I found that decreasing the proportion of high quality forage parts decreased the asymptotic maximum rate of forage intake and changed the shape of the functional response curve from a linear Holling's type I (at 100 % leaf) to an asymptotic type II (at 50 % leaf). A further decrease in the proportion of high quality forage (to 25 % leaf) depressed the maximum rate of forage intake even more and the relationship between forage intake and total forage availability ceased to exist. It appeared that increasing forage availability for a low proportion of high quality forage in fact decreased forage intake, though this effect could not be proven statistically (Figure 2.3).

In the same chapter (Chapter 2), I demonstrated the effects of the local aggregation of high quality forage in a matrix of low quality forage (stems) on forage intake. I showed that an increasing aggregation of high quality forage led to an increase in the rate of forage intake, even when the overall proportion of high quality forage was low (25 % leaf, Figure 2.5). Thus, local aggregation of high quality forage, to a certain extent, was counteracting the negative effect of the decreasing proportion of high quality forage. However, this effect was limited to small aggregations and I found indications that this effect might be linked to the size of the foraging apparatus of the forager: When the aggregations were smaller than the maximum cropping area of the forager, then increasing the size of the aggregations led to an increase in forage intake. However, when the aggregations were larger than the maximum

cropping area, the effect was lost. I suspected that my foragers not only selected actively against low quality forage, but that they experienced a physical hindrance due to the low quality forage. Consequently, I questioned what actual mechanism was responsible for the observed changes in forage intake.

Bite formation and functional response

In Chapter 3 I presented a hierarchical concept of the foraging process on feeding station level (Figure 3.1). The purpose of this concept was to clarify the interactions between the elements of the foraging process. I intended to use the concept as a guide in identifying the elements of the foraging process which were affected most by changes in forage resource structure. Also I wanted to identify the elements which because of their magnitude had the largest effect on other elements of the foraging process. These elements of the foraging process would then be the major sources of variation in the rate of forage intake for foraging in complex swards at feeding station level. I found that the number of tillers cropped per bite was the single most important element in controlling the rate of forage intake. Video observations of the foraging experiments delivered strong evidence that the interference of low quality forage parts (stems) with the bite formation process (cropping of tillers) caused a decrease in the number of tillers cropped per bite and therefore in forage intake rate with increasing density of low quality forage.

Also, I found strong indications that in fact it was not the proportion of high or low quality forage which affected the rate of forage intake, as I previously thought. Instead, the interacting densities of high and low quality forage affected the rate of forage intake. In the course of this study I developed simple models of forage intake rate. These models showed that even if the proportion of high quality forage parts remained at a constant, intermediate level, e.g., at 50 % leaf, increasing forage abundance could lead to a decrease in forage intake due to increased 'crowding' of low quality forage parts, which were interfering with the bite formation process. This mechanism could generate a range of shapes of functional response curves, including a dome-shaped type IV response curve (Figure 3.6), and could give a mechanical explanation for the decreasing rate of forage intake with increasing forage abundance in natural forage resources as suggested in other studies (e.g., Fryxell, 1991; Van de Koppel *et al.*, 1996; Van der Wal, 1998; Bos, 2002). The described mechanism is different from previously suggested mechanisms which usually are based on the competition between forage acquisition and forage processing (e.g., Spalinger and Hobbs, 1992; Laca *et al.*, 1994; Parsons *et al.*, 1994; Farnsworth and Illius, 1996). In fact, the evidence of a dome-shaped

functional response curve as shown by the forage intake model in this Chapter 3, supported the supposed, though statistically unproven, negative effect of increasing forage availability on forage intake from complex forage resources, as indicated by the experimental data which formed the basis of the previous Chapter 2.

Diet choice at feeding station level

At this point it is important to note that the observed effects of density and proportion of high and low quality forage on forage intake, are contingent on the selectivity of the forager. In my studies, foragers were selecting strongly against low quality forage. To investigate what the foragers gained by foraging so selectively, I compared their actual diet to a hypothetical diet, truly representative of the composition of the forage on offer. This hypothetical diet is the diet the foragers would have achieved if they would have foraged indiscriminately. I found, that selective foraging increased the metabolizable energy content of the ingested diet by 11 - 13% and the protein content by between 36 - 48 %, compared to an indiscriminate diet. However, selective foraging depressed the rates of intake of energy by between 230 - 530 % and of protein by 130 - 270 %. Even if we assumed that ingesting low quality forage (stems) will slow down the rate of intake by a maximum of 30 %, as can be derived from the work of Bergman et al. (2000) for wood bison, selective foraging would still depress the rates of intake of energy by 130 - 340 % and of protein by 70 - 160 %, relative to an indiscriminate diet. Selective foraging, if maintained throughout the course of a day, often would not even have provided the foragers with enough energy to fulfil their daily maintenance requirements, varying from 36 – 43 MJ (Commonwealth Agricultural Bureaux, 1980). Even if we assumed that the foragers would forage a maximum time of 650 minutes (Chacon, 1976), daily energy intake often would have been too low (40 MJ) at intermediate proportion of high quality forage (50 % leaf) and always too low (28 MJ) at low proportions of high quality forage (25 % leaf). Indiscriminate foraging, on the other hand, always would have provided high enough energy intake rates to meet daily requirements. So why did these foragers choose a diet, which was of high quality, but not sufficient to provide them with a high enough short-term nutrient intake rate to meet their daily requirements? Strong selection for leaf material cannot be explained by the shorter retention times of leaves in the rumen, as leafy material is retained only 30 % shorter in the rumen than is stem material (Poppi et al., 1981). Neither did the foragers always select strongly against low quality forage. This was illustrated by the incidental 'stealing' of left-over stem material by foragers when they were not involved in the current experimental session (personal observation). Studies on the fracture properties of grasses showed that the energy required to tear and grind stems is often several times higher than for leaves (Wales et al., 1990; Wright and Illius, 1995; Wilson and Kennedy, 1996). Taking the data given by Wales et al. (1990) for the grinding energy of leaves and stems of wheat $(70 - 90 \text{ J g}^{-1} \text{ and } 200 - 230 \text{ J g}^{-1}$, respectively) as an indication, I calculated the grinding energy expenditure for the different diets (selective, indiscriminate, indiscriminate with 30 % intake depression), which comprises the largest part of energy expenditure during active foraging (Illius et al., 1995). I found that indiscriminate foraging and indiscriminate foraging with intake depression would have required energy expenditure rates of 100 - 130 % and 40 - 60 % higher, compared to the selective diet. However, as the absolute energy expenditure rates were small compared with the rates of energy intake, the net energy gain rates were still very similar to the gross intake rates of metabolizable energy as reported above. Thus, energy intake and expenditure differences between the diets do not offer a satisfying explanation for the diet choice of the foragers. Illius et al. (1995, 1999) noted that goats selected a diet that maximised their intake rate and that bite mass in goats is negatively related to the number of grass tillers in a sward as these increase the force required to crop bites. Shipley et al. (1999) suggested that large bites including fibrous material may offer a high energy return per bite, however such bites may just be too tough, making it physically impossible to harvest them and therefore they might be selected against. In line with this, I suggest, that the diet chosen in my study might just be related to limiting physical parameters, like the force required to crop stems and the ease of grasping them, and not to forage quality *per se.* In support of this point is the fact that the diet choice of my foragers did not change towards including low quality forage after the high quality forage parts (leaves) were depleted. This it should have, if diet choice was based on selection for quality and contingent on the composition of the forage currently available (Fryxell and Lundberg, 1994; Farnsworth and Illius, 1998).

Therefore I suggest that diet selection in this study probably was not directed by quality criteria, but by energy expenditure and effort criteria, though these undoubtedly were correlated in the experimental situation. This strategy only makes sense, if forage intake by the experimental foragers, in the course of the day outside of the experimental setting, was not constrained by forage availability, but by forage quality or by the foragers' digestive capacity. Thus, a link presents itself here, connecting the foragers' intake and diet choice at the level of the feeding station with the condition and structure of the forage resource at the next higher spatial and temporal scales, the levels of the patch and of the camp.



Figure 6.1. Forage intake rate in free-ranging herbivores foraging in a natural, semi-arid grassland in relation to grass mass.

Forage intake at patch level

In Chapter 4 I presented the results of the investigation of the foraging behaviour of freeranging herbivores in relation to forage resource availability, quality and structure on patch level in a natural grassland. Previous studies had shown that the proportion of high quality forage parts and plant nutritional quality were negatively correlated with increasing forage availability in natural forage resources (Hamilton *et al.*, 1973; Stobbs, 1973; Prins and Olff, 1998; Hassall *et al.*, 2001). It has been suggested that due to digestive constraints or due to decreasing foraging efficiency, decreasing forage resource quality at high levels of forage availability causes forage intake rates to decrease in many foragers, thus causing a domeshaped functional response curve (Fryxell, 1991; Van der Wal, 1998; Bos, 2002).

Also in my experimental site I found a decrease in the proportion of high quality forage parts (leaves) and in plant tissue nitrogen content with increasing forage availability (Figure 5.1). Thus, I also expected to find a dome-shaped functional response curve in my intake data at patch level. But instead I found that a linear type I functional response curve gave the best fit to the data, explaining 69 % of the variation in forage intake (Figure 6.1). This compares favourable to an asymptotic type II model, which explained 53 % of the variation in forage intake, and to a domed-shaped type IV model, which in fact reduced to the linear type as its quadratic term approached zero. Above that, there were no statistically detectable effects of forage resource quality or structure at all on forage intake. So the question arises: What counteracted the negative effects of decreasing resource quality on forage intake? I focus my

argument on the aspect of heterogeneous spatial arrangement of high and low quality forage parts within the forage resource up to patch level. Large mammalian herbivores cannot select for high quality forage parts within individual plant organs, because of the shear size of the foraging apparatus. To large herbivores, their 'grain' (sensu Kotliar and Wiens, 1990), which is the smallest unit on which they base their response to the forage resource, is an individual plant organ. The scale at which they choose between individual plant organs, e.g., between high quality leaves and low quality stems, is the single plant (Ruyle et al., 1987; Orians and Jones, 2001). At the next higher scale, the level of the feeding station, herbivores can choose for potential bites from within or between individual plants, which might be differing in the composition, density and quality of plant organs. At patch level, herbivores choose between feeding stations, differing in the availability of profitable bites within the feeding station and in the degree of accessibility of neighbouring feeding stations. Finally, at the highest scale addressed in this section, herbivores can choose between patches, differing in the availability of profitable feeding stations within the patches. Previous studies on the negative effects of decreasing availability of high quality forage parts and decreasing plant tissue quality with increasing forage availability, were based on the assumption that the forage resource was a homogeneous structure at least up to patch or camp level (Fryxell, 1991; Bos, 2002). However, while this might be true for intensively managed production grasslands, there can be considerable local spatial variation in the distribution and density of high and low quality forage parts below these levels in natural or extensively managed grasslands.



Figure 6.2. Sward roughness, *i.e.*, the divergence of sward height transects from a straight line, in relation to the average patch sward height in a natural, semi-raid grassland of South Africa.

Evidence of the significance of this variation is the positive effect of leaf aggregation on the rate forage intake as presented in Chapter 2 of this thesis, and the positive effects of variation in forage availability on forage intake as shown in some other studies (Allden and Whittaker, 1970; Ungar and Noy-Meir, 1988). Also in the present study, there was pronounced variation in the distribution of high and low quality forage parts below patch level. Leaves are not distributed uniformly throughout a grass plant. Instead, owing to the need to receive light for photosynthetic activity, green leaves are mainly present on the sides or on top of individual grass plants (Stobbs, 1973), depending on the vegetation density and the resulting competition for light. Thus, while a whole grass plant on average might be rather low in green leaf density and nitrogen content, it might still be possible to crop large bites of high quality from the sides or top of the plant. Besides of this variation at plant level, there was also considerable variation at patch level. I found that there was variation in local plant height indicating variation in forage availability and accessibility within patches. I determined sward roughness, which is defined here as the divergence of the upper sward surface from a level plain, and which I derived from the fractal dimension of sward height transects (1.00 =straight line, 2.00 = full plane), *i.e.*, the divergence of sward height transects from a straight line (Farina, 1998). Sward roughness is a measure of the variation in sward height. But different from the non-spatial term 'variation in sward height', it also accounts for the spatial distribution of this variation, and its numerical value is increasing with increasing distribution of the variation. I found that sward roughness initially increased with forage availability, here represented by average patch sward height. However, it turned out that sward roughness did not increase linearly with average patch height, but approached a maximum roughness of about 1.4 (Figure 6.2). Visual inspection of the sward height transects revealed a possible explanation for the sigmoid shape of the curve. In patches of low average sward height the variation in sward height was distributed rather uniformly through space. However, with increasing average sward height the auto-correlation in height of neighboring transect points increased and patches, which appeared rather homogeneous at first sight, turned out to be fragmented into low and tall parts (Figure 6.3). These parts of locally low sward height turned out to be starting points of foraging bouts of the herbivores in tall patches. Short parts within the tall patches were utilized, first, directly by foraging on the vegetation within the short parts, and, second, as areas from where to attack green leaves growing low on the sides of tall grass plants in neighboring parts of the patches. The importance of low growing vegetation for forage intake in fragmented swards is indicated by the amount of bites taken in lower horizons of the vegetation.



Figure 6.3. Sward height transects in three patches of differing average sward height (h = 11 cm, 20 cm, 38 cm). Bars at top indicate parts of the height transect in the tallest patch with locally low and high roughness (r).

In Chapter 4 we showed that even in tall patches (frequently >180 cm) the majority of bites (70 - 100 %) were taken from below 50 cm high, and that the proportion of bites taken from below 50 cm explained 81 % of the variation in forage intake.

On basis of the argument I presented in this section I want to answer the question I voiced previously: What was counteracting the negative effects of decreasing resource quality on forage intake? I suggest that it was the spatial variation in the arrangement of high quality forage parts at the plant and patch level, which created locally improved opportunities for forage intake, thus maintaining high rates of forage intake even in patches of high forage availability but low average resource quality.

Diet quality at patch level

In Chapter 4 of this thesis, I presented the results on the relationship of diet quality with forage quality. I showed that diet quality was consistently higher than forage quality, but otherwise not related (Figure 6.4). Stobbs (1973) found that diet quality in cattle was high compared to the average quality of forage. He found a negative correlation between diet quality and forage availability, which he attributed to a decrease in forage quality with increasing availability and a lack of selective ability in the cattle. Hamilton *et al.* (1973) on the other hand, found a positive relationship between diet quality and forage availability in sheep, which they attributed to increased selection opportunity for high quality forage parts with increasing forage availability.



Figure 6.4. The digestible matter content of simulated bites in relation to the digestible matter content of patches of grass. Equality of the digestible matter content of bites and grass is indicated by a solid line. There was no significant correlation of bite digestibility with grass digestibility (P = 0.445), but bite digestibility was consistently larger than grass digestibility (P < 0.001), as indicated by the data points lying on the left from the line of equality.

The apparently contradictory results can be explained by the differences in body size and forage intake requirements between cattle and sheep. Neither Stobbs (1973) nor Hamilton *et al.* (1973) gave the body masses of their experimental animals. However, the sheep were 4 months-old Marinos, so they probably weighed some 20 kg (Agricultural Research Council, 1980). Further I assume that the cattle must have been at least ten times heavier than the sheep. Accordingly, forage intake in the cattle must have been at least 3.5 kg daily, while that of the sheep must have been some 0.3 kg (Agricultural Research Council, 1980). As the foraging apparatus and the forage intake requirements of cattle were much larger than that of the sheep, the cattle could not forage as selectively and diet quality in cattle was more alike to average forage quality than in sheep. Thus, increasing forage availability might open opportunities for selection in sheep, but might limit diet quality in cattle. But why then did diet quality not decline with increasing forage availability in the current study? The main difference between the current study and the study by Stobbs (1973) is that in spatial variation. In the study by Stobbs (1973) herbivores apparently were foraging on a uniform production grassland, without much spatial structure. Yet in the current study, herbivores

were foraging in a natural grassland, with much spatial variation in the availability and quality of forage (Figure 6.3). Thus, I suggest that locally improved foraging opportunities, created by the spatial variation in the distribution, density and accessibility of high quality forage parts, are the reason for the independence of diet quality from the average quality of the forage resource in the current study.

Interactions between foragers and a complex non-spatial forage resource

In the Chapters 2 through to 4 of this thesis I presented the results on the effects of the quality and structure of the forage resource on forage intake and diet quality. Throughout these studies I ignored that the foraging process changes the structure of the forage resource and that this might feed-back on the forager and its behaviour. In the experiments at the level of the feeding station (Chapters 2 and 3), I deliberately ignored the depletion of the resource which might lead to intake depression (Laca et al., 1994; Ginnet et al., 1999). I calculated forage intake rates averaged over the period of the grazing session, instead of the instantaneous rate of intake. This was justified because I could not detect any systematic differences between forage intake in the beginning of the grazing session (the first 6 bites) and the remainder of the grazing session (the remaining bites). Also at patch level, I deliberately ignored that foraging in fact means the removing of a part of the forage resource and therefore, by its very nature, causes the structure of the forage resource to change. In this case, this was justified because at any feeding station foragers took few bites (on average seven bites), and Laca et al. (1992) considered six to be so few that bites do not overlap and therefore the forager does not suffer from intake depression. Further, because the amount of forage removed during each period of observation was very small compared to the totally available forage in any patch, the effects of forage intake on resource structure were to small to be detected. However, changes in forage resource structure might be detected if the foraging activity is spatially or temporally concentrated on a resource patch, or if the period of observation is long enough to register the repeated utilisation of a resource patch. In this case it might be worthwhile not only to investigate the effects of forage resource structure on foraging behaviour, but also the effects of foraging behaviour on resource structure.

Such an approach was chosen in Chapter 5 of this thesis, where I presented the results of a model study on predator-prey interaction, with focus on a herbivore-vegetation system. Though I suggest that the results of this study are also relevant to many other types of predator-prey interaction. The predator-prey-system consists of three parts: A predator population, a high quality prey population and a low quality prey population. Growth of the high quality prey population depends on its own density, while growth of the low quality prey does not depend on its own density, but instead on the density of the high quality prey (see Equations (8) and (9) in Chapter 5). The link between the forager and the vegetation , of course, is the functional response. We modelled the functional response curve as a variable function, depending on the proportion of high quality forage in a resource consisting of high and low quality forage. Herewith, we were offering a mechanistic link between changes of forage intake and increasing forage availability, instead of a priori assuming a negative effect high forage availability on forage intake (Fryxell, 1991; Van de Koppel et al., 1996; Bos, 2002). In the model, forage intake can be with different degrees of selectivity and is changing the composition and structure of the forage resource. This again is changing the shape of the functional response curve and therefore is feeding-back on the forager. We found that the herbivore-vegetation system can have multiple stable states, depending on the initial density of foragers and on the profitability of the low quality forage. Essentially it showed that if the initial forager density is to low, the vegetation accumulates low quality forage, which depresses forage intake and drives foragers into extinction. However, if the profitability of the low quality forage is sufficient, e.g., if the digestive capacity of the forager is high enough, foragers can survive a much higher accumulation of low quality forage. On the other hand, if the density of foragers is initially high, they can maintain the forage resource in a state of lower forage availability but higher proportion of high quality forage. This affects forage intake per capita positively enabling foragers to survive. These multiple stable states are very much comparable to observations in natural foraging systems (Van de Koppel et al., 1996; Bos, 2002). Opposite to this, a predator-prey system with a constant functional response, *i.e.*, when the functional response does not depend on the proportion of high quality forage, cannot grasp this complex feed-back mechanism between the forage resource and the forager population.

Seasonal effects on dynamic interactions between foragers and a complex spatial forage resource

Drawing on the information presented so far, now I want to develop a concept of the dynamic interactions between foragers and a forage resource, which is spatially and temporally variable in availability and in the proportion of high quality forage.

The concept relies heavily on the predator-prey-model presented in Chapter 5. The predator-prey-system consists of the three parts mentioned earlier: a predator population, a high and a low quality prey population. Growth of both the high and the low quality prey

population depend on the density of the high quality prey (see Equations (8) and (9) in Chapter 5). In other words, the growth of the low quality forage depends on the high quality forage, but not the other way round. Besides of this asymmetric relationship, the exact shape of the growth curves of the high and low quality forage (asymptotic or sigmoid, slope etc.) are not a of major importance for the behaviour of this conceptual model. However, if the concept was to be worked out in detail, this point would deserve more attention. Forage intake is derived from a variable functional response, which depends on the proportion of high quality prey as shown in Chapters 2 and 3 (Figures 2.3 and 3.6). Apart from these main aspects, here we are taking the arguments further by making a number of assumptions about the forager and the forage resource. In that way we are increasing the similarity of the conceptual model to a seasonal grazer-grassland-system:

(i) The concept is extended with the effects of spatial variation in the distribution of forage parts (aggregation of high quality forage). As has been demonstrated in Chapter 2 and as was elaborated about previously in this current Chapter 6 (within-plant distribution of photosynthetically active material and sward roughness), I assume that increasing spatial variation in forage mass increases the accessibility of high quality forage parts (leaves). This has a positive effect on forage intake if foraging is selectively for high quality forage parts. A number of earlier studies support the notion of the positive effect of spatial variation in forage mass on forage intake (Allden and Whittaker 1970; Ungar and Noy-Meir, 1988).

(ii) The maximum specific growth rate of the high (leaves) and of the low (stems) forage parts is seasonally variable, depending on soil moisture content which is driven by rainfall (e.g., Whiteman, 1980). Here, I simplistically assume, that growth of the high and low quality forage is high in the early wet season and is zero in the dry season (Prins, 1988). In the course of the dry season all forage turns into moribund low quality forage.

(iii) Generally, foraging is selective for high quality (Hamilton, *et al.*, 1973; Stobbs, 1973, Prins, 1996; Heitkönig and Owen-Smith, 1998; Chapters 2 and 4). However, high quality always is high relatively to the range of qualities on offer and therefore the quality of the selected diet is variable (Fryxell and Lundberg, 1994; Farnsworth and Illius, 1998). Further, I assume that the degree of selectivity depends on the overall availability of forage: When availability is high, foragers are limited by digestive constrains rather than by ingestion and are foraging with high selectivity to increase diet quality and nutrient intake (Stobbs, 1973). When availability is low, foragers are limited by ingestive constrains rather than by digestion and are foraging with low selectivity to maintain nutrient intake as high as possible (Hamilton *et al.*, 1973).



Figure 6.5. The growth of high and low quality forage during the early and late wet season in an ungrazed patch and in a patch grazed once in the early wet season. Growth of high quality forage is a function of high quality forage, while growth of low quality forage is a function of high quality and of low quality forage (see Equations (8) and (9) in Chapter 5). Forage intake in the early wet season is with low selectivity (arrows) and limits the growth of the low quality forage stronger than the growth of the high quality forage.

(iv) In the current concept foragers are non-migratory, discrete individuals whose foraging impact on the resource is spatially defined, *i.e.*, which are locally removing parts of the forage resource.

(v) Further, foragers have a non-perfect knowledge of the availability and quality of the forage resource and follow an intake satisficing strategy on daily time-scale (Greenwood and Demment, 1988; Chapter 4).

In a thought experiment, I want to investigate the properties of this conceptual foragervegetation-model through the seasons. I start with the early wet season, proceed to the late wet season, then the early dry season and will finally end with the late dry season. I assume that the overall forager density in the beginning of the early wet season, is limited by the low availability and quality of forage at the end of the dry season.

In the early wet season, growth of forage starts from residual or storage material which survived the previous dry season. In the beginning, the availability of forage is low, but it is increasing quickly because of the high growth rate of the high quality forage. The proportion of high quality forage is increasing quickly, too, because the growth rate of high quality forage, which only depends on its own density, is initially higher than that of the low quality forage, which is growing delayed because of its dependency on the high quality forage



Figure 6.6. The growth of forage of high and low quality during the early and late wet season as in Figure 6.5. Shown is an ungrazed patch and a patch re-grazed with low selectivity during the early wet and late wet season. Grazing limits the growth of the low quality forage stronger than the growth of the high quality forage This results into localities with lower forage availability but higher proportion of high quality forage, compared to patches grazed once or ungrazed.

(Figure 6.5, as explained in the beginning of this section). Thus, as the proportion of high quality forage is high, forage intake is increasing linearly with forage mass (Figure 2.3). In this situation, forage intake is with low selectivity (assumption iii), and therefore forage intake does not change the proportion of high quality forage. Because the proportion of high quality forage is high, also most ingested forage is of high quality. The intake of forage logically decreases the local availability of forage. However, it limits the growth of the low quality forage stronger than the growth of high quality forage (Figure 6.5). Therefore, after foraging, the proportion of high quality forage quickly regains relatively high values. Because the overall density of foragers has been reduced by previous (end of dry season) low quality and low availability, the density of foragers is now to low to check the overall forage production. Because foragers have non-perfect knowledge of the availability and quality of the forage resource and are following a satisficing strategy (assumption v), they are less likely to intensely explore the total forage resource in search of opportunities for maximum forage intake. Instead, they are more likely to re-graze the same location, which they know has been providing them with foraging opportunities previously (Wallis de Vries, 1994). In that way, they are maintaining localities with lower forage availability but higher proportion of high quality forage (Figure 6.6).





Figure 6.7. (This and opposite page) A diagram of the main processes of a conceptual model describing the dynamic interactions between foragers and a complex forage resource from the early wet season to the late dry season. Arrows indicate the direction of effects, '+', '0' and '-' are a positive, absent or negative effect. a) Foraging in the early wet season is not selective, because low proportions of low quality forage are tolerated in the diet. Accordingly, foraging does not change the proportion of high quality forage and both high and low quality forage contribute to forage intake. Regrazing of localities creates spatial variation in forage mass. b) In the late wet season, foraging in regrazed localities is like in the early wet season, but in ungrazed patches, with high availability but low proportion of high quality forage, grazing is selectively thus further decreasing the proportion of high quality forage. Re-grazed patches get depleted by increasing foraging aggregation and easily accessible patch edges get utilised. c) In the early dry season, growth of forage ceases. Re-grazed plots become depleted and previously ungrazed localities, with high availability but low proportion of high quality forage, get increasingly utilised. Selective foraging and decay of forage material cause the proportion of high quality forage to decrease. d) In the late dry season, utilisation of previously ungrzed localities causes overall forage availability and proportion of high quality forage to decline. Increasingly low quality forage gets included in the diet, causing digestive limitation of forage intake.

Opposite to this, continuous growth in localities with little grazing results in an increase in forage availability and a decrease in the proportion of high quality forage. Therefore, because of the inability to check the overall forage production and because of localised foraging, foragers create spatial variation in forage availability and in the proportion of high quality forage. A conceptual sketch of the main processes is presented in Figure 6.7a.

In the late wet season, the contrasts in forage availability and in the proportion of high quality forage between localities are increasing. In localities which were less frequently grazed, forage availability is high, but the proportion of high quality forage is low. In these localities, high local forage availability leads to highly selective foraging. However the low proportion of high quality forage leads to decreased forage intake, which nevertheless might reduce the proportion of high quality forage even more. When the utilisation of forage intake in such localities decreases so far that the average daily nutrient intake drops below the satisficing level, grazing of these localities becomes increasingly unlikely. Instead, re-grazing

of localities of lower forage availability but higher proportion of high quality forage, increases in frequency, thus leading to a spatial or temporal aggregation of foragers in these localities which may create so-called grazing lawns (Vesey-FitzGerald, 1969; McNaughton, 1984). However, the increasing grazing pressure in these localities, though it is maintaining the high proportion of high quality forage, also depresses local forage availability (Figure 6.8). When the increasing grazing pressure in these localities depresses the forage intake so far that the average daily forage intake drops below the satisficing level, the utilisation of forage at the edges of these localities becomes more likely. Here, forage availability and the proportion of high quality forage still are relatively high (assumption i), enabling higher forage intake than in either frequently or seldomly re-grazed localities. Further more, foraging on these edges increases the area of frequently re-grazed localities, thereby relieving grazing pressure per unit area and increasing per capita intake there. A conceptual sketch of the main factors is presented in Figure 6.7b.

In the early dry season, growth of high and of low quality forage ceases (assumption ii). Frequently re-grazed localities quickly become depleted and less often utilised. Instead, previously seldom re-grazed localities are utilised with increasing frequency, thus leading to an decreasing aggregation of foragers in previously re-grazed localities. In the former localities, forage availability initially is high, but the proportion of high quality forage is relatively low and ever decreasing since high quality forage parts turn moribund (assumption ii). Forage intake is selectively for high quality forage (assumption iii), causing a depletion of high quality forage parts. As the availability of high quality forage is decreasing because of decay and depletion, increasingly lower forage qualities become acceptable to the foragers (assumption iii). See Figure 6.7c for a conceptual sketch of the main processes.

In the late dry season, continuous foraging even in previously ungrazed localities decreases the availability of forage and the proportion of high quality forage to low levels over the total forage resource. To maintain a nutrient intake as high as possible, foraging is with low selectivity, *i.e.*, diet quality is low. However, as low quality forage decreases the passage rate of forage through the digestive system forage intake is relatively low (Poppi *et al.*, 1981), thus further limiting the rate of nutrient intake. This is the critical period of scarcity for forager survival. The availability and quality of forage and during this period is limiting the density of foragers in the area. In Figure 6.7d the main factors are presented.


Figure 6.8. The growth of forage of high quality and of low quality during the late wet and early dry season. Frequent re-grazing in the late wet season with low selectivity, maintains a relatively high proportion of high quality forage, but depresses forage availability, compared to seldom grazed or ungrazed localities. In the dry season, growth of high and of low quality forage ceases and utilised patches quickly become depleted.

Coping with temporal variability in forage availability

In the previous sections I presented the results of a thought experiment investigating the dynamics of a conceptual forager-vegetation-model through the course of the seasons (early wet to late dry season). A defining characteristic of the model is the temporal variability in forage availability and forage quality. As formulated in the assumptions to this model, the forager population is responding to this temporal variation with a low population density determined by the forage availability and forage quality during the dry season, which is well below the temporal 'carrying capacity' during the wet season. Instead of seeing this population response as a passive process, in which the forager population is suffering in number because of resource limitation, one might also see it as a result of adaptation to variable resource availability. However, I am very well aware of the fact that in this conceptual model I used just one hypothetical type of forager, whose behavioural characteristics I based on my experimental data and a number of assumptions. Certainly, other types of foragers might follow other strategies in order to cope with temporal resource limitation, in an attempt to avoid an excessive decrease in condition and a reduction in fitness. Possible strategies might include the following:

(i) Small-sized resident foragers might hoard durable forage items, e.g., seeds, during the period of high forage abundance, following a maximising strategy instead of a satisficing strategy with regards to forage collection (e.g., Jansen, 2003). The hoarded forage reserves may then be utilised during a period of rest or scarcity. Hoarding can be found in different types of foragers like birds (shrikes), rodents or marsupials.

(ii) Resident foragers might be able to switch their diet. By including a previously inferior forage type or a forage type, which is only available when the primary forage resource is unavailable, foragers might bridge the period of scarcity of the primary forage resource (Mnene *et al.*, 1997; Papachristou *et al.*, 1999).

(iii) Also large-sized resident foragers might follow a nutrient intake maximising strategy instead of a satisficing strategy. The surplus of acquired nutrients during the period of abundant high quality, might then be stored as large body reserves (e.g., fat) and might be utilised in periods of scarcity (Wallis de Vries, 1996). This type of hoarding of reserves within the body opposite to outside the body in depots, makes sense for large foragers which might be unable to safely hide the necessarily larger absolute quantities of food, compared to small-sized foragers.

(iv) Foragers might be able to escape local resource limitation by regional migration to areas of temporary increased foraging opportunities (Voeten, 1999; Wilmshurst *et al.*, 1999a). This strategy occurs in a wide variety of types of foragers from insects (locusts), over birds, sea mammals and large terrestrial herbivores.

Temporal variability in forage availability as a promoter of species co-existence

The competitive exclusion principle states that two forager species with very similar requirements cannot co-exist if they are foraging on the same resource. Often the requirements of a diversity of sympatric large herbivore species are not obviously different, as is the case in many large African grazers. Furthermore, the forage resource which these species are foraging on, *i.e.*, the grass sward, is rather homogeneous if ungrazed (Prins and Olff, 1998). It appears that there must be a great potential for severe competition between such herbivore species. Generally, it is assumed that competitive exclusion is not taking place when there is no resource limitation, when there disturbance of the system before one species gets excluded, or when there is spatial or temporal variation in the resource. The conceptual forager-vegetation-model, described earlier in this chapter, illustrates a potential mechanism for this. The creation of spatial variation in forage availability, quality and structure through foraging on a temporally variable, though originally spatial homogeneous, forage resource, as explained above, could form a basis for the partitioning of the forage resource. Forager

compete less strong on another patch type. For example, biting foragers like Thompson's gazelle, may crop forage more effectively on short patches of low forage availability, while they may be less competitive on tall patches of high forage availability (Wilmshurst *et al.*, 1999b), where tongue-grasping foragers like African buffalo may forage more effectively. Thus, the heterogeneity in the forage resource created by the foragers themselves, may offer an explanation for the diversity of co-existing large herbivore species in African grasslands.

Grass growth forms, forager types and natural resource management

The experiments I have been reporting on in this thesis were performed making use of cattle as experimental animals. However, this study was not aimed at researching the foraging behaviour of cattle as such. Instead, cattle served as a model for other large herbivores, wild and domestic. Similarly, though we used *Panicum maximum* as the forage species in the grazing experiments on feeding station level, this study was not aimed at investigating the grazing of *P. maximum* as such. Also this grass species merely served as a model for other grasses. Therefore, in this section I will extrapolate my findings and will point out implications for other herbivore species foraging on other grass species with different growth forms. Furthermore, I will briefly reflect on some implications of my findings for biodiversity and natural resource management in temperate regions.

In this study I showed that the proportion of high quality forage parts, *i.e.*, grass leaves, the local aggregation of leaves and their accessibility have positive effects on forage intake by large grazing herbivores. This implies that bite mass from tufted grasses, which are grasses with leaves clustered around the plant base, could be high, because grazers can crop bites with a high proportion and density of leaves within the cropped bite volume. In doing so, grazers have to make only comparatively little efforts to select against low quality stems, because these tend to be concentrated towards the centre of the plant base. However, as tufted grasses thus comprise a mosaic of dispersed high and low quality forage items (potential bites with a high or a low proportion of leaves), searching times may be increased in selective foragers with a negative effect on bite rate. Forage intake from cauline grasses, which are grasses with leaves growing scattered along the stems, can expected to be lower, because the density of leaves within any cropped bite volume, and thus bite mass, is low. At the same time, the intimate contact of leaves and stems means high selection efforts, if a high proportion of leaves within the bite volume, and thus a high diet quality, is to be maintained, therefore decreasing bite rate. Different from bunch grasses (i.e., tufted and cauline perennials), creeping grasses tend to invest relatively little biomass in stemmy support tissue and show a

more homogeneous distribution of leaves. The distance between potential bites is therefore likely to be small and search times should not be limiting forage intake rate. At the same time, in creeping grasses there might be less need for selection against stems, because these tend to be thin or low in fibre compared to bunch grasses, thus enabling decreased handling times and increased bite rates. However, as short, creeping grasses typically accumulate lower biomasses, this may lead to low bite mass and accordingly may limit the rate of forage intake.

Mammalian herbivore species often are distinguished by means of their digestive system (e.g., ruminants and non-ruminants; e.g., Hofmann, 1973; Van Wieren, 1996), their main dietary components (grazers, browsers and mixed feeders; Hofmann, 1973) and their metabolic requirements in relation to body size (e.g., Jarman, 1974; Illius and Gordon, 1987). In this study I focussed on grazers, so in the remainder of this section I distinguish only between larger and smaller bodied grazers and between ruminants and non-ruminants, though the following reflections also have implications for browsers and mixed-feeders. Firstly, the metabolic requirements of a herbivore increase with its body mass to the power of 0.75, while the digestive system is linearly related with body mass. Therefore it has been argued that larger herbivores should be able to tolerate a lower quality diet than small herbivores (Jarman, 1974). Larger herbivores however, require a larger absolute amount of nutrients than small herbivores. Secondly, the principal groups of ruminants and non-ruminants I distinguish are bovids and equids. It has been suggested that, because of their more effective digestive system, bovids could forage more efficiently on medium quality grass then equids, while equids, because of the higher throughput of their digestive system, could forage more efficiently on low quality grass than bovids (e.g., Janis, 1976). Taking these arguments into account, it follows that compared with other grazing species, large equids could forage efficiently on tall, leafy bunch grasses, offering high forage intake rates and high quality diet, but also tolerate tall, stemmy bunch grasses, offering high intake rates on the expense of a high quality diet. Smaller bovids, however, could forage more efficiently on short, creeping grasses, tolerating low bite mass and intake rate, if the proportion of leaves, and accordingly diet quality, is high. Nevertheless, they could also forage efficiently on tall, leafy bunch grasses, tolerating low bite rates that may result from long handling or searching times when selecting for leaves. Both large bovids and small equids should be rather intermediate in the efficiency of their digestive systems. However, the large bovids would have higher absolute nutrient requirements than the small equids. Therefore the large bovids would forage more efficiently in tall, dense grasslands, while the small equids would forage more efficiently in short or sparse grasslands.

On the basis of the above mentioned differences in foraging efficiency between grazers of varying size and different digestive systems, and taking into account the effects of grazing on the structure of the vegetation as suggested in an earlier section of this chapter, I now want to reflect on the implications of this study for natural resource management in temperate regions. In many nutrient rich grasslands plant species diversity decreases without grazing, as perennial grasses exclude other plant species (Bakker and Van Wieren, 1998). Horses, with their tolerance of a low quality diet but high absolute nutrient requirements, are especially suitable to remove large amounts of the relatively low quality grass mass (Menard et al., 2002) and therefore can prevent or slow down the competitive exclusion of other plant species through perennial grasses. Further, horses tend to create grazing lawns, even at low grazer densities (Amiaud, 1998). The creation of such spatial structures may serve to partition the forage resource and can facilitate the forage availability for smaller herbivore species (Farnsworth et al., 2002). The use of cattle, on the other hand, has different effects from horses. Because of their lower mass, cattle have smaller absolute nutrient requirements compared with horses, and larger numbers of the former are necessary to prevent perennial grasses from gaining dominance (Menard et al., 2002). However, because of their lower tolerance of a low quality diet (Janis, 1976; Wallis de Vries, 1994) and because of their preference for other resource structures compared with horses (Menard et al., 2002), cattle include other forage types in their diet than horses and have a qualitatively different effect on grasslands. For example, because broadleaved plant species make a greater part of the diet of cattle than of horses, cattle are better suited to prevent or slow down the encroachment of grasslands by woody species (Menard et al., 2002). The use of water points, salt licks or protein/molasses licks has the potential to manipulate the spatial distribution of grazers (Wallis de Vries, 1994, Ganskopp, 2001). A more evenly or clustered utilization of the grazing resource can be achieved by temporary opening or closing water points or re-locating supplement licks. Side effects of the directing of the spatial distribution of grazing are the accompanying effects of trampling and localized nutrient deposition through defecation (Georgiadis and McNaughton, 1990). All these effects can influence the local plant species composition and structure of the vegetation. The use of water points, of supplemental licks, and of different herbivore species as management tools can be instrumental in the creation of (shifting) mosaics of grassland patches, differing in plant species composition and vegetation structure. A (shifting) mosaic of vegetation patches appears desirable from a biodiversity conservation point of view. It provides opportunities for the successional recruitment of plant species of different growth forms (Olff et al., 1999) and creates spatial heterogeneity in the

availability of micro-climates and of forage types which appear essential for the maintenance of a diversity of vertebrate and non-vertebrate herbivores (Wallis de Vries and Franssen, 2001).

Conclusion

Foraging on a temporally variable forage resource necessitates specific adaptations in the foraging strategy and the way of resource use. The population density of large resident foragers likely is adapted to the low resource availability during the periods of scarcity. This low population density may cause a temporary under-utilisation of the forage resource during the periods of plenty. Forage production temporary exceeding forage consumption can then lead to an accumulation of forage material and a decrease in the proportion of high quality forage. A likely response of foragers to this is a spatial or temporal aggregation of their foraging activity. Through re-grazing, foragers might maintain localities of intermediate forage availability and proportion of high quality forage, which enable high forage intake rates. The creation of spatial variation in forage availability and quality, *i.e.*, the partitioning of the forage resource into localities of low availability and high quality and localities of high availability and low quality, might serve as a basis for the maintenance of large diversity of herbivore and plant species.

The experiments and observations I conducted in the course of the last four years and which I presented in this thesis, enabled me to sketch, in the form of a conceptual model, a concise picture of the interactions of a large herbivore with a forage resource, which is complex in its structure and varies spatially and temporally in availability and quality. However, this conceptual model rises at least as many questions as it answers:

(i) Does the degree of selectivity in large foragers really depend on forage availability and on the proportion of high quality forage? (ii) How much do foragers really know about the distribution and condition of their forage resource? (iii) It has been shown that foragers can learn about toxicity in forage items (e.g., Provenza, 1996). But, can free-ranging foragers really learn to recognise precisely the quality of forage types, when there is no immediate and strong detrimental effect for their fitness? (iv) How do own experience, the example by elders and peers, and genetic inheritance contribute to diet choice? (v) What is the proof that foragers can really benefit from the uneven distribution of high quality forage parts throughout the forage resource? (vi) How can we utilise different species of herbivores most effectively for natural resource management and the maintenance of a high diversity of plant and herbivore species? And these are but a few of the important questions which still have to be answered. I would not have been able to see the relevance of these questions before I started my experimental work. And I would not even have seen it, before I synthesised all data and brought them into the shape of a conceptual model. Clearly, besides of being a tool to integrate all the knowledge, which I acquired during my studies, the main function of this model is to show where knowledge is lacking and to help generate new hypotheses. These hypotheses can only be verified by doing new experiments and observations, making the creation of knowledge an iterative process with alternating employment of models and experiments.

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Summary

In this thesis I report on my studies on the effects of forage resource structure on foraging behaviour in large ruminant herbivores. I focus on the effects (i) of the proportion of high quality forage, and (ii) of the spatial arrangement of forage parts, on the functional response and on diet quality. The functional response, which is the relationship of forage intake with forage availability, is the main process of interaction of a forager with a forage resource. It has been shown that the shape of the response curve depends on the type of foraging process (see Figure 1.2). Because the functional response is linking the trophic levels of the producer and the consumer, its understanding as such is fundamental to our insight into animal ecology.

The majority of large herbivores world-wide forage on grasslands. Natural grasslands are mosaics of patches, differing in the availability and quality of forage. This variation mainly is brought about by the differences in nutritional quality between high quality leaves and low quality stems. In natural grasslands, high and low quality forage parts are intimately mixed, but unevenly distributed.

At the smallest spatial scale this uneven distribution of forage parts originates from the heterogeneous distribution of leaves and stems within a grass plant. Intimate mixing of leaves and stems decreases the accessibility of the high quality leaves. This results in a decrease in forage intake in selectively foraging herbivores by decreasing bite mass or bite rate, or it results in a decrease in diet quality when selectivity is low. As a consequence, foragers are confronted with a trade-off between forage intake and diet quality. Spatial aggregation of high quality forage parts, e.g., clustering of leaves at the base of grass tufts, increases the accessibility of high quality forage, resulting in an increase in forage intake and diet quality. At larger spatial scales, variation in soil properties or disturbances like grazing, fire or flooding, can cause variation in forage availability and quality forage parts, with forage availability.

Besides of forage intake and diet quality being affected by forage resource structure, foraging also affects the structure of the resource. On a short temporal scale, foraging causes the local decrease of forage availability, and selective foraging can result in a decrease in the proportion of high quality forage parts, *i.e.*, in forage resource quality. However, on longer temporal scales, foraging can lead to the temporal arresting of a forage resource patch in a state of intermediate forage availability and quality, enabling an optimal compromise between forage intake and diet quality and resulting in a maximisation of long-term nutrient intake.

Apart from the spatial variation in the forage resource, seasonal fluctuations in temperature and rainfall cause temporal variation in forage availability and quality. Marked periods of plenty and of scarcity require special strategies to survive the periods of low forage availability and quality. Spatial variation in forage resource structure, in part, is a result of the temporary increased concentration of foraging during times of plenty, creating the before mentioned patches of intermediate forage availability and intermediate quality.

I performed my practical studies by carrying out grazing experiments and field observations in South Africa using Nguni cattle, which served as a general model for wild and domestic large ruminant herbivores. Nguni cattle are a breed of cattle indigenous to southern Africa and they were exposed to the conditions of natural, unmanaged grasslands for at least the last 1000 years. It can therefore be assumed that these cattle are well adapted to the natural grazing conditions in complex and seasonally variable grasslands.

In the Chapters 2 and 3 of this thesis, I report on the results of foraging experiments involving hand-constructed micro-swards. These swards of the size of a single feeding station, i.e., the area the herbivores could reach without moving their front legs, varied in (i) mass, (ii) the proportion of high quality forage, and (iii) the spatial arrangement of forage parts. In Chapter 2 I show that decreasing the proportion of high quality forage parts changes the shape of the functional response curve from a linear type I to a asymptotic type II. It appears that by decreasing the proportion of high quality forage, the factor limiting forage intake changes from forage availability to forage acquisition. Clustering high quality forage parts counteracts the negative effect of a decreasing proportion of high quality forage, but only partially. The positive effect of clustering is restricted to small-sized clustering up to about 200 cm², supporting the hypothesis that the negative effect of decreasing proportion of high quality forage parts with the cropping process.

In Chapter 3, I present a detailed investigation of the mechanism causing the decrease in forage intake with decreasing proportion of high quality forage. I found that the main factor limiting forage intake is the decrease of bite area which results in a decrease of plant parts cropped per bite and thus in bite mass. I show that for a given intermediate proportion of high quality forage an increase in forage availability initially results in an increase in bite mass as more plant parts can be cropped per bite. However, when forage availability is increasing further, the negative effect of crowding of low quality forage parts on bite area overcompensates for the increasing density of high quality forage parts in the cropped bite area, resulting in decreasing bite mass. Ultimately this mechanism causes a dome-shaped type IV functional response curve. On basis of these mechanics I constructed a simple regression model, which is generating a family of functional response curves, from linear type I, over

asymptotic type II, to dome-shaped type IV, depending on the range of forage availabilities and the proportion of high quality forage.

In Chapter 4, I present the results of field observations of the foraging behaviour of free-ranging Nguni cattle. I expected to find that forage intake and diet quality were decreasing with increasing forage availability and with decreasing proportion of high quality forage. However, I was not able to detect any such effect. Probably, the existing spatial variation in forage availability and in the distribution of high quality forage parts within patches offered opportunities for simultaneously high forage intake and high diet quality, despite a decrease in average resource quality.

With the aid of a simple simulation model I explored the effects of a variable functional response, which is depending on the proportion of high quality forage, on the forager-resource interaction. The results of this study are presented in Chapter 5. It shows that such a system of a forager and a forage resource consisting of two types, a high and a low quality forage type, can take multiple stable states: (i) a trivial stable state with high forage availability but a low proportion of high quality forage and without foragers, or (ii) a non-trivial stable state with lower forage availability but a high proportion of high quality forage and with foragers. Which of these two states is reached depends on the initial density of the forager population, the growth rate of the high and low quality forage, and on the consumption-to-growth conversion factor of both forage types to the forager population.

In the last chapter of this thesis, Chapter 6, I synthesise the results of the earlier chapters and add previously unreported data and the results of other studies. I sketch a concise picture of the interactions between a forager and a complex forage resource over a range of spatial scales, from the single bite up to patch level. On basis of this, I constructed a conceptual model of the interactions of a forager and a complex, seasonal forage resource, which I investigated in a thought experiment. The results of this thought experiment suggest the creation of spatial variation in forage availability and quality as a result of the temporal concentration of foraging activity in some localities during times of high forage production. In these localities, regrazing causes forage availability and forage quality to stay at intermediate levels, promoting high forage intake, while other localities remain underutilised, resulting in an accumulation of forage and a decrease in forage quality. In the context of the competitive exclusion principle I suggest that the creation of this spatial variation in forage availability and quality may cause a partitioning of the forage resource in natural grasslands. Such a resource partitioning may form the basis for species co-existence and is a potential mechanism for causing the observed species diversity of ruminant grazer assemblages. At the same time, I suggest that the creation of a (shifting) mosaic of grassland patches can be instrumental in natural resource management, as it is expected to have positive effects on the diversity of plant species and of vertebrate and non-vertebrate herbivore species.

Samenvatting

In dit proefschrift bericht ik over de resultaten van mijn onderzoek naar de effecten van de structuur van een voedselbron op het foerageergedrag van grote herkauwende herbivoren. Ik concentreer mij hierbij op de effecten (i) van de proportie van voedsel van hoge kwaliteit, en (ii) van de ruimtelijke ordening van delen van voedsel, op de functionele respons en op de dieetkwaliteit. De functionele respons, welke gedefinieerd is als de relatie van voedselopnamesnelheid met voedselbeschikbaarheid, is de meest belangrijke verbinding tussen een foeragerend organisme en een voedselbron. Uit eerder onderzoek bleek dat de vorm van de functionele respons afhankelijk is van het type van het foerageerproces (zie Figuur 1.2). Omdat de functionele respons de verbinding vormt tussen de trofische niveaus van producenten en consumenten is het begrijpen van de functionele respons essentieel voor ons het vergroten van ons inzicht in de dierecologie in het algemeen.

De meerderheid van alle grote herbivoren wereldwijd foerageert in graslanden. Natuurlijke graslanden zijn mozaïeken waarvan de onderdelen verschillen in de beschikbaarheid en de kwaliteit van voedsel. De variatie in de kwaliteit wordt voornamelijk veroorzaakt door verschillen in de concentraties van nutriënten tussen de bladeren en de stengels van grassen. In het algemeen zijn de concentraties van nutriënten in bladeren hoger dan in stengels en daarom zijn bladeren voedseldelen van hoge kwaliteit, maar stengels voedseldelen van lage kwaliteit. In natuurlijke graslanden is voedsel van hoge en van lage kwaliteit sterk gemengd, maar onregelmatig verdeeld.

Op de kleinste ruimtelijke schaal heeft de onregelmatige verdeling van voedsel van lage en hoge kwaliteit haar oorsprong in de ongelijkmatige verdeling van bladeren en stengels binnen een grasplant. De sterke menging van bladeren en stengels in de grasplanten heeft als gevolg dat de bladeren niet makkelijk bereikbaar zijn. Voor selectief foeragerende herbivoren betekent dit een afname van de voedselopnamesnelheid omdat de massa van happen met bladeren of de snelheid van het nemen van deze happen afneemt. Anderzijs veroorzaakt het een daling van de dieetkwaliteit voor niet selectief foeragerende herbivoren door het opnemen van stengels in de happen. Als gevolg hiervan moeten herbivoren een compromis zien te vinden tussen de snelheid van voedselopname en dieetkwaliteit. De ruimtelijke aggregatie van voedsel van hoge kwaliteit, welke voornamelijk ontstaat door de concentratie van bladeren aan de basis van graspollen, verhoogd echter de toegankelijkheid van voedsel van hoge kwaliteit en verhoogd daarom ook de voedselopnamesnelheid en de dieetkwaliteit.

Op grotere ruimtelijke schaal kan variatie in de beschikbaarheid en kwaliteit van voedsel veroorzaakt worden door bijvoorbeeld variatie in bodemfactoren of door plaatselijke verstoringen door vuur of overstromingen. Voedselbeschikbaarheid en voedselkwaliteit, dat wil zeggen de concentratie van nutriënten in voedsel of de proportie van voedsel van hoge kwaliteit, laten in het algemeen een negatieve verhouding zien.

Niet alleen de structuur van de voedselbron heeft effecten op de voedselopnamesnelheid en de voedselkwaliteit, maar ook de voedselopname zelf heeft effecten op de structuur van de voedselbron. Op korte termijn veroorzaakt voedselopname een afname van de voedselbeschikbaarheid en gemiddelde voedselkwaliteit door het selectief eten van voedsel van hoge kwaliteit. Niettemin, op langere termijn kan voedselopname leiden tot het tijdelijke vasthouden van een gedeelte van een voedselbron in een toestand van gemiddelde beschikbaarheid en kwaliteit van voedsel. Dit maakt een optimaal compromis tussen voedselopname en dieetkwaliteit mogelijk en leidt over langere tijd tot een maximalisering van de opname van nutriënten.

Behalve de ruimtelijke variatie in de voedselbron bestaat er ook tijdelijke variatie in de beschikbaarheid en kwaliteit van voedsel, veroorzaakt door seizoensfluctuaties van temperatuur en regenval. Sterke verschillen in de voedselbeschikbaarheid tussen de seizoenen maken speciale aanpassingen nodig voor tijden van lage beschikbaarheid en kwaliteit van voedsel. De ruimtelijke variatie in de voedselbron, dat wil zeggen het mozaïek van delen van lage en hoge voedselbeschikbaarheid, is gedeeltelijk ook het gevolg van kortstondige, lokale concentraties van herbivoren in tijden van algemeen hoge voedselbeschikbaarheid.

Ten behoeven van dit onderzoek voerde ik begrazingsexperimenten uit en deed veldobservaties in Zuid Afrika. Ik gebruikte hiervoor Nguni runderen welke een model zijn voor wilde en gedomesticeerde grote herbivoren in het algemeen. Nguni runderen zijn een inheemse Afrikaanse ras en zijn al sinds ruim 1000 jaar blootgesteld aan de condities van de natuurlijke graslanden in zuidelijk Afrika. Daarom is dit ras goed aangepast aan de omstandigheden van ruimtelijke en seizoenale variatie in voedselbeschikbaarheid en kwaliteit.

In de hoofdstukken 2 en 3 bericht ik over begrazingsexperimenten met kleine, handvervaardigde grasmatten. Deze grasmatten hadden de grote van een *feeding station*, welk gedefinieerd is als het oppervlak waarin een herbivoor kan foerageren zonder zijn voorpoten te bewegen. De grasmatten verschilden van elkaar in (i) massa, (ii) de proportie van voedsel van hoge kwaliteit en, (iii) de ruimtelijke ordening van de voedseldelen. In hoofdstuk 2 laat ik zien dat de vorm van de functionele respons curve verandert van een lineaire type I naar een asymptotische type II als gevolg van een afname van de proportie van voedsel van hoge kwaliteit. Het blijkt dat hierbij de beperkende factor van de voedselopname verschuift van voedselbeschikbaarheid naar voedselhanteerbaarheid. De lokale, ruimtelijke concentratie van voedsel van hoge kwaliteit gaat het negatieve effect van een afnemende proportie van voedsel

van hoge kwaliteit gedeeltelijk tegen. Maar het positieve effect van de ruimtelijke concentratie is beperkt tot concentraties met een oppervlak van kleiner dan 200 cm². Omdat deze waarde overeenkomt met het maximale hapoppervlak, ondersteunt deze vondst de hypothese dat het negatieve effect van de afnemende proportie van voedsel van hoge kwaliteit veroorzaakt is door de fysieke belemmering van het nemen van happen van voedsel van lage kwaliteit.

In hoofdstuk 3 presenteer ik de resultaten van een onderzoek naar het mechanisme dat ten grondslag ligt aan de afname van de voedselopname met afnemende proportie van voedsel van hoge kwaliteit. Ik vond dat de meest belangrijke factoor hiervoor de afname van het hapoppervlak is. De afname van het hapoppervlak leidt tot een afname van het aantal plantendelen welk per hap geoogst wordt en dus tot een afname van de hapmassa. Ik laat zien dat voor een gemiddelde proportie van voedsel van hoge kwaliteit een toename van de voedselbeschikbaarheid aanvankelijk leidt tot een toename in het aantal van geoogste plantendelen per hap en dus in hapmassa. Als de voedselbeschikbaarheid echter verder toeneemt, wordt het negatieve effect van de toenemende dichtheid van voedsel van lage kwaliteit sterker. Het hapoppervlak neemt hierdoor af en de toenemende dichtheid van voedseldelen van hoge kwaliteit binnen het geoogste hapoppervlak kan dit niet compenseren, resulterend in een afname van de hapmassa. In het extreem geval leidt dit mechanisme naar het ontstaan van een klokvormige, type IV functionele respons curve. Op basis van dit mechanisme heb ik een simpel regressie model gemaakt welk in staat is een verzameling van verschillende respons curven te genereren, beginnend bij het lineaire type I over het asymptotische type II naar het klokvormige type IV. Welk van deze types gegenereerd wordt hangt alleen af van de voedselbeschikbaarheid en de proportie van voedsel van hoge kwaliteit.

In hoofdstuk 4 presenteer ik de resultaten van veldobservaties van het gedrag van vrij lopende Nguni runderen. Ik verwachtte dat de voedselopnamesnelheid en de dieetkwaliteit af zouden nemen met toenemende voedselbeschikbaarheid en de daaraan verbondene afnemende proportie van voedsel van hoge kwaliteit. Niettemin heb ik een dergelijk effect niet kunnen aantonen. Het is waarschijnlijk dat de ruimtelijke variatie in de voedselbeschikbaarheid en in de verdeling van plantendelen in delen van de grasmat lokaal mogelijkheden schepte voor een hoge voedselopnamesnelheid en een hoge dieetkwaliteit, terwijl de voedselkwaliteit gemiddeld laag was.

In hoofdstuk 5 presenteer ik de resultaten van een onderzoek naar de effecten van een variabele functionele respons voor consument-voedselbron interacties. Hiervoor werd gebruik gemaakt van een simpel simulatiemodel, waarin de vorm van de functionele respons curve

afhing van de proportie van voedsel van hoge kwaliteit. Het blijkt dat een systeem bestaande uit consumenten en een voedselbron welk onderverdeeld is in een deel van hoge en een deel van lage kwaliteit, verschillende stabiele toestanden kan aannemen: (i) een triviale stabiele toestand met een hoge voedselbeschikbaarheid maar een lage proportie van voedsel van hoge kwaliteit en zonder consumenten, en (ii) een niet triviale stabiele toestand met een lagere voedselbeschikbaarheid maar een hogere proportie van voedsel van hoge kwaliteit en met consumenten. Welk van deze twee toestanden bereikt wordt hangt af van de initiële dichtheid van de consumentenpopulatie, de groeisnelheid van voedsel van lage en van hoge kwaliteit, en van de consumptie-naar-consumentengroei conversiefactor van beide voedseltypes naar de consument.

In het laatste hoofdstuk van dit proefschrift, hoofdstuk 6, breng ik de resultaten van de eerdere hoofdstukken samen en betrek daarbij ook data welk ik nog niet eerder presenteerde en data van andere studies. Over een reeks van schalen, beginnend bij een enkele hap tot naar het niveau van een grasland, schets ik een samenhangend beeld van de interacties van een herbivoor met een heterogene voedselbron. Dit diende als basis voor de constructie van een conceptueel model van de interacties van een herbivoor met een heterogene, seizoenale voedselbron, welk ik onderzocht heb in een gedachtenexperiment. De resultaten van dit gedachtenexperiment suggereren het ontstaan van ruimtelijke variatie in voedselbeschikbaarheid en kwaliteit als gevolg van kortstondige, lokale concentratie van het foerageren in tijden van verhoogde algemene voedselbeschikbaarheid. In deze gebieden leidt herbegrazing tot het vasthouden van een toestand van gemiddelde voedselbeschikbaarheid en kwaliteit. In andere gebieden echter wordt het geproduceerde plantenmateriaal niet volledig geconsumeerd wat lokaal leidt tot een accumulatie van biomassa en een daling van de voedselkwaliteit. Met het oogmerk op het principe van *competitive exclusion* suggereer ik dat in natuurlijke graslanden het ontstaan van ruimtelijke variatie in de beschikbaarheid en kwaliteit van voedsel een opdeling zou kunnen veroorzaken van de voedselbron. Deze opdeling zou de basis kunnen vormen voor de co-existentie van verschillende soorten herbivoren en zou mogelijk de opvallende soortendiversiteit in groepen van herbivoren in Afrikaanse graslanden kunnen verklaren. Tegelijk suggereer ik dat het genereren van een mozaïek van gebieden met verschillen in voedselbeschikbaarheid en kwaliteit, instrumenteel zou kunnen zijn in het beheer van natuurlijke graslanden. Het kan namelijk verwacht worden dat zo een variatie door het ontstaan van verschillende microklimaten positieve effecten zal hebben op de diversiteit van plantensoorten en van vertebraten en niet-vertebraten.

Zusammenfassung

In dieser Doktorarbeit berichte ich über die Ergebnisse meiner Studie zu den Effekten der Struktur von Nahrungsressourcen auf die Nahrungssuche und das Fressverhalten von grossen, wiederkauenden Herbivoren. Hierbei konzentriere ich mich auf die Effekte (i) der Proportion der Nahrung von hoher Qualität in der Nahrungsressource und (ii) der räumlichen Anordung der Nahrungsressource, auf die *functional response* und auf die Diätqualität. Die *functional response*, welche definiert ist als das Verhältnis zwischen der Nahrungsaufnahmegeschwindigkeit und der Nahrungsverfügbarkeit, ist das wichtigste Bindeglied zwischen einem Nahrung suchenden Organismus und der Nahrungsressource. In früheren Studien wurde gezeigt, dass die Form der *functional response* abhängig ist von der Art der Nahrungssuche und des Fressverhaltens (siehe Figur 1.2). Da die *functional response* die trophischen Niveaus von Produzenten und Konsumenten verbindet, ist unser Verständnis der Faktoren, welche die *functional response* beeinflussen, essentiel für unser Verständnis der Tierekölogie im allgemeinen.

Die Mehrheit aller grossen Herbivoren weltweit lebt auf Grasländern. Natürliche Grasländer sind Mosaike, deren Elemente sich in der Verfügbarkeit und der Qualität der Nahrung unterscheiden. Die Variation in der Qualität wird grösstenteils verursacht durch Konzentrationsunterschiede von Nutrienten zwischen Blättern und Stengeln von Gräsern. Im allgemeinen sind die Nutrientenkonzentrationen in Blättern höher als in Stengeln und darum sind Blätter Nahrung von hoher Qualität, Stengel hingegen Nahrung von niedriger Qualität. In natürlichen Grasländern ist Nahrung von hoher und von nierdriger Qualität stark vermischt und unregelmässig verteilt.

Auf der kleinsten räumlichen Skala betrachtet, wird die unregelmässige Verteilung der Nahrung von hoher und von niedriger Qualität verursacht durch die ungleichmässige Verteilung von Blättern und Stengeln in den Grasbüscheln. Wegen dieser starken Vermischung von Blättern und Stengeln sind die Blätter schwierig erreichbar. Selektiv Blätter fressende Herbivore müssen in einer solchen Situation das Bissgewicht oder die Bissgeschwindigkeit reduzieren um eine hohe Diätqualität aufrecht zu erhalten, welches eine Abnahme der Nahrungsaufnahmegeschwindigkeit zur Folge hat. Nicht selektiv fressende Herbivore andererseits nehmen die Stengel mit den Blättern auf, welches eine Abnahme der Diätqualität verursacht, wobei aber die Nahrungsaufnahmegeschwindigkeit hoch bleiben kann. Als Konsequenz müssen Herbivore einen Kompromiss zwischen Nahrungsaufnahmegeschwindigkeit und Diätqualität finden. Die räumliche Aggregation von Nahrung von hoher Qualität jedoch, welche grösstenteils durch die Konzentration von Blättern an der Basis von Grasbüscheln verursacht wird, erleichtert die Zugänglichkeit von Nahrung von hoher Qualität und erhöht damit die Nahrungsaufnahmegeschwindigkeit und die Diätqualität.

Auf grösseren räumlichen Skalen betrachtet, kann die Variation in der Verfügbarkeit und der Qualität von Nahrung die Folge sein von Variationen in Bodenfaktoren oder von lokalen Störungen durch Feuer oder Überflutungen. Im allgemeinen sind die Verfügbarkeit und die Qualität von Nahrung, das heisst die gemittelte Nutrientenkonzentration oder der Anteil von Nahrung von hoher Qualität, negativ korreliert.

Neben den Effekten, welche die Struktur der Nahrungsressource auf die Nahrungsaufnahmegeschwindigkeit und die Diätqualität hat, hat auch die Nahrungsaufnahme selbst Effekte auf die Struktur der Nahrungsressource. Wegen des selektiven Aufnehmens von Nahrung von hoher Qualität, verursacht die Nahrungsaufnahme kurzfristig einen Abnahme der Nahrungsverfügbarkeit und der gemittelten Nahrungsqualität. Längerfristig allerdings kann die Nahrungsaufnahme Teile der Nahrungsressource zeitweise in einem Zustand von mittlerer Verfügbarkeit und Qualität fixieren. In einer sochen Situation können Herbivore einen optimalen Kompromiss zwischen Nahrungsaufnahmegeschwindigkeit und Diätqualität finden, welches eine Maximalisierung der langfristigen Nutrientenaufnahme möglich macht.

Ausser der räumlichen Variation in der Nahrungsressource gibt es auch zeitliche Variationen in der Verfügbarkeit und in der Qualität der Nahrung, die grösstenteils durch jahreszeitliche Schwankungen in der Temperatur und im Regenfall verursacht werden. Grosse Unterschiede in der Nahrungsverfügbarkeit zwischen den Jahreszeiten erfordern spezielle Anpassungen an die Zeiten in denen die Verfügbarkeit und die Qualität der Nahrung niedrig sind. Zum Teil ist die räumliche Variation der Nahrungsressource, dass heisst das Mosaik von Gebieten mit hoher und niedriger Nahrungsverfügbarkeit und Nahrungsqualität, die Folge von kurzzeitigen, lokalen Konzentrationen Herbivoren in Zeiten allgemein von von hoher Nahrungsverfügbarkeit.

Im Zusammenhang mit dieser Studie führte ich Begrasungsexperimente aus und machte Feldbeobachtungen in Südafrika. Hierfür verwendete ich Nguni Rinder, die als Model dienen für wilde und domestizierte Herbivore im allgemeinen. Nguni Rinder sind eine einheimische afrikanische Rasse, die vor mindestens 1000 Jahren im südlichen Afrika durch Bantu und KhoiKhoi Völker eingeführt worden ist. Man kann also davon ausgehen, dass diese Rinder gut angepasst sind an die lokalen Verhältnisse und auch an die räumliche und jahreszeitliche Variation der Nahrungsverfügbarkeit und Nahrungsqualität.

In den Kapiteln 2 und 3 berichte ich über Begrasungsexperimente mit kleinen, handgemachten Grasmatten. Jede Grasmatte hatte die Grösse einer *feeding station*, welche

definiert ist als das Gebiet, in welchem ein Herbivor Nahrung suchen kann, ohne seine Vorderbeine zu bewegen. Die Grasmatten unterschieden sich in (i) ihrer Masse, (ii) der Proportion der Nahrung von hoher Qualität in der Grasmatte und (iii) der räumlichen Anordung der Nahrung. In Kapitel 2 zeige ich, wie sich die Kurvenform der functional response von einem lineären Typ I zu einem asymptotischen Typ II verändert, wenn die Proportion hochwertiger Nahrung vermindert wird. Es scheint, dass sich hierbei der Faktor, der die Nahrungsaufnahme begrenzt, von der Nahrungsverfügbarkeit zu der Nahrungszugänglichkeit verschiebt. Lokale, räumliche Konzentrationen der Nahrung von hoher Qualität können zu einem Teil den negativen Effekt der abnehmenden Proportion der Nahrung hoher Qualität kompensieren. Dieser positive Effekt der räumlichen Konzentration ist jedoch beschränkt auf kleine Konzentrationen mit einer Oberfläche von bis zu 200 cm². Weil dieser Wert übereinstimmt mit der maximalen Bissoberfläche, understützt dieses Resultat die Hypothese, dass der negative Effekt der abnehmenden Proportion der Nahrung hoher Qualität die Folge einer physischen Behinderung des Beissvorganges durch Nahrung von niedriger Qualität ist.

In Kapitel 3 präsentiere ich die Resultate einer Studie nach dem Mechanismus, der die Abnahme der Nahrungsaufnahmegeschwindigkeit mit abnehmender Proportion von Nahrung von hoher Qualität verursacht. Es stellte sich heraus, dass der wichtigste Faktor hierbei die Abnahme der Bissoberfläche war. Die Abnahme der Bissoberfläche führt zu einer Reduzierung der Anzahl der Planzenteile, die mit jedem Biss gepackt worden können, und somit zu einer Abnahme der Bissmasse. Es war mir möglich zu zeigen, dass für eine mittlere Proportion der Nahrung von hoher Qualität, eine Zunahme der Nahrungsverfügbarkeit anfänglich zu einer Zunahme der Anzahl der Pflanzenteile, die mit jedem Biss gepackt werden können, leitet. Wenn die Nahrungsverfügbarkeit aber weiter zunimmt, dann überwiegt der negative Effekt der Zunehmenden Dichtheit der Nahrung von niedriger Qualität. Die Bissoberfläche nimmt hierdurch ab und auch die zunehmende Dichtheit der Nahrung von hoher Qualität in dem greifbaren Bissvolumen kann dies nicht kompensieren, so dass es zu einer Abnahme der Bissmasse kommt. Im Grenzfall verursacht dieser Mechanismus das Entstehen einer glockenförmigen Typ IV Kurve der functional response. Diesen Mechanismus als Basis nehmend, konstruierte ich ein simples Regressionsmodel, welches eine Reihe von verschiedenen Kurven der functional response generieren kann, beginnend bei dem lineären Typ I über den asymptotischen Typ II bis zum glockenförmigen Typ IV. Welche dieser Formen generiert wird, hängt vor allem ab von der Nahrungsverfügbarkeit und der Proportion der Nahrung von hoher Qualität.

In Kapitel 4 präsentiere ich die Resultate einer Feldstudie des Nahrungssuch- und Fressverhaltens von sich frei bewegenden Nguni Rindern. Ich erwartete, dass die Nahrungsaufnahmegeschwindigkeit und die Diätqualität mit zunehmender Nahrungsverfügbarkeit und der daran verbundenen Abnahme des Anteils hochwertiger Nahrung abnehmen würden. Ein solcher Effekt konnte jedoch nicht gezeigt werden. Es scheint, dass die räumlichen Variationen der Nahrungsverfügbarkeit und der Verbreitung von Pflanzenteilen, in begrenzten Bereichen der Grasmatte, Möglichkeiten schafften, eine hohe Nahrungsaufnahmegeschwindigkeit und eine hohe Diätqualität zu kombinieren, obwohl die Nahrungsqualität gemittelt niedrig war.

In Kapitel 5 berichte ich über die Resultate einer Studie zu den Effekten einer variablen *functional response* auf Konsumenten-Nahrungsressource Interaktionen. Hierfür wurde ein simples Simulationsmodel benutzt, in welchem die Form der *functional response* von der Porportion der Nahrung von hoher Qualität abhängig ist. Es erwies sich, dass ein solches System, bestehend aus Konsumenten und einer Nahrungsressource, die unterteilt ist in Nahrung von hoher und von niedriger Qualität, verschiedene stabiele Zustände annehmen kann: (i) ein trivialer stabieler Zustand, in welchem die Nahrungsverfügbarkeit hoch, aber der Anteil hochwertiger Nahrung niedrig ist, und in welchem keine Konsumenten existieren; (ii) ein nicht-trivialer stabieler Zustand, in welchem die Nahrungsverfügbarkeit nideriger, aber der Anteil hochwertiger Nahrung höher ist, und in welchem Konsumenten existieren. Welchen dieser Zustände das System erreicht, hängt ab von der initiellen Dichtheit der Konsumentenpopulation, der Wachstumsgeschwindigkeit der Nahrung von hoher und von niedriger Qualität und von dem Aufnahme-zu-Konsumentenwachstum Konversionsfaktor beider Nahrungstypen.

Im letzten Kapitel dieser Doktorarbeit, Kapitel 6, synthetisierete ich die Resultate welche in den vorangehenden Kapiteln präsentiert wurden und beziehe hierbei auch bisher noch nicht präsentierte Daten und die Resultate anderer Studien ein. Über eine Serie von Skalen skizzierte ich ein zusammenhängendes Bild der Interaktionen eines Herbivoren mit einer heterogenen Nahrungsressource, vom einzelnen Biss bis zum Niveau eines Graslandes. Daraufhin diente diese Skizze als die Basis für ein konzeptuelles Model der Interaktionen eines Herbivoren mit einer heterogenen, jahreszeitlich variablen Nahrungsressource, welches ich in einem Gedankenexperiment studierte. Die Resultate dises Gedankenexperimentes suggerieren, dass räumliche Variation in der Nahrungsverfügbarkeit und Qualität die Folge einer kurzzeitigen und lokalen Konzentration von Konsumenten sein kann, in Zeiten allgemein hoher Nahrungsverfügbarkeit. In solchen Gebieten führt wiederholte Begrasung zu der Fixierung eines Zustandes mittlerer Nahrungsverfügbarkeit und Qualität. In Gebieten in denen jedoch nicht durch wiederholte Begrasung die produzierte Biomasse konsumiert wird, leitet dies zu einer Akkumulation von Biomasse und einer Abnahme der Nahrungsqualität. Unter dem Gesichtspunkt des Prinzips der *competitive exclusion* verweise ich darauf, dass die räumliche Variation in der Nahrungsverfügbarkeit und Qualität zu einer Aufteilung der Nahrungsressource führen könnte. Diese Aufteilung könnte die Basis formen für die Koexistenz verschiedener Arten von Herbivoren und könnte so möglicherweise die auffallende Artenvielfalt in Gruppen von Herbivoren in afrikanischen Grasländern erklären. Auch suggerierte ich, dass das Enstehen eines Mosaiks von Gebieten mit unterschiedlicher Nahrungsverfügbarkeit und Qualität, als Instrument gebraucht werden könnte im Management von natürlichen Grasländern. Es ist nämlich zu erwarten, dass diese Variation zur Entstehung von verschiedenen Microklimaten führt, welches einen postiven Effekt haben kann auf die Artenvielfalt von Pflanzen sowie von höheren und niedrigeren Tieren.

Acknowledgements

The start of my work at the Tropical Nature Conservation and Vertebrate Ecology Group was kind of strange. I always had these romantic ideas about doing research in the tropical rainforests of South America, where I also did the fieldwork for my first graduation thesis. I guess, this whole idea about the rainforest and such originates from my love for forests and for trees. Animals, I thought, are just a nuisance. They never hold still, they never do want one wants them to, they have a mind of their own. Very annoying! Thus when I read the announcement of a vacancy for a Ph.D. working on large herbivores in Africa, I thought: 'This is not really what I want to do. It is not in South America. It is not about trees. Instead it is about, well, cows. And in any case, I am a vegetation ecologist, not an animal ecologist. What do I know about animals?' But I applied anyway. I thought it might be a good exercise in learning how to write a letter of application. To my surprise I got invited for an interview. In fact, that was more than I had bargained for. Even worse, a few days after the talks, to my complete horror, Ignas Heitkönig called and said that they would like me to do the job. I said that I wanted to think it over. Of course, that was merely because I did not want to feel like being sucked into something without having made a conscious decision myself. Anyway, finally I accepted the offer and I never regretted it. I consider it a privilege having got the chance to do work at the Tropical Nature Conservation and Vertebrate Ecology Group and to do research in the Africa savanna. And by the way: I changed my mind about cattle, too. Sometimes they are a pain and mostly they look quite dumb. But actually they are really amazing animals and are always good for a surprise.

This work would not have been possible without the support of many people. First, of course, I want to mention my promoter and my co-promoter. Herbert, thanks for accepting me as your Ph.D.-student. You were always willing to listen and to give advice. You taught me a lot about science and about ecology. And I think I also learned a few lessons about life, at least I hope so. Ignas, your patience and integrity always amazed me. Once in a while I must have given you quite a bit of headache. But you never gave up on me, or did you? I want to thank the two of you. It was a pleasure working with you.

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Michael Drescher, Wageningen, August 2003
Curriculum Vitae

Michael Drescher was born on the 22nd of March 1971 in Hannover, Germany, as the second child of Marlies Drescher, née Burgard, and Günter Drescher. He followed secondary school at the Städtisches Gymnasium, Herten, Germany, where he obtained his senior highschool graduation diploma (Abitur) in 1991. Having passed this exam he took a well deserved timeout to visit the Australian outback. Later, this trip into the wilderness would proof decisive for the choice of his scientific specialisation. In the course of his obligatory civil service he worked from 1991 to 1992 at the departments of internal and geriatric diseases of the Gertrudis Hospital, Herten. Thereafter, in 1992, he started his studies of biology at the Ruhr-Universität Bochum, Germany. He obtained his intermediate diploma (Vordiplom) in 1994 and deemed the time ripe for another time-out. Therefore, with the aid of the Erasmusnetwork, he went to the Netherlands and spent a year as an exchange student at Utrecht University. In 1995 he enrolled as bona fide student at Utrecht University, and doubted whether to specialise in genetics or in ecology. Remembering his visit to Australia he realised that his heart lay with nature, not with the lab, and he decided for ecology. For his first graduation thesis (afstudeeronderwerp) he did an internship with the Instituut voor Bos en Natuuronderzoek, currently Alterra, Wageningen, Netherlands. With the aid of a simulation model he investigated the long-term forest dynamics of European broadleaf forests. Of course, working on a computer is not the "real thing". So his second graduation thesis took him into the forests of the Bolivian Amazon. In co-operation with the non-governmental organisation Programa Manejo de Bosques de la Amazonía Boliviana he studied the patterns of the spatial distribution of tropical tree species. In 1998 he graduated (doctoraal) at Utrecht University and in the same year he was employed with the Netherlands Foundation for the Advancement of Tropical Research. He started working as a researcher in training (onderzoeker in opleiding) at the Tropical Nature Conservation and Vertebrate Ecology Group, Department of Environmental Sciences, Wageningen University, Wageningen. In the course of his employment he investigated the effects of vegetation structure on the functional response of large mammalian herbivores. The results of this study are presented in this doctoral thesis. After this employment, Michael was working as a Marie Curie Fellow at the Centre d'Etudes Biologique de Chizé, France.

Affiliations of co-authors

Heitkönig, I.M.A. Tropical Nature Conservation and Vertebrate Ecology Group Wageningen University Bornsesteeg 69, 6708 PD Wageningen Netherlands

Prins, H.H.T. Tropical Nature Conservation and Vertebrate Ecology Group Wageningen University Bornsesteeg 69, 6708 PD Wageningen Netherlands

Van den Brink, P.J. Alterra Green World Research Wageningen University and Research Centre P.O. Box 47, 6700 AA Wageningen Netherlands

Van Langevelde, F. Tropical Nature Conservation and Vertebrate Ecology Group Wageningen University Bornsesteeg 69, 6708 PD Wageningen Netherlands



And then the bovine watchers were given a *real* treat. On a small knoll, in full splendor, there suddenly appeared a Guatemalan cow of paradise.