PIOSPHERES IN SEMI-ARID RANGELAND: CONSEQUENCES OF SPATIALLY CONSTRAINED PLANT-HERBIVORE INTERACTIONS

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DECLARATION

I certify that this thesis was composed by myself, and that the work reported herein is my own.

[Julian F. Derry]

ACKNOWLEDGEMENTS

Inspiration to study piospheres came from Jem Perkins. A memorable first (and subsequent) visit to his rock-hewn home replete with houseguest Black Mambas, on the outskirts of Gaborone, provided me with an enticing glimpse of an alien lifestyle and a strange culture. My wanderlust peaked at the imagined excuses. I could justify venturing back to southern Africa and particularly the Kalahari, and Zimbabwe from where I had just travelled, to find out more about pans and dambos, vleis and kops, and the incredible African wildlife that I was just starting to glimpse. Jem was equally enthusiastic about African ecology and his soft-spoken descriptions of 4-wheel drive expeditions into remote wilderness rekindled the sense of adventure first lit in youth by the grand panoramas of many David Attenborough Serengeti specials. There was something of the hedonist about Jem too. Fuzzy recollections of every bar and casino in a Castle Lager-addled night of *Fear and Loathing in Gaborone*. A fitting inauguration for the fledgling ecologist looking for a subject on which to hone his academic chops. So, thank you Jem, for your generous hospitality, and the initial impetus to study piospheres, in whatever forms it came.

My primary supervisor was Andrew Illius. His task has not been easy. I have not been the model student, and our student-supervisor relationship has been compromised by our collaborative work carried out in parallel with this study, for which purposes we were recast as employee and boss, respectively. The conflict in ensuring separation of thesis content and contractual work mainly impacted schedules, with time regularly being lost from one endeavour to the other, making deadlines a figment of the imagination and frustrating delays far too common. Even so, Andrew did negotiate the fine line between supervisor and boss, and not only do I have this thesis to show from our shared anguish, but we have also produced end-user modelling software that is probably second-to-none for simulating semi-arid grazing systems. Additionally, my fieldwork involved protracted periods when I would be out of contact, and it must have proved difficult monitoring my experimental progress and providing feedback to developments on the ground. Nonetheless, Andrew has guided me through the disciplines of this thesis, patiently introducing me to the subject matter of animal foraging and nutrition; always steering me away from inadequately precise questions in favour of the more exacting scientific interrogation expected for a doctorate. Long enough has he suffered my verbal dyslexia, suffice for me to offer huge thanks to him for his supervisory skills and deep gratitude for introducing me to Miles Davis' "electric period". In the words of Miles, "If you understood everything I say, you'd be me!".

My second supervisor was Graham Russell. When I started my study, I read that part of the role of the second supervisor is to moderate the advice of the first supervisor (Phillips & Pugh 1994). Graham has done more than this and I thank him for giving the perfect complementary guidance that helped fuse the disparate pieces of work from which this thesis has emerged. Without him it certainly would have been less than the sum of its parts.

I have been fortunate enough to have had a third, unofficial, supervisor in Iain Gordon, a long-term friend and colleague of Andrew's, and therefore well-placed to smooth over the difficulties between us. Iain also gave me great direction in my studies, emotional support and well-needed approval, the rare occasions it was due. Iain, thank you for all you have done for me, and I am profoundly sorry for the loss of your irreplaceable Leica binoculars, last peeked bouncing down the Fort Hare road. I did return to look under every pebble and blade of grass for miles around, that winter, and the next, but as we guessed, sadly they're probably still on some mantelpiece, collecting dust as a bookend.

The broad ideas and concepts leading to the hypotheses tested in this thesis originated during travel through South Africa, Zimbabwe and Botswana, partly supported by the Bath & West Agricultural Society and the James Rennie Bequest from the School of Biological Sciences at the University of Edinburgh. During my time in Pietermaritzburg, the people in the [old] Department of Range & Forage Resources made me most welcome. The Klugs welcomed me into their home. Tim O'Connor took time from his busy schedule to be interested in my work, included me on his field trips and introduced me to his students for inclusion on theirs. Looking at black rhino browsing with Brent in Weenen; lion calling with Byron in Hluhluwe-Umfolozi; pine plantations in St. Lucia with Barry "Leecence" James; grasses, watering holes and aerial counts at Malilangwe with Sarah and Bruce Clegg, who also accommodated me in PMB. My independent travels were made possible by use of Richard Fynn's Toyota bakkie, an ancient and forgiving war-horse of a lifeline and inanimate friend. Most thanks go to Craig Morris at UNP for the many hours that we have spent chewing the cud, for the successful collaborations and for the projects that didn't make it. Best wishes to him and Anita. Visits to Kruger were always exciting and made all the better by Harry Biggs who made sure I was comfortable and made arrangements for me to stopover with rangers as I made my way through the Park, such as the cordial Paul Funston. There I also met Ivan Thrash, another inspiring piosphere worker. I also enjoyed productive visits to Mkuzi where Pete Goodman shared his wildlife expertise, and Matopos where Shadrack NCube made me welcome.

The people in the Department of Livestock and Pasture Science at the University of Fort Hare were incredibly generous with their time, hospitality and patience. Difficulties with experiment design and preparation did involve some heated debate. The head of department Jan Raats remained civil when faced by this extra pressure, especially for times of such emergency from land repossession in South Africa. In retrospect, the scale of the operations that we attempted in such a short period was unrealistic (particularly in preparation for the experiment in Chapter 4), and it was unfair of me to coerce certain individuals, although, I would like to think that we parted friends.

Sue Milton, Nkobi Moleele, Jeremy Perkins, Chris Stokes, Ivan Thrash, Noel Van Rooyan and Craig Morris generously and willingly donated the piosphere data analysed in my introductory chapter. Data was also collected in person accompanied by Sarah and Bruce who, I hope, now see the method in my madness - I was right after all!

In particular I would like to thank the following for their invaluable help particularly during the fieldwork for Chapter 2. Helping with data collection was Wellington, Lethando Dziba and Dumi, in addition to Mweli, Mpendu and James who also assisted with the GPS and theodolite measurements. Peter Scogings put his excellent botanical knowledge to good use in assessment of the plant communites. Wiseman Mthozami Goqwana and Peter helped to collect defoliation data. Vuyani Bonyela was the goat herder. The Departments of Geology and of Survey and GIS at the University of Fort Hare supplied the GPS and theodolite equipment, respectively, along with advice on their use. Tony Palmer provided the aerial infrared photograph of the study site. Nick Colegrave, Trimble Navigation Europe Limited (UK), Optron (SA) and Telkom (SA) contributed towards assessment of the GPS accuracy. Nick also commented on an early draft of the chapter. Craig Morris and Tony Hunter gave advice on statistical analysis. David Baird patiently and unfailingly provided his GIS expertise. Hilary Third helped to capture the large volume of data. Visits to Fort Hare were carried out with assistance from The UK Royal Society and NRF Link Programme. Felicity Jones provided additional statistical assistance.

Kerstin Olsson was very generous and donated much of the goat physiology literature reviewed in Chapter 3. Thanks to Garry Yates for donating his extensive library of African livestock literature collected during his prestigious career with ILCA/RDP.

For the fieldwork in Chapter 4, many of the same personnel were involved as above for Chapter 2. In addition Peter spent many hours discussing how to adapt experiment design when the original plans failed. Luthando was incredibly diligent, invaluable company and a trusted friend. Wiseman was equally enthusiastic and always had a hugely infectious smile. Winston Trollope made useful comments during development of the vegetation survey. John Deag's data collection software provided inspiration for my own animal data capture software.

Thanks to Donato Bergandi, Martyn Murray, Andrew Illius and Iain Gordon for invaluable discussions regarding aspects of Chapter 5. David Baird and Paul Christie advised on statistical analysis. Thanks to Martyn Murray, David Baird, Iain Gordon and Andrew Illius for suggested improvements to earlier drafts of the manuscript. Financial support was gratefully received from the UK Government's Department for International Development under the Livestock Production Programme. I consider Chapter 5 my most prophetic. It is dedicated to Arthur C. Clarke and Stanley Kubrik, with thanks for providing a more interesting future and a pleasanter past.

Mareike Möller-Holtkamp (German), Luthando Dziba (Xhosa) and Danie Pienaar (Afrikaans) carried out translations.

Perhaps most deserving of thanks are my close friends who have had to suffer the brunt of my lamentations on the evils of Ph.D.'s. Stuart Blackman, Martyn Murray, David Baird and Lucy Odling-Smee have all been there and were understanding of the pressures. True friends indeed.

Most of all I want to thank Hilary Third, my best friend, wife and mother of our daughters, Kaya and Nadia, who also contributed with their baby innocence and rejuvenating fun. But it is Hils who gave the most. Her love, time, support and reassurance kept this thesis alive. Without her I would have given up through the difficulties of contract work and thesis running in parallel over the course of nearly 8 years of our shared life. For her dedication and companionship, this PhD is as much part hers, as it is mine, although I think her favourite bit of it is to see that it is finally finished.

ABSTRACT

This thesis explains two aspects of animal spatial foraging behaviour arising as a direct consequence of animals' need to drink water: the concentration of animal impacts, and the response of animals to those impacts.

In semi-arid rangelands, the foraging range of free-ranging large mammalian herbivores is constrained by the distribution of drinking water during the dry season. Animal impacts become concentrated around these watering sites according to the geometrical relationship between the available foraging area and the distance from water, and the spatial distribution of animal impacts becomes organised along a utilisation gradient termed a "piosphere". During the dry season the temporal distribution of the impacts is determined by the day-to-day foraging behaviour of the animals. The specific conditions under which these spatial foraging processes determine the piosphere pattern have been identified in this thesis.

At the core of this investigation are questions about the response of animals to the heterogeneity of their resources. Aspects of spatial foraging are widely commented on whilst explaining the consequences of piosphere phenomena for individual animal intake, population dynamics, feeding strategies and management. Implicated are our notions of optimal foraging, scale in animal response, and resource matching. This thesis addressed each of these. In the specific context of piospheres, the role of energy balance in optimal foraging was also tested.

Field experiments for this thesis showed a relationship between goat browsing activity and measures of spatial impact. As a preliminary step to investigating animal response to resource heterogeneity, the spatial pattern of foraging behaviour/impacts was described using spatial statistics. Browsing activity varied daily revealing animal assessment of the spatial heterogeneity of their resources and an energetic basis for foraging decisions. This foraging behaviour was shown to be determined by individual plants rather than at larger scales of plant aggregation. A further experiment investigated the claim that defoliation has limited impact on browser intake rate, suggesting that piospheres may have few consequences for browser intake. This experiment identified a constraining influence of browse characteristics at the small scale on goat foraging by relating animal intake rate to plant bite size and distribution.

Computer simulation experiments for this thesis supported these empirical findings by showing that the distribution of spatial impacts was sensitive to the marginal value of forage resources, and identified plant bite size and distribution as the causal factors in limiting animal intake rate in the presence of a piosphere. As a further description of spatial pattern, piospheres were characterised by applying a contemporary ecological theory that ranks resource patches into a spatial hierarchy. Ecosystem dynamics emerge from the interactions between these patches, with piospheres being an emergent property of a natural plant-herbivore system under specific conditions of constrained foraging. The generation of a piosphere was shown to be a function of intake constraints and available foraging area, whilst piosphere extent was shown to be independent of daily energy balance including expenditure on travel costs. A threshold distance for animal foraging range arising from a hypothesised conflict between daily energy intake and expenditure was shown not to exist, whereas evidence for an intermediate distance from water as a focus for accumulated foraging activity was identified.

Individual animal foraging efficiency in the computer model was shown to be sensitive to the piosphere, while animal population dynamics were found to be determined in the longer term by dry season key resources near watering points. Time lags were found to operate in the maintenance of the gradient, and the density dependent moderation of the animal population. The latter was a direct result of the inability of animal populations to match the distribution of their resources with the distribution of their foraging behaviour, because of their daily drinking requirements. The result is that animal forage intake was compromised by the low density of dry season forage in the vicinity of a water point.

This thesis also proposes that piospheres exert selection pressures on traits to maximise energy gain from the spatial heterogeneity of dry season resources, and that these have played a role in the evolution of large mammalian herbivores.

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SCIENTIFIC NAMES

Alphabetical list of scientific names for animals appearing in the text.

Common name (as in text)	Scientific name
Bison (North American)	*Bison bison* (Linnaeus)
Buffalo	*Syncercus caffer* (Sparrman)
Bushbuck	*Tragelaphus scriptus* (Pallas)
Bushpig	*Potamochoerus porcus* (Linnaeus)
Cattle (unspecified)	*Bos taurus* (Linnaeus)
Donkey	*Equus asinus* (Linnaeus)
Dik-Dik	*Madoqua kirkii* (Günther)
Duiker (Common)	*Sylvicapra grimmia* (Linnaeus)
Eland	*Taurotragus oryx* (Pallas)
Elephant	*Loxodonta africana* (Blumenbach)
Gemsbok	*Oryx Gazella* (Linnaeus)
Gerenuk	*Litocranius walleri* (Brooke)
Giraffe	*Giraffa cameleopardalis* (Linnaeus)
Goat (Domestic)	*Capra hircus* (Linnaeus)
Goat (Wild)	*Capra aegagrus* (Erxleben)
Grant's Gazelle	*Gazella granti* (Brooke)
Grysbok (Cape)	*Raphicerus melanotis* (Thunberg)
Hartebeest	*Alcelaphus buselaphus* (Pallas)
Hereford Cattle	*Bos taurus* (Linnaeus)
Hippopotamus	*Hippopotamus amphibius* (Linnaeus)
Impala	*Aepyceros melampus* (Lichenstein)
Klipspringer	*Oreotragus oreotragus* (Zimmermann)
Kongoni	*Alcelaphus buselaphus* (Pallas)
Kudu	*Tragelaphus strepsiceros* (Pallas)
Moose	*Alces alces* (Linnaeus)
Oryx	*Oryx beisa* (Ruppell)
Ostrich	*Struthio camelus* (Linnaeus)
Peter's Gazelle	*Gazella granti petersi* (Peters)
Reedbuck	*Redunca arundinum* (Boddaert)
Reindeer	*Rangifer tarandus tarandus* (Linnaeus)
Roan Antelope	*Hippotragus equinus* (Desmarest)
Roe deer (European)	*Capreolus capreolus* (Linnaeus)
Sable	*Hippotragus niger* (Harris)
Sheep	*Ovis aries* (Linnaeus)
Springbok	*Antidorcas marsupialis* (Zimmerman)
Steenbok	*Raphicerus campestris* (Thunberg)
Thomson's Gazelle	*Gazella thomsonii* (Günther)
Topi	*Damaliscus lunatus* (Burchell)
Tsessebe	*Damaliscus lunatus* (Burchell)
Wapiti	*Cervus elaphus* (Linnaeus)
Warthog	*Phacochoerus aethiopicus* (Pallas)
Waterbuck	*Kobus ellipsiprymnus* (Ogilby)
Wapati	*Cervus elaphus* (Linnaeus)
White-tailed deer	*Odocoileus virginianus* (Boddaert)
Wildebeest	*Connochaetes taurinus* (Burchell)
Zebra	*Equus burchelli* (Gray)
Zebu Cattle	*Bos indicus* (Linnaeus)

Sources: Estes (1991), Stuart & Stuart (1993), Kingdon (1997), IEA (2000)

ACRONYMS AND ABBREVIATIONS

Standard units, terms for statistical tests and variable names not included.

acronym or abbreviation	Definition
ADDS	Africa Data Dissemination Service
AIC	Akaike Information Criterion
ANOVA	Analysis of Variance
BOA	Board on Agriculture
C++	C Object-Oriented Programming Language
CEP	Circular Error Probable
CV	Coefficient of Variation
DLL	Dynamic link library
DM	Dry matter
DSR	Dry season range
DWR	Dry-Weight-Ranking method
ESRI	Environmental Systems Research Institute
EWMA	Exponentially Weighted Moving Average
FAO	Food and Agriculture Organization (United Nations)
Fig.	Figure
FMR	Field metabolic rate
GIS	Geographic Information System
GLM	Generalized Linear Model
GPS	Global Positioning System
GUD	Giving up density
HAL	Herbivore Assessment Lexicon
IFD	Ideal Free Distribution
ILCA	International Livestock Center for Africa
ILCA/RDP	Joint Ethiopian Rangelands Development Project
IRC	International Rangelands Congress
KNP	Kruger National Park
LAT	Latitude
LE	Livestock equivalents
LONG	Longitude
Ma	Million years ago
M A.S.L.	Metres above sea-level
Max(a,b)	Maximum value of a and b
MLE	Maximum Likelihood Estimation
MVT	Marginal Value Theorem
N and n	Number / population size
N(μ,σ)	Normal distribution
NDVI	Normalised Difference Vegetation Index

ACRONYMS AND ABBREVIATIONS (continued…)

acronym or abbreviation	Definition
NMSU	New Mexico State University
NRF	National Research Foundation (South Africa)
NW	Northwest
ODI	Overseas Development Institute (United Kingdom)
OFT	Optimal Foraging Theory
PMB	Pietermaritzburg (South Africa)
RDP	Rangelands Development Project
REML	Residual maximum likelihood method
RMS	Root Mean Square
SA	South Africa
SE	Southeast
S.E.	Standard error
SR	Stocking rate
UBRule	“Use Biomass” rule
UK	United Kingdom
UNP	University of Natal, Pietermaritzburg (South Africa)
US	United States (of America)
W	Animal weight
WSR	Wet season range

CHAPTER 1 - INTRODUCTION

1.1 Introduction

> *When Coleridge's Ancient Mariner said 'Water, water, everywhere, nor any drop to drink', he gave a fair picture of the global situation. The 'drop to drink' is a hundredth of a percent of the world's water: about one drop in every bucketful. The proportion of planetary water that is fresh is rather larger - around 3.5 per cent - but most is frozen in the ice caps and mountain glaciers. As sea water is corrosive and toxic to land-based animals and plants, nearly all of the water that we use must come from that precious one hundredth of a per cent.*
>
> Ball (2000)

The small proportion of global water that is available for plant and animal consumption is not distributed evenly in time and space, especially in the earth's drier zones. As a result livestock managers in semi-arid areas need to cope with the insecurities arising from climatic variation and frequent droughts (*e.g.*, Scoones 1994). Additionally, growing evidence shows that they also need to carefully manage watering points in order to preserve key resources required for the survival of animals when constrained to their dry season range (Illius & O'Connor 2000). Imprudent depletion of winter forage can be catastrophic (*e.g.*, Sinclair & Fryxell 1985).

Mammalian herbivores require drinking water to differing degrees (*e.g.*, Western 1975). The congregation of these animals around focal points on rangeland from where they acquire this supplementary water results in a concentration of environmental impacts (Andrew 1988). The subsequent land modification is considered by some to be localised degradation (Perkins & Thomas 1993b) or desertification (*e.g.*, Dean *et al.* 1995), and is especially noticeable in arid and semi-arid landscapes. The affected area has been termed a piosphere (Lange 1969). Gradient sampling strategies have been used to quantify the piosphere effect (*e.g.*, Tolsma *et al.* 1987), revealing remarkable consistency in their mathematical characterisation (Graetz & Ludwig 1978). How much of this response is due to the animal component, independently and via interaction with other components, and how much influence each component has on the system dynamics has yet to be determined.

Part 1 of this introductory chapter (Section 1.1) defines the piosphere effect and deals with its ecology. The second part (Section 1.2) is a review of modelling literature relevant to piospheres. This part is adapted from Thrash & Derry (1999) and includes a review of more recent literature (Section 1.2.11) and further investigates piosphere characteristics by application of a generalized piosphere model to piosphere data sets collected for African savanna. The final part (Section 1.3) describes the objectives and structure of this thesis.

1.1.1 Spatial resource heterogeneity

Rainfall infiltration and the spatial redistribution of runoff water are the predominant factors determining patterns in semi-arid vegetation (Friedel 1990, Maestre *et al.* 2003), but grazing impacts also contribute to the generation and maintenance of spatial heterogeneity (Adler *et al.* 2001). It is probable that animals must therefore respond to this spatial variation in their food distribution (Pyke 1984) implying a capacity for assessment of resource patchiness (Ford 1983). This assessment must operate at a scale that is functionally meaningful to each animal (Wiens 1976) and will elicit a response relative to how much they are affected by the fragmentation of their habitat (Hester *et al.* 1999).

It is a pervading question in spatial ecology, yet little is known about the scale or scales that this assessment operates (Levin & Pacala 1997) to dictate foraging behaviour and landscape utilisation. Our assessments of animal behaviour must be in terms of function rather than resource organisation (Li & Reynolds 1995) to ensure quantification of the animal’s perceived heterogeneity of its environment (Wiens 1976, Bailey *et al.* 1996).

1.1.2 Optimal spatial foraging

Large mammalian herbivores prospect their environment for an optimal diet (Illius & Gordon 1993), but because they perceive their environment at differing scales

(Kotliar & Weins 1990, With 1994, Levin & Pacala 1997), they also differ in the cues that they use to do so (Eztenhouser *et al.* 1998).

The landscape components that may act as potential cues for animal behaviour are present across regional, landscape and plant community scales (Senft *et al.* 1987), providing a hierarchical framework for animal foraging decisions (Orians & Wittenberger 1991). However, while animal diet selection may be sensitive to the small-scale variation in food distribution (Edwards *et al.* 1994, Turner 1999), there is little evidence in support of daily decisions at large scales, other than the apparent behaviours of seeking shade and water (Senft 1989, Cowley 2001).

Foraging strategies within landscapes seek to maximise daily energy gain (Fryxell *et al.* 2001) which is sufficient to motivate large-scale animal movements (Wilmshurst *et al.* 1999). It follows that animals are expected to make decisions about diet selection based on the balance between forage profitability (a function of the satisfaction of nutritional requirements) and the distance travelled to reach this forage. This is encapsulated by Optimal Foraging Theory (Stephens & Krebs 1986) which predicts that animals assay the energy balance underlying travel and intake against the profitability of their resource (Bailey *et al.* 1998).

Resource profitability is energy gained in excess of costs, the rate of which is constrained by the logistics of food detection and ingestion. Intake rate constraints depend on the initial locating of food items, the travel between those food items, and, once arrived, the speed of cropping, chewing and swallowing of food (Spalinger & Hobbs 1992). Feeding strategies also need to account for the instantaneous decline in intake rate associated with the successive removal of food from a single location. The Marginal Value Theorem (Charnov 1976) predicts that feeding should only occur for locations while resource profitability is above the environmental average. If all the profitable locations are exploited, it can be said that there has been a degree of *matching* between animals and their resource, and the resulting spatial pattern of resource utilisation will describe the Ideal Free Distribution (Fretwell & Lucas 1970).

1.1.3 Animal water dependency

It is evident that water dependency means that the opportunity for an animal to forage is defined by the interval between drinking events (*e.g.*, Tolkamp *et al.* 1999). Thus, the need to forage is constrained by the requirement to drink, and ranging patterns determined by foraging behaviour are constrained by the location of water to differing degrees as dictated by animal water dependency (Ayeni 1975). Naturally, foraging ranges are most constrained during the dry season (Ayeni 1975). The obvious question is whether water requirement is related to the distance that animals are typically observed from water during the dry season. There is some evidence for this in birds (Harrington 2002), but not large mammalian herbivores.

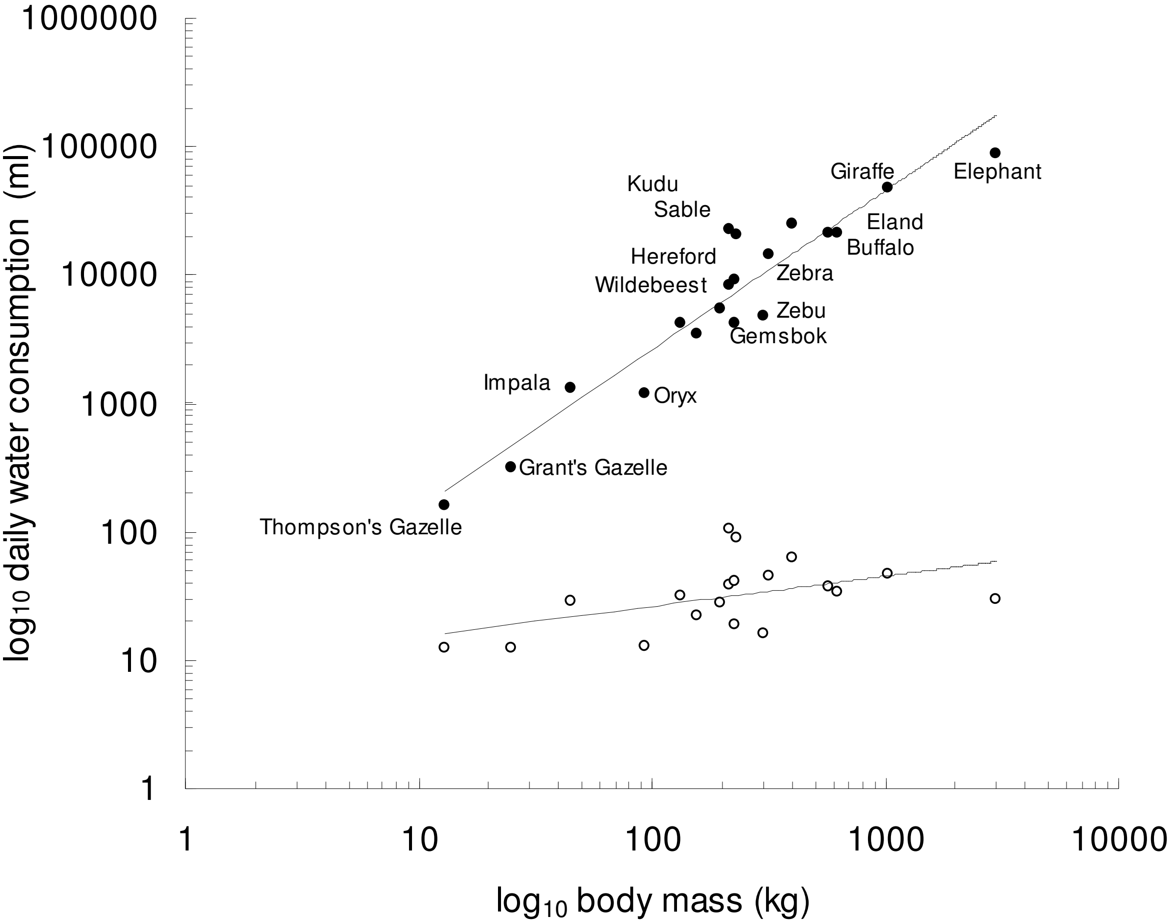
Water dependent	Feeder type	Water independent	Feeder type
Zebra	G	Oryx	G
Wildebeest	G	Eland	B
Hartebeest*	G	Grant's gazelle	M/B
Thomson's gazelle	M/G	Giraffe	B
Buffalo	G	Ostrich	B
Elephant	M	Lesser Kudu	B
Cattle	G	Gerenuk	B
Sheep	G	Dik-Dik	B
Goat	M		
Donkey	G		
Warthog	G		
Waterbuck	G		
Reedbuck	G		
Hippo	G		

*water independent in some cases

Table 1.1: Distribution of feeding strategies (Grazer, Browser and Mixed) between water-bound and non-water-bound communities (*after* Western 1975).

We know that free-ranging, herbivorous animals congregate around surface water for the simple fact that they need to drink it (*e.g.*, Senft 1989). Grazers are most dependent on watering points for their drinking water and therefore tend to need more access to supplementary drinking water than do browsers (Western 1975), with the notable exception of the oryx, which famously supplements its water with that stored in Tsama melons (*Citrullus lanatus*) (Knight 1995a). Water independent animals are mainly browsers because of the greater water storage within their food (Estes 1991) than that provided by comparatively dry grass (Table 1.1). Grazers also tend to be larger in size as an adaptation to the low quality of their diet (Gordon & Illius 1996), which carries with it a larger total water requirement than smaller animals (Taylor 1968), although there are notable exceptions (Table 1.2).

After accounting for body size (W, kg), it is apparent that factors other than mass are involved in determining water requirements (Fig. 1.1). Re-expressing water consumption in terms of unit mass of water turnover ($\log_{10} y = \log_{10} 8.831 + 0.377 \log W^{0.86}$, $R^2 = 0.40$, $F_{1,17} = 13.06$, $P<0.01$, but see Chapter 3 Section 3.6) and unit of metabolic mass ($\log_{10} y = \log_{10} 8.831 + 0.487 \log W^{0.75}$, $R^2 = 0.54$, $F_{1,17} = 21.80$, $P<0.001$) confirms a physiological basis for water requirement above the basic need to support a larger body.



(*Data source*: Bothma 1996, Taylor 1968, Young 1970)

Fig. 1.1: Log-log plot of drinking water consumption (y) across a range of body sizes (W), expressed in ml/day (closed circle, $\log_{10} y = \log_{10} 8.831 + 1.237 \log_{10} W$, $R^2 = 0.89$, $F_{1,17} = 140.70$, $P < 0.0001$) and ml/kg/day (open circle, $\log_{10} y = \log_{10} 8.831 + 0.237 \log W$, $R^2 = 0.19$, $F_{1,17} = 5.16$, $P < 0.05$).

Species (alphabetical)	W (kg)	Water requirement per unit mass (ml/kg)	Source	W (kg)	Distance from water (km)	Source
Buffalo	625	32.71	Young 1970	500	1.00	Western 1975
				N/A	4.90	Ayeni 1975
				450	7.5	Cumming & Cumming 2003
Bushbuck				30	3.1	Cumming & Cumming 2003
Bushpig				50	3.6	Cumming & Cumming 2003
Cattle (unspecified)	400	42.25	Bothma 1996	277	4.54†	Western 1975
				225	5.9	Cumming & Cumming 2003
Donkey				130	2.20	Western 1975
				120	4.9	Cumming & Cumming 2003
Duiker				15	2.75	Cumming & Cumming 2003
Eland	575	37.00	Young 1970	340	6.8	Cumming & Cumming 2003
Elephant	3000	29.53	Young 1970	3000	1.66	Western 1975
				N/A	3.83	Ayeni 1975
				1725	11.7	Cumming & Cumming 2003
Gemsbok	225	18.80	Young 1970			
Giraffe	1030	46.41	Young 1970	725	10.62†	Western 1975
				N/A	3.63	Ayeni 1975
				828	9.2	Cumming & Cumming 2003
Goat / Sheep	53	18.2‡	MacFarlane & Howard 1972	16	3.43†	Western 1975
				42	3.4	Cumming & Cumming 2003
Grant's Gazelle	25	12.50¥	Taylor 1968	50	8.29†	Western 1975
Grysbok				6	1.8	Cumming & Cumming 2003
Hereford Cattle	225	41.10¥	Taylor 1968			
Impala	45	28.89	Young 1970	45	3.00	Western 1975
				N/A	6.21	Ayeni 1975
				45	3.5	Cumming & Cumming 2003
Klipspringer				10	2.1	Cumming & Cumming 2003

Table 1.2 (*and overleaf*): Literature values for body size, water requirements and foraging distance from water for African large mammalian herbivores.

Table 1.2 (*Continued*)

Species (alphabetical)	W (kg)	Water requirement per unit mass (ml/kg)	Source	W (kg)	Distance from water (km/kg)	Source
Kongoni				136	2.03†	Western 1975
				N/A	5.30	Ayeni 1975
Kudu	215	105.12	Young 1970	135	5	Cumming & Cumming 2003
Oryx	92.5	13.00¥	Taylor 1968	167	1.74	Western 1975
				N/A	6.15	Ayeni 1975
Ostrich				114	12.93†	Western 1975
				N/A	4.53	Ayeni 1975
Peter's Gazelle				45	5.53	Ayeni 1975
Reedbuck				40	3.4	Cumming & Cumming 2003
Roan Antelope				220	5.9	Cumming & Cumming 2003
Sable	230	88.70	Young 1970	185	5.6	Cumming & Cumming 2003
Springbok				39	3.4	Cumming & Cumming 2003
Steenbok				10	2.1	Cumming & Cumming 2003
Tsessebe				110	4.7	Cumming & Cumming 2003
Thomson's Gazelle	13	12.50¥	Taylor 1968	20	1.48	Western 1975
Warthog				45	3.5	Cumming & Cumming 2003
				N/A	3.63	Ayeni 1975
Waterbuck				160	5.3	Cumming & Cumming 2003
				N/A	3.25	Ayeni 1975
Wildebeest	215	38.61	Young 1970	165	2.16†	Western 1975
				165	5.4	Cumming & Cumming 2003
Zebra	315	45.71	Young 1970	238	4.77†	Western 1975
				N/A	5.53	Ayeni 1975
				200	5.7	Cumming & Cumming 2003
Zebu Cattle	300	16.10¥	Taylor 1968			

† mean of studies from 1968, 1969 and 1973 dry seasons ‡ allometric prediction (see Chapter 3 Section 3.4) ¥ Taylor (1968) used captive animals N/A Ayeni (1975) omits body sizes

This implies that the relationship between water location and animal foraging range is most affected by adaptations leading to improved water conservation (see Chapter 3 Section 3.4), but may also be modified by adaptations to diets with differing water content.

1.1.4 Foraging range

So are adaptations related to how far animals travel from water? The data is scant: there is no obvious relationship between water requirement per unit mass of water turnover (ml/W$^{0.86}$) and foraging range (km), ($F_{1,19}$=1.53, P=0.23, *not shown*). Expressing the data per unit of mass normalises observations for different sized animals (Fig. 1.2). This was only possible for overlaps between the four unrelated data sets presented in Table 1.1, but involved discarding data that did not occur in co-ordinate pairs. Also, distance observations were of wild individuals while some of the requirement measurements were made under experimental conditions on captive stock (*e.g.*, Taylor 1968).

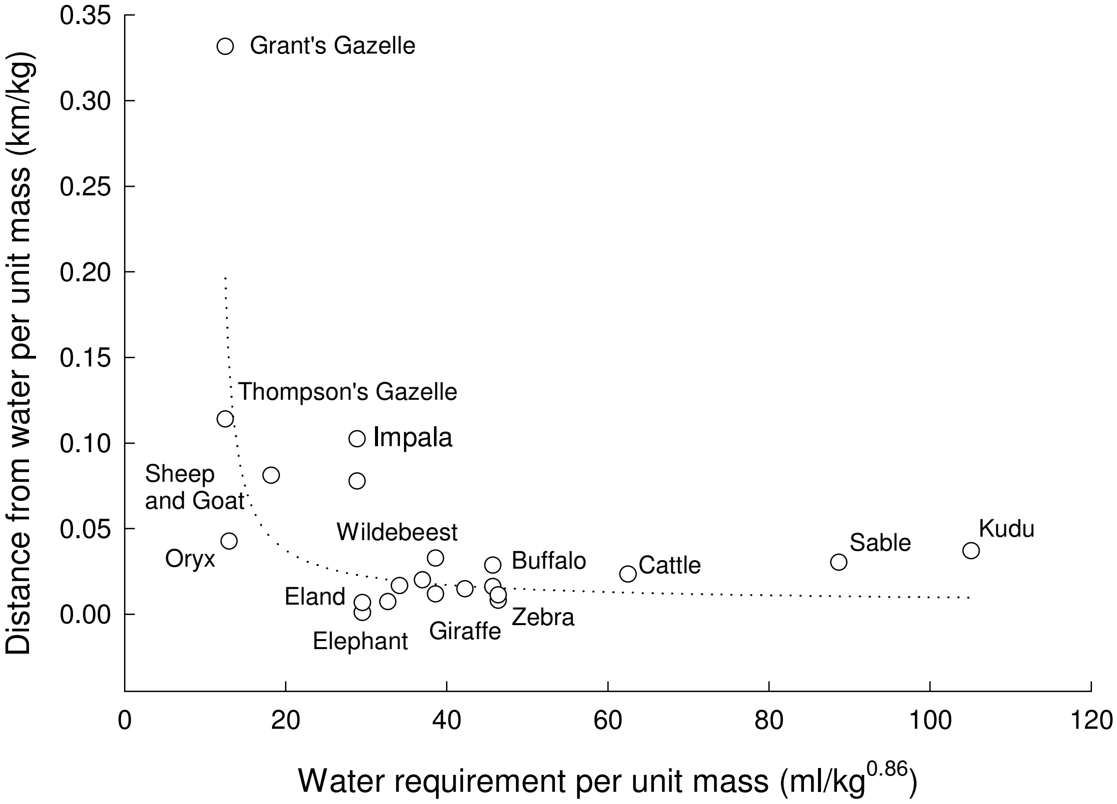


Fig. 1.2: Can water requirement predict foraging distance from water? Dotted line shows a best-fit reciprocal logarithm plot (R^2 = 0.59, F1,19=27.12, P<0.0001).

Although regression of the data plotted in Fig. 1.2 proves significant, it's predictive value is limited because of the outlier for the small bodied Grant's Gazelle (25 kg). From this it would be not be possible to state that animals requiring the least water travel further in relation to their size. Water requirements scale with body weight raised to the power of 0.82 (MacFarlane & Howard 1972) implying that smaller animals have larger water requirements relative to their body size than larger animals. But, it does not necessarily follow that the most water dependent animals, whether that is the largest species, or those with the driest diets, will be found closest to water (particularly for closely spaced water sources, Redfern *et al.* 2003).

Wildlife have a hierarchy of water use, with elephants taking priority at the individual waterhole (Owen-Smith 1996), with bulls dominating breeding groups (Parker 1997). Landscape features (Jarman 1972), dietary and mineral preferences (Weir 1967, Child *et al.* 1971, Ayeni 1977), association with other species, or avoidance of predators and competition (Hitchcock 1996) and tourists (Weir & Davison 1965) and larger or dominant species, especially elephants (Peters 1983, Parker 1997) may all influence where an animal spends most time foraging. An increase in the frequency of waterholes introduces bulk grazing into areas that were previously refugia for more water-independent, and typically rare, species (Owen-Smith 1996). As well as depleting forage resources, the influx brings with it a following of predators. The result is displacement or local extinction of the rare species, as seen for Roan antelope on the northern plains of Kruger National Park, South Africa (P. Funston *pers. comm.*, Owen-Smith 1996).

1.1.5 Spatial impacts

> *Grass grows by the inch and is ruined by the foot*
> From a sign in Bekonscot Model Village, Beaconsfield, England

Animals move between places used for feeding and places used for drinking. The localisation of impacts associated with the congregation of animals at water points and the declining grazing pressure with distance from water gives rise to a utilisation gradient termed the *piosphere* pattern (*see* review by Thrash & Derry 1999). The name 'piosphere' was introduced by the Australian Robert Lange when describing sheep movement in shrubland west of Port Augusta (Lange 1969). In the name he wished to imply an area of influence arising from the need for animals to drink water.

The need to find drinking water is most extreme in arid and semi-arid areas during the dry season when this water is often only available via artificial supply (Ayeni 1975), usually pumped from below ground using wind or oil powered pumps and stored in tanks for release into troughs (*pers. obs.*). If we can represent the watering point as a hub, then distances from the hub can be marked off with concentric rings as shown in Fig. 1.3.

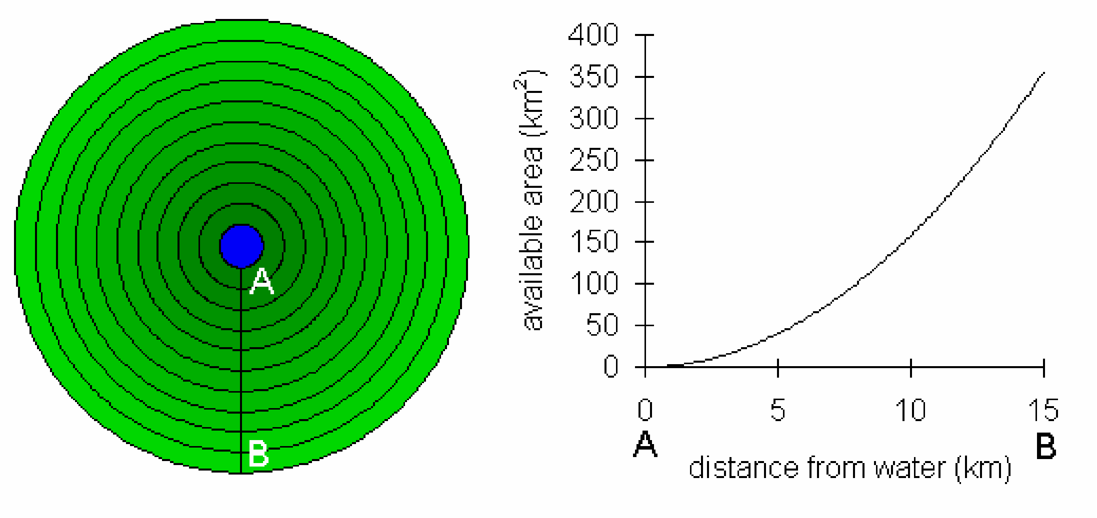


Fig.1.3: The reduction in available foraging area on approaching a watering point.

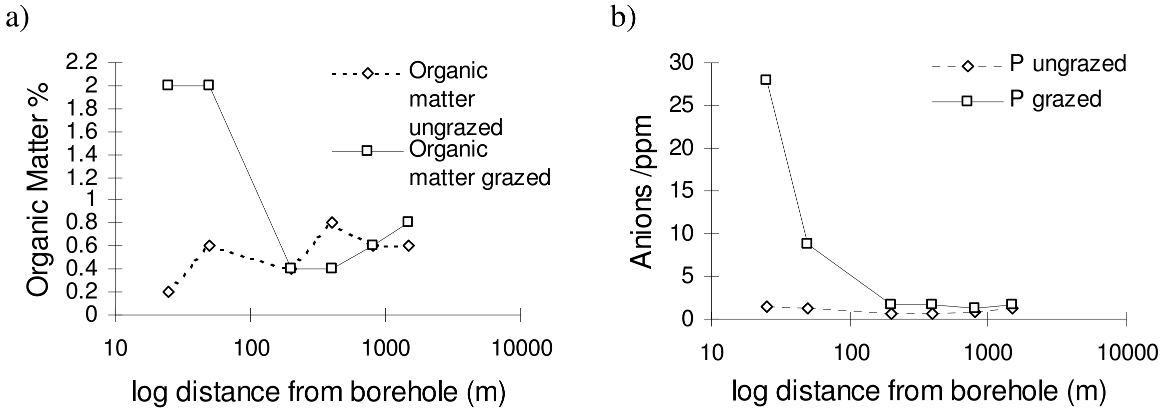
The space within each of these areas *between* the rings is the available foraging area at that distance from the water, equal to $\pi x^2 - \pi(x-1)^2$ where x is a discrete distance interval from water. From this it can be seen that the available area decreases rapidly on nearing the watering point (Perkins 1991) and as animals move in towards it, their cumulative foraging effort becomes concentrated into less space. The result is a gradient of stocking pressure, which is greatest nearest the watering point and decreases as a function of distance from it (Andrew 1988). For herbivores, along with the gradient of stocking pressure comes a gradient of grazing intensity, greatest at the centre and least at the furthest distance from water an animal may travel during the period before returning to drink. This defines the extent of the piosphere (Graetz

& Ludwig 1978). This is a maximal model for available foraging area at distance from water. Real-life examples are more likely prone to restriction by landscape features, *e.g.*, aspect, fences, watercourses and other boundaries, and may not conform to geometric prediction (*e.g.*, Weir 1971) because of variations in the animal behavioural response to wind, topography and spatially heterogeneous vegetation (Nash *et al.* 1999).

By definition then a piosphere may occur at any point in the landscape where there exists a focal point for animal convergence. This has been mostly documented for artificial watering points in semi-arid livestock systems (*e.g.*, Foran 1980, Andrew & Lange 1986a, 1986b, Stroleny & Mentis 1989) and naturally occurring waterholes in wildlife systems (Goodman 1982, Thrash *et al.* 1991, Gaylard *et al.* 2003), but for large herbivores generally and livestock in particular, similar patterns occur around other foci, for example, shady trees, rest sites and saltlicks (Andrew 1988). Smaller animals may add to the piospheres of larger animals, or create their own, like the areas surrounding rabbit warrens, prairie dog towns, termitaria, nesting colonies of rooks and reefs that shelter tropical fish, to name but a few (Andrew 1988). As animals tend to frequent particular watering points along rivers, most probably due to ease of access, semi-circular piospheres also occur along their banks.

The utilisation gradient in forage biomass provides feedbacks for animal foraging and intake, and the redistribution of nutrients and seeds in the landscape (*see* Thrash & Derry 1999 plus Redfern *et al.* 2003). In addition to foraging activity, trampling exposes topsoil by destroying canopy structure and disturbing litter, increasing soil compaction and reducing infiltration of rainwater (Kelly *&* Walker 1976, Thrash 1997). Reduced microtopography limits collection of runoff water and nutrients (Nash *et al.* 2003) and increases bare soil by removal of plant-soil interactions that maintain vegetated patches (Rietkerk *et al.* 2000). Exposed topsoil dust is eroded by wind action or fixed by rainwater into a soil crust (Andrew & Lange 1986a), further reducing infiltration and increasing run-off (Beukes & Ellis 2003, Thrash 1997). Soil dust collects on leaf surfaces where it inhibits stomatal closure or photon entrapment and absorption, and thus photosynthesis and transpiration (Andrew & Lange 1986a).

At the centre of the piosphere, experiencing the highest herbivore pressure, trampling usually generates an area reduced to nothing but mud (Thrash & Derry 1999) called the *sacrifice zone* (Graetz & Ludwig 1978). Defecation and urination elevate nutrients (Fig. 1.4), affecting herbaceous production (especially phosphorus-availability gradients, Turner 1998a, 1998b) or to levels above the toxicity tolerance of plants (Perkins & Thomas 1993a). Nutrient levels are also higher because trampling of lichen crusts reduces nitrogen fixation (Andrew & Lange 1986a) as a function of distance from water (Hodgins & Rogers 1997).



(*Data source* Perkins 1991)

Fig. 1.4: Elevated soil nutrients are a product of defecation and urination. Organic matter (a) and Phosphorous (b) are examples of this.

Both univariate (*e.g.*, Graetz & Ludwig 1978) and multivariate (*e.g.*, Perkins 1991) techniques have been used to analyse these data. Ordination (ter Braak & Prentice 1988) and Principal Components Analysis (Jongman *et al.* 1995) can show which environmental variables have dominant effects by separating species-by-site data from environmental data (*e.g.*, distance from water, soil moisture and nutrients. *e.g.*, Fernandez-Gimenez & Allen-Diaz 2001, Heshmatti *et al.* 2002).

1.1.6 Plant response

Plant response within the piosphere is a local effect, largely determined by edaphic and environmental factors (Kalikawa 1990, Makhabu *et al.* 2002). The dynamics of savanna vegetation depend on the competition between plants for light and space to grow in, soil nutrients and soil water, whereas compositional changes depend on the life histories of individual plant species present and on their location along the gradient of grazing pressure (Lailhacar *et al.* 1993). Therefore, disturbances by herbivores bias this competition according to plant life histories (Lailhacar *et al.* 1993). For example, the growth of some grasses is promoted by grazing but reduced in others (Andrew *&* Lange 1986b). Species may be described as 'increasers' or 'decreasers' or unaffected (*e.g.*, Rogers & Stride 1997). Landsberg *et al.* (1997) found Australian biota evenly split into 38% increasers and 33% decreasers. The result is that, a grazing gradient will not only be expressed via a defoliation gradient but also by a change in the composition of the vegetation. As a result, piospheres have been used (Moleele 1994, Hosten & West 1995, Fernandez-Gimenez. & Allen-Diaz 1999, Lind *et al.* 2003) to test Clementsian succession (Connell & Slatyer 1977), State and Transition (Westoby *et al.* 1989) and nonequilibrium models (Ellis & Swift 1988) of rangeland vegetation dynamics (see Section 5.5.2). Within the herbaceous layer, poor quality, hardier (centripetal) increaser grasses will be favoured by the high grazing pressure towards the centre, displacing higher quality, less hardy (centrifugal) decreasers to the perimeter of the piosphere (Perkins & Thomas 1993a). Near the centre one might expect to find a short sward of annual grasses, moving out to a taller stand of annuals with some perennials, and open grassland of decreasers farthest away, being predominantly perennials (Fig. 1.5). This is a rule of thumb, an aid to a conceptual model, for which some studies are in good agreement (*e.g.*, Friedel 1988, Thrash *et al.* 1993), and others contradict wholly (*e.g.*, Stroleny & Mentis 1989, van Rooyan *et al.* 1994, Nangula & Oba 2004), or at least in part (*e.g.*, Foran 1980, Andrew & Lange 1986b, Heshmatti *et al.* 2002). Proximate sites experiencing similar grazing pressures may differ in plant composition through soil differences (*e.g.*, sandveld pans versus clay pans, Makhabu *et al.* 2002) without the effect of distance from water within sites.

All piospheres do not match the conceptual model because of complicating factors such as grazing-induced vigour (Andrew & Lange 1986b). Clearly, the community response to disturbance is complex (Perkins & Thomas 1993a). In addition, ‘palatability’ is often used in association with diet quality, but is subjective, based on our assumptions about the desirable qualities of forage, and the comparative qualities of proximal forage (Illius *et al.* 1996a). A mechanistic understanding of animal diet is better interpreted in terms of nutritional optimality (*e.g.*, Owen-Smith 1994).

Compositional changes detected using multivariate analysis and direct measurements tend to negatively reflect increasing grazing pressure towards water (*e.g.*, Thrash *et al.* 1993), reaching a maximum at distances from the watering point where the piosphere is not detectable through subsequent measurement of species.

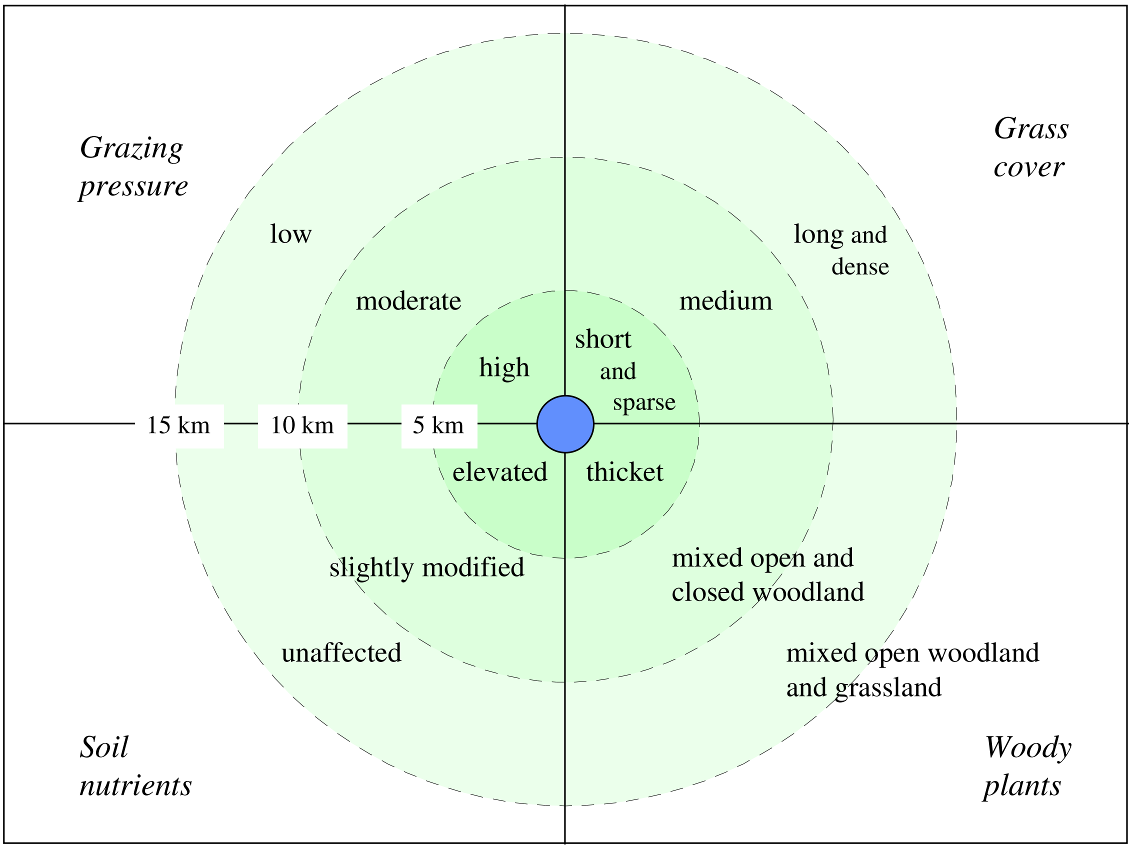


Fig. 1.5: Diagrammatic illustration of how distance from permanent water is an important determinant of the habitat diversity of an area. Adapted from Collinson (1983).

The extent of the impact as reflected by the response of a measured variable, and our interpretation, depends upon which variable is being measured (Fernandez-Gimenez & Allen-Diaz 1999), when it is being measured (*i.e.*, in which season and the age of the site) and where it is being measured (*i.e.*, dependencies on climate and vegetation type). For example, a gradient may be generated in soil surface characteristics up to only a few tens of metres away from a watering trough (Andrew & Lange 1986a), whereas trends in herbaceous plant basal cover may be detected up to 7 km from the focal point (Thrash *et al.* 1991), and 'desert patches' (areas of exposed soil around well sites) have been reported to have radii of 30 km and 50 km (Glantz 1977 and Rapp 1976, respectively, cited in Hanan *et al.* 1991).

In addition to herbaceous vegetation changes, high grazing and trampling intensities towards the centre deplete grass cover of shorter species allowing shrub and tree growth to encroach in those areas fuelled by the centripetal carriage of shrub and tree seed in fæces (Perkins & Thomas 1993a). Changes in herbaceous cover tend to be more consistent across all studies, essentially because of the sacrifice zone. Woody cover is more variable between regions of differing climate, soil and vegetation types, and management (*e.g.*, compare the Kalahari, Tolsma *et al.* 1987, with Kruger National Park, Gaylard *et al.* 2003). Cattle ranching can produce piospheres that feature a band of shrubs in the near vicinity of a borehole (Kalahari 20-400 m , Perkins 1991; Tanzania 300-2500m, Tobler *et al.* 2003). For savanna, encroachment may displace palatable leaf-succulent shrubs in favour of unpalatable woody species (*e.g.*, in the Kalahari, Moleele & Perkins 1998 and in the Succulent Karoo, Riginos & Hoffman 2003). A wildlife equivalent typically lacks a central woody band because the effect of elephants and other browsers is to override this bush encroachment and open up the area. This in itself leads to a gradient in shrub density (extending to 2.8 km from the watering point, Brits *et al.* 2002) or tree damage (Gaylard *et al.* 2003). Cowley (2001) found quite different rates of woody cover change for separately stocked sheep and kangaroo compared to mixed stock. Bush encroachment may also be suppressed anthropogenically around settlements (Fernandez-Gimenez & Allen-Diaz 2001). Anti-herbivory responses may reduce effective forage availability (Cooper & Owen-Smith 1986). Although not reported to occur in response to the grazing gradient of the piosphere, increased chemical protection (Whitham *et al.* 1991) and spinescence (Dangerfield *et al.* 1996) occur in woody species under concentrated grazing.

The processes that generate, maintain and modify utilisation gradients are dependent on temporally dynamic quanta (*e.g.*, rainfall volume and animal density, van Rooyan *et al.* 1990, Parker & Witkowski 1999). This would be expected to give rise to temporal variation in piosphere extent and the shape of the response, but not sufficient to restore the system to its previous state (Parker & Witkowski 1999, Rietkerk & van de Koppel 1997, Rietkerk *et al.* 1997). However, Perkins has consistently argued that the Kalahari is more resilient to permanent modification, and that restoration is possible (*e.g.*, Perkins & Thomas 1993b). For example, bush encroached zones may revert to open savanna (Perkins 1996), even though they have been noted to spread outwards during development (Perkins 1991). During the dry season some of the piosphere characteristics, such as the amount of defoliation of the forage will reach its maximum. The nature of some of those relationships will then change for the wet season; for example, grass growth will increase the herbaceous cover and therefore decrease the amount of bare soil (van Rooyan *et al.* 1994). So although there will be an overriding tendency for the piosphere to grow out, depending on climate and stocking rates (Heshmatti *et al.* 2002), there will also be a seasonal flux in piosphere dimensions, and complexity from site-specific sensitivity to degradation (Perkins & Thomas 1993b), making it difficult to assess the extent of impact. It is therefore unfortunate that no long-term piosphere data exists but only a few years of basal cover measurements made at artificial watering points in the Kalahari (van Rooyan *et al*. 1990, 1994; Parker & Witkowski 1999 was not a gradient analysis), which generally followed rainfall levels suggesting that when monitoring the piosphere effect it is important to account for climate (KNP 1997).

1.1.7 Management

Justification and siting of artificial water sources, especially in Game reserves and other protected areas within semi-arid regions, has never been a more contentious issue in Africa than at present. Some sites have undergone a holistic re-evaluation of water resource management (*e.g.*, Kruger National Park), for which managers have had to account for the external pressures that also tax the water supply, *i.e.*, rivers running in to game reserves get tapped and depleted by human intervention (H.Biggs *pers. comm.*, Braak 1997). Decisions then taken to supplement that inadequate supply must be informed with respect to the consequences of supplementary water provision (Braak 1997). Central to this discussion is the large-scale damage to the landscape from water provision characterised as the piosphere effect. Previous management policies typically advocated an even distribution of watering points to increase the carrying capacity of the land by accessing waterless zones and evenly spreading out the grazing pressure (*e.g.*, Kalahari Gemsbok National Park and the Northern Plains of Kruger National Park). This has resulted in high borehole densities in the Kalahari (Perkins 1996) and a decline in water independent species (Walker *et al.* 1987, Owen-Smith 1996).

The Botswana government erected the infamous veterinary cordon fences to separate wildlife and livestock, impinging on the Central Kalahari Game Reserve (*e.g.*, Owens & Owens 1986). The little that remains of the reserve is increasingly under threat from cattle farming. As there is no drinking water in the Kalahari sandveld, commercial ranchers are opening up areas that were previously unusable by drilling boreholes (Perkins 1991). The piospheres that resulted have been measured over 30 km in diameter and are visible from satellites (Hanan *et al.* 1991). Suggestions to increase borehole separation have been ignored, and Botswana's New Agricultural Policy has recently reduced the recommended distance between boreholes from 8 km to 4 km (J.S.Perkins *pers. comm.*).

The sacrifice zones for dams such as found in Kruger National Park have been found to extend for nearly half a kilometre (I.Thrash *pers. comm.*). The loss of this vegetation to primarily trampling is an issue in itself but perhaps more important is that the influence of these dams on the herbaceous cover is still apparent over seven kilometres from the watering point (Thrash *et al.* 1991). This implies that if watering points are located too close to one another, there will be an overlap of their piospheres and overall reduction in the forage potential of the grassland (de Leeuw *et al.* 2001). Evidence for this is given by a low grazing intensity zone above 1.6 km from water originally identified (Van der Schijff 1959), but which is absent in more recent studies (Thrash *et al.* 1993, Thrash 1998b). In Mkuzi Game Reserve, Natal, too high a frequency of water provision has been shown to result in the destruction of refugia for rarer species (*c.f.* Kruger National Park), and the loss of species diversity (Goodman 1982). There is also a belief that this leads to instability in the dynamics of the system as a whole (Goodman 1982). In livestock scenarios, crowding of watering points, feed troughs etc. is also thought to result in the loss of forage abundance and pasture quality (*e.g.*, Verlinden *et al.* 1998). The problem is now at a larger scale than the individual piosphere unit within the landscape, dependent on the extent of the impact associated with each piosphere and the number of piospheres involved (Owen-Smith 1996).

There are lessons learned from past strategies of even distribution of permanent water points throughout a protected area,

i. A change in the cover, biomass and species composition of plants for a certain radial distance around the newly established water points.
ii. An increase in soil erosion on susceptible soils for a certain radial distance around the water point.
iii. A reduced spatial heterogeneity of the landscape.
iv. A reduction in dry season and drought food reserves.
v. A gradual decline, and possible local extinction of animal species with a greater degree of water independence.
vi. A decreased temporal stability of large herbivore populations.

Points (i) and (ii) are processes causing localised rangeland degradation. The last four points are a function of watering point distribution and watering point saturation now considered counterproductive for the re-establishment and maintenance of the pristine system of optimal biodiversity stated as the desired target for contemporary management practice (Pienaar *et al.* 1996). Managers are considering the landscape in terms of integrated dynamic watering point units (Goodman 1982, Collinson 1983, Perkins & Thomas 1993b, Owen-Smith 1996).

1.1.8 Permanency of effect

Most authors agree that detrimental impacts result from too high a frequency of watering points. Where the literature tends to polarise is over the issue of whether the impact is dynamic or static, permanent or temporary, and if the original rangeland condition may be restored, or is irretrievable.

Desertification has become a broadly used term to describe a permanent loss of rangeland functionality (Dean *et al.* 1995), whereas other authors prefer the term 'dryland degradation'. Perkins & Thomas (1993b) have captured the essence of the argument involving piospheres in the ongoing desertification/degradation discourse with their paper title *Spreading deserts or spatially confined environmental impacts*? They incline towards 'spatially confined environmental impacts', describing piospheres as being complex and dynamic, with dimensions a function of the interaction between stocking rates and environmental factors. Spread of the effect is probably mediated by natural processes, (*e.g.*, physical suppression of sacrifice zone growth by the bush zone for Kalahari examples) with an overall dominance by climatic variability (but see Section 5.5.2), thereby diminishing any detrimental impacts. Much of their argument disputes Botswana's New Agricultural Policy, in favour of traditional pastoral practices.

While some authors conclude inevitable desertification resulting from high density stocking practices (*e.g.*, Sefe *et al.* 1996), other reports show minimal, or no existence of a piosphere effect at all (*e.g.*, Hanan *et al.* 1991), usually in support of claims that an incursive activity (*e.g.*, deep-drilling for borehole water) is not leading to degradation. The failure to detect a piosphere may have originated from experimental methods that do not resolve the scale of effect with the variables being measured. Examples include dry matter production measured using NDVI at 1.1 km resolution (Hanan *et al.* 1991) and radial transects with 5 km-interval measurements in western Botswana (G.Techeba *pers. comm.*). Where NDVI methods have successfully detected piospheres, negative effects on primary productivity were rejected due to the inconsistency and transience of the response in one instance (Lind *et al.* 2003), while rangeland assessment using persistent responses was considered possible in another (Harris & Asner 2003).

Some field surveys also suggest that the negative effects of water provision are temporary and reversible, with relaxation to the previous condition upon termination of the grazing pressure (*e.g.*, Seitshiro 1978). Perkins & Thomas (1993a) argue that Kalahari vegetation can be resilient, recovering after good rains, however, they also note that the complexity of the processes involved deem it unlikely that a rangeland's recovery will result in reproduction of its initial state. Dean and MacDonald (1994) supply a history of borehole management that has purportedly lead to irreversible degradation at the landscape level.

1.2 Modelling

1.2.1 Simplification of a complex system

Antagonistic to any generalized piosphere modelling effort is the range of responses that have been found for vegetation and soil properties with distance from water across different study sites. That is to say, the piosphere effect is a multivariate system response, further complicated by its particularity to the site of interest. The spatial extent of vegetation impact is largely determined by soil and vegetation type (*e.g.*, Kalikawa 1990 and Section 1.1.6). However, within the detectable extent of impact for any given site, characteristic zones of compositional change in the vegetation and particularly in the tree-grass ratio may be recognised. This has enabled the representation of the individual piosphere as annuli in the form of conceptual models in the presence (Collinson 1983) and absence (Perkins & Thomas 1993a) of woody layer mediation by browsers.

1.2.2 Conceptual models

Whilst being parsimonious treatments of a complex system, the conceptual models do provide a reasonable basis upon which to design an improved understanding of the piosphere response (*e.g.*, one that includes temporal dynamics). Changes in composition with time depend on the life histories of individual plant species present, the selectivity of animals, the plant response to that grazing pressure, and on the plant location along the gradient of grazing pressure (Lailhacar *et al.* 1993). A notional pattern displaces less hardy (centrifugal) species, from the centre, outwards, towards the perimeter, and replaces them with hardier (centripetal) species (*c.f.* Fig. 1.5). This is a rule of thumb, an aid to the conceptual models, for which some studies are in good agreement (*e.g.*, Friedel 1988, Thrash *et al.* 1993), and others contradict wholly (*e.g.*, Stroleny & Mentis 1989, Perkins 1991, van Rooyan *et al.* 1994), or at least in part (*e.g.*, Foran 1980; Andrew & Lange 1986b). Why all piospheres do not conform to the concept may be due to complicating factors such as grazing-induced vigour (Andrew & Lange 1986b), implying a complex community response to disturbance (Perkins & Thomas 1993b).

1.2.3 The use of conceptual models in rangeland management

Further abstraction allows these models to be used as units of landscape management (Foran 1980, Collinson 1983). Incorporating knowledge about livestock behaviour and patterns of home-range use (*e.g.*, dietary preference, wind direction) and paddock design, will highlight areas most susceptible to impact (Pickup & Stafford Smith 1987). Consideration of these areas allows the construction of management strategies for optimal rangeland use and minimal degradation (Cridland & Stafford Smith 1993). Application to wildlife areas involves additional levels of complexity. These include notions regarding the stabilising qualities of heterogeneity on system dynamics (Goodman 1982), wet and dry season ranges (*e.g.*, Funston *et al.* 1994), and the importance of maintaining rare species refugia in the landscape (Owen-Smith 1996).

1.2.4 The general logistic model

The piosphere effect that underlies the conceptual models is the pattern that results from the amalgamation of animal impacts and the separate graded responses of vegetation and soil characteristics. The separate responses fall into two categories; those in which there is a concomitant increase in the level of the variable with distance from water, and those that decrease. Graetz & Ludwig (1978) recorded vegetation and soil data that appeared sigmoid when plotted against distance from water. This led them to suggest that a generalised regression model could be used to describe both the increasing and decreasing variable response types in terms of a logistic curve (Fig. 1.6). The parameters of this model lend themselves well to mathematically describing the shape of the piosphere pattern depicted by the conceptual models. The upper asymptote, K, and the slope parameter, b, are easily measured in the field and therefore supply us with a convenient way to assess the impact of water provision for a single site but also to make comparisons across sites. The sacrifice zone is described by the lower asymptote.

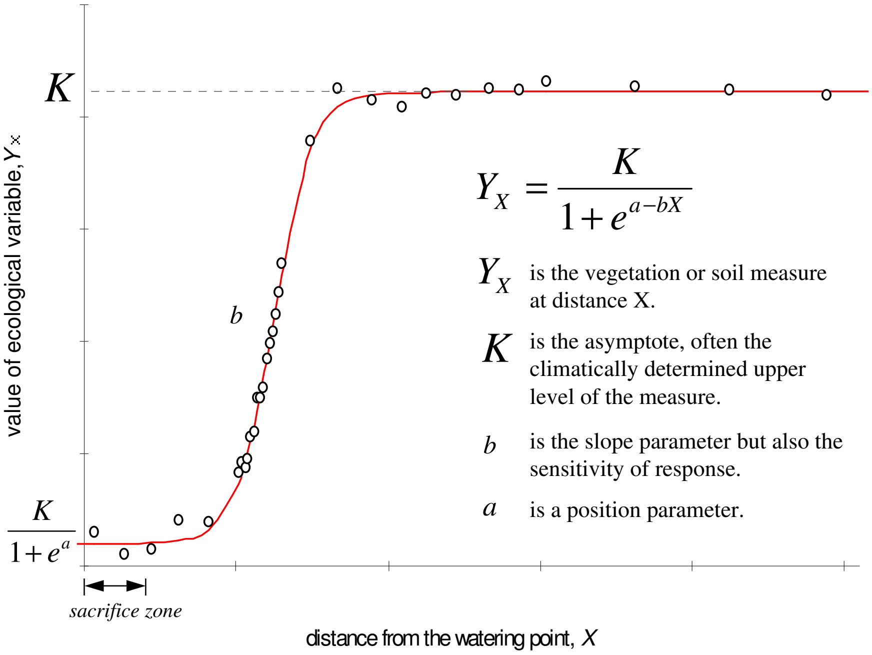


Fig. 1.6: The logistic curve adopted from population biology can be used to describe the piosphere effect. The parameters of the curve are convenient for representing the response of variables to the decrease in stocking pressure with distance from water. Positive relationships are modelled by negative values for parameters *a* and *b*. Adapted from Graetz & Ludwig (1978).

In addition to proving to be an acceptable fit for their own data collected in the Australian chenopod shrubland of New South Wales, the generality of Graetz and Ludwig's model is supported by examples collected for studies in southern and central Africa (Table 1.3). These include an additional term to account for nonzero y-intercepts (Thrash 1998b; Verlinden *et al*. 1998). However, it can be seen that large negative values for parameters *b* and *a* typically result for left-hand truncated forms of the positive relationship of a variable with distance. Also, because truncation produces a curve with no upper asymptote, values for *K* exceed the maximum value of 1 for the normalized data. "Forcing" the logistic model in this way can also give rise to nonsensical values for y_0, although a significant fit does indicate the piosphere pattern. Therefore, while the logistic model is useful for the affinity of its parameters to the real world, its universality is questionable (see Section 1.2.5). Also, there is no apparent variation due to climate, site age or stocking history, although more work is necessary to carry out a valid meta-analysis and one that includes a measure of piosphere extent.

Location	Vegetation	Rainfall	Animals	SR	Age	y_0	*K*	*a*	*b*	SE	R^2	F	*P*	Data	n	Source
Malilangwe Nature Trust, S.E. Zimbabwe	Limpopo lowveld	300-500	Wildlife[1]	57 ha/head	Unknown	-	0.96	1472.64	-319.95	0.101	0.90	37.05	<0.0001	Canopy distance	115	Unpublished. S. & B. Clegg & J.F. Derry.
Gonarezhou, S.E. Zimbabwe	Limpopo lowveld	300-500	Wildlife[1]	90 ha/head	Unknown	-	0.91	59.03	7.90	0.090	0.96	23.86	0.0402	Tree density	50	Rodriguez 1995
						-	1.02	501.61	-114.98	0.006	0.99	1168.0	0.0009	Tree damage	50	
Tierberg, South Africa	Karoo Dwarf Shrublands	167	Sheep	6 ha/ssu	Closed 20 yr	0.09	25.12	-26.16	-6.96	0.164	0.12	3.52	0.0187	Total cover	84	Unpublished. S.J. Milton, Percy FitzPatrick Institute, University of Cape Town.
Sandrivier, South Africa	Karoo Dwarf Shrublands	167	Smallstock[2]	6 ha/ssu	1/2 yr rotation	-	0.48	174.80	-127.54	0.198	0.15	6.07	0.0038	Total cover	70	
						0.08	3.34	-6.50	-17.04	0.062	0.95	74.82	<0.0001	Dung cover	16	
Kgatleng District, S.E. Botswana	Kalahari sandveld	350-400	Cattle	475 head	29 yr	-	0.85	31.20	19.43	0.108	0.89	32.35	0.0001	Tree cover	88	Moleele 1994
						0.47	2.34	-56.50	-48.64	0.071	0.92	28.19	0.0003	CEC[3]	88	
						0.57	0.32	86.83	-8.73	0.068	0.89	18.10	0.0011	Soil organic carbon	88	
						0.68	0.20	164.01	-48.46	0.070	0.71	5.79	0.0260	Plant nitrogen	88	
						-	11.35	-48.51	-20.68	0.077	0.96	87.19	<0.0001	Bare ground	88	
						0.70	0.51	14.98	-53.38	0.023	0.97	85.92	<0.0001	Soil pH	88	
						-	0.76	50.06	-6.99	0.123	0.91	39.26	<0.0001	Soil phosphorus	88	
						0.20	3.52	-35.78	-29.24	0.064	0.96	61.46	<0.0001	Soil calcium	88	
						0.21	13.64	-84.05	-29.76	0.065	0.96	52.56	<0.0001	Soil magnesium	88	
						-	48.20	-133.03	-34.06	0.084	0.95	76.59	<0.0001	Soil potassium	88	
						0.08	44.72	-50.48	-13.06	0.027	0.99	354.06	<0.0001	Soil sodium	88	
						0.42	0.60	92.80	-28.61	0.037	0.99	172.54	<0.0001	Plant phosphorus	88	
Makgadikgadi Basin, E. Botswana	Kalahari sandveld	400-500	Cattle	17 ha/LU	25 yr	-	1.11	19.46	-12.17	0.056	0.94	228.18	<0.0001	Grass composition[4]	34	Perkins 1991
						-	2.32	-10.08	-21.97	0.049	0.95	418.12	<0.0001	Shrub composition[4]	46	
						-	1.08	18.97	-7.47	0.002	1.00	76467	<0.0001	HUI[5]	56	
						-	0.98	45.04	-2.05	0.029	1.00	447.52	0.0002	Soil sodium	64	
						-	0.97	46.64	-2.05	0.073	0.98	71.50	0.0029	Soil potassium	64	
						-	0.99	48.47	-2.05	0.079	0.98	64.91	0.0034	Soil phosphorus	64	
						-	0.87	177.56	-11.68	0.183	0.91	14.58	0.0285	Soil nitrogen	64	
Makhi, N. Botswana	Kalahari sandveld	451	Cattle	12 ha/LU	21 yr	0.72	1.05	-223.21	-210.52	0.033	0.93	21.13	0.0029	Soil pH	41	Mphinyane 2001
						0.53	19.12	-965.35	-257.81	0.073	0.87	11.51	0.0111	Soil magnesium	41	
						-	0.93	438.94	556.16	0.080	0.94	24.57	0.0138	Phytomass[6]	100	
						-	79.57	-5749.99	-1299.03	0.109	0.94	23.18	0.0150	Utilisation[7]	400	
						0.42	25.87	-639.26	-168.85	0.029	0.99	116.02	<0.0001	Soil phosphorus	41	
						0.45	1.40	-107.40	-246.82	0.031	0.98	106.40	<0.0001	CEC[3]	41	
						0.27	42.82	-1264.23	-309.42	0.038	0.99	113.27	<0.0001	Soil calcium	41	
Tierberg, South Africa	Karoo Dwarf Shrublands	167	Unknown	Unknown	Unknown	-	5.72	137.67	50.57	0.164	0.32	8.654	0.0008	Total cover	40	Stokes & Yeaton 1994
Worcester, South Africa	Karoo Dwarf Shrublands	150	Unknown	Unknown	Unknown	0.44	0.27	18.26	-1.11	0.124	0.54	12.15	<0.0001	Canopy cover	35	
Kruger National Park, South Africa	Transvaal lowveld	530	Wildlife	35 LSU/km^2	28 yr	-	1.77	6.57	-15.72	0.046	0.98	607.07	<0.0001	Grass composition[8]	23	Thrash 1993
Kalahari Gemsbok National Park, Botswana	Kalahari sandveld	209-230	Wildlife	Unknown	Unknown	-	7.98	-28.69	-14.75	0.027	0.99	1937.7	<0.0001	Grass composition[8]	44	van Rooyen *et al.* 1994
Eastern subalpine and alpine mountains, Lesotho	*Themeda Festuca* Alpine Veld	900-1100	Smallstock + cattle	Unknown	Unknown	-	0.57	389.98	267.30	0.194	0.11	5.46	0.0057	*Festuca caprina*	94	Morris 2002
						-	0.58	-23.26	-52.58	0.135	0.16	8.83	0.0003	*Bromus uniloides*	94	
Ceel Dhere, Somalia	Coastal grassland	275	Wildlife + livestock	9 ha/AU	Unknown	-	0.95	11.50	10.77	0.106	0.90	53.83	<0.0001	Range condition	15	Barker *et al.* 1989
						-	0.90	3.12	2.11	0.072	0.93	76.20	<0.0001	Bare ground	15	

[1] especially elephant [2] sheep and goats [3] cation exchange capacity [4] Detrended Correspondence Analysis [5] herbivore use intensity [6] dry weight [7] biomass removed [8] Canonical Correspondence Analysis

Table 1.3: Regression of generalised piosphere model (Graetz & Ludwig 1978) for variables measured in Africa. Site age and location, vegetation and animal types, annual rainfall (mm/yr.), regression statistics (standard error, SE; R^2; F and *P*), sample size (n) and data source are given, along with model parameters (*K*, *a* and *b*) plus adjustment term y_0 introduced by Thrash (1998b) for non-zero lower asymptotes, equivalent to $K/(1+e^a)$. These regressions were carried out for this thesis. To enable comparisons, each variable was normalised with respect to its maximum value. Only significant fits are presented. Model selection between 3- and 4-parameter versions was based on SE, R^2 and PRESS (Press 1992, *not shown*) statistics.

1.2.5 The use of the logistic model in rangeland management

Although the logistic curve is a convenient tool to estimate piosphere dimensions, by adopting the logistic equation and not selecting a more complex empirical model that may better satisfy statistical selection criteria for a piosphere data set, the loss in estimator precision may outweigh the logistic curve's usefulness. Conversely, the process of selecting the most suitable model will have some bearing on what we may infer from the analysis (Buckland *et al.* 1997). For example, one dimension of a piosphere that may be estimated using this graphical model is the distance to the extent of its impact as measured by the abscissa upon negligible change in the asymptotic gradient (*e.g.*, Thrash 2000). This value would be useful to managers when trying to assess the spacing of watering points. Keys of 3 models, exponential, logistic and Gompertz, were fitted to compositional vegetation data collected at nine sites in Kruger National Park (Thrash *et al.* 1993). Whilst there was no overall effect on estimating the impact extent by selecting the logistic curve in favour of a 'best-fit' alternative if one existed ($t_{0.05,8} = -0.16$; $p >> 0.05$), the error in doing so for individual sites ranged between approximately a fifth (0.18) and nearly four times (3.91) the distance estimated by selection of the 'best-fit' model, and on average the distance estimated by the logistic equation was over twice (2.06) that estimated by the 'best-fit' model (J.F.Derry & C.D.Morris, *unpublished*). Alternatives have been used: an exponential decay model, offering similar interpretation by its parameterization, was favoured for the change in cover with distance from water for a site on the Nullarbor Plain, Australia (Cridland & Stafford Smith 1993).

1.2.6 Regression models

Semi-arid environments exhibit high temporal and spatial variability (Ellis *et al.* 1993), this spatial heterogeneity being found at a range of spatial scales; locally, within plants, through the whole plant communities and up to landscape and regional scales (Kotliar & Weins 1990). Foraging animals respond to the spatial heterogeneity of their environment by making diet selection decisions that need to account for the distribution of their forage resource (Laca & Demment 1991). A grazing gradient occurs where there exists a relationship between foraging behaviour and a trend in this spatial distribution. At the landscape scale, animal distributions are the simplest method we have to study the behavioural response. Relating direct measurements of animal density to watering point location can show species interaction, especially wildlife displacement by livestock (de Leeuw *et al.* 2001). If measurements are analysed using statistical modelling techniques (*e.g.*, kriging), they can also highlight the impact zones associated with animal distributions along grazing gradients (Verlinden *et al.* 1998).

1.2.7 The prediction of animal densities

A large number of models have been developed, each an attempt to shed some light on the behavioural response underlying what appears to be a complex grazing pattern. Techniques that have been employed include, regression analysis (*e.g.*, Senft *et al.* 1983), probability densities (*e.g.*, Arnold *&* Maller 1985) and GIS (*e.g.*, Wade *et al.* 1998). Disquietingly, Stafford Smith (1990) achieved realistic results from an elementary random-walk model of sheep movement. The only adjustments made were to keep animals within the scope of the paddock, motivate them through previously utilised areas, and probabilistically tailor their movement with respect to wind direction.

1.2.8 Looking for gradients from outer space

More analytically, the flux of animal movements to and from watering points has been captured by using a convection-diffusion process calibrated with remote-sensing measurements (Pickup *&* Chewings 1988, Pickup 1994). Remotely-sensed Landsat images of vegetation cover are typically translated into animal distributions via the design of a filter that accounts for vegetation growth and temporal variation in vegetation cover. The filter incorporates growth, originally modelled as an exponential decay of a growth peak following satisfactory rain, however since then more sophisticated rainfall-driven growth models have been devised (Pickup 1995). Additional terms account for natural decline in vegetation cover, and species gradient effects (compositional changes) assumed to reduce forage quality under heavy stocking. Animal density is then assumed to be proportional to the depletion of vegetation cover and can be modelled using families of inverse Gaussian distribution functions. The approach is effective in extrapolating information from satellite imagery and linking animal densities to range utilisation. Animal densities were shown to be highest at intermediate distances from water (Pickup & Chewings, 1988).

Landsat data has proved useful for the prediction of herbage production and the subsequent distribution of animals along a grazing gradient. It is also effective for the monitoring of rangeland (Pickup *et al.* 1994) and estimation of rangeland degradation (Pickup *et al.* 1998). To date the approach lacks a two-dimensional treatment, and requires further development of the biological component for application to other sites (Stafford Smith 1990). It is noteworthy that this remote sensing technique uses defoliation as a predictor of animal distribution. Heterogeneity in rangeland utilisation is assumed to be equivalent to spatial difference in the removal of vegetation cover related to distance from the nearest watering point.

1.2.9 Productivity gradients

General relationships between animal densities and primary production (*e.g.*, Coe *et al.* 1976, Fritz & Duncan 1994) might imply an alternative predictor of animal distribution and thus herbivore impacts. Gradients may be found in standing crop biomass, as well as vegetation cover (Cridland & Stafford Smith 1993), and appropriately, herbage production may be estimated using remotely-sensed data (Pickup 1995). However, animal responses to gradients of primary production do not fully reflect large-scale dependencies. Functional responses may be complex (Spalinger & Hobbs 1992). van de Koppel *et al.* (1996) detected reduced foraging efficiency in tall, dense grasses at the upper end of a productivity gradient. To model this, negative relationships between plant density and consumption rate, and plant density and digestion efficiency were introduced into a typical predator-prey formulation to reduce the herbivore numerical response. The model predicted a maximal grazing pressure at intermediate levels of standing crop. Under these conditions, multiple stable states may occur for systems of intermediate productivity. Under high productivity, there is a potential for unchecked domination by vegetation. Utilisation thresholds in tall, dense swards are due to dietary and other factors.

Reduced digestibility and preference of plant material, reduced intake of structural tissues and increased vertical resource partitioning constrain diet quality and quantity. Other effects are physical impediment (*e.g.*, impenetrable swards of *Cenchrus ciliaris*, Tuli Block, South Africa, *pers. obs.*), increased threats of predation through obstructed vigilance (Lamprey 1963), and substitution of foraging time to heightened vigilance (Illius *&* Fitzgibbon 1994).

1.2.10 System models

Simulation models seek to emulate ecosystem behaviour by the integration of system components (sometimes packaged in submodels) by various means (*e.g.*, Starfield *&* Bleloch 1991, Balzter *et al.* 1998, Derry 1998), allowing independent dynamics (*e.g.*, growth) as well as interaction (*e.g.*, competition). The representation of the need, to differing degrees, for animals to drink water, depends largely on a model's iteration interval and the nature of the animal component. At one extreme, highly mechanistic, spatial models that attempt to predict foraging behaviour within small time steps may simulate animal movements that are responsive to physiological stress. Constraint within a home range as a function of water requirement becomes a model output. Simpler models that are not so concerned with the fundamentals of foraging behaviour and its associated spatial impacts may simply superimpose a grazing gradient over the modelled region.

1.2.11 Patterns in forage production and utilisation

Adler & Hall (*subm.*) have produced similar results to Pickup *&* Chewings (1988) and van de Koppel *et al.* (1996), also predicting a peak in grazing intensity at intermediate distances, but with a dedicated piosphere systems model. An accompanying field study provided real examples of higher utilisation at intermediate distances for subhumid and semi-arid biomes. In a parallel arid case study, utilisation was highest close to water. There is a shortage of other real world examples, however, Western (1975) measured peak biomass of water-bound livestock for his middle distance class.

For their model, Adler & Hall (*subm.*) coupled an individual-based herbivore foraging submodel to a two species vegetation submodel of Lokta-Volterra plant growth and competition. Versions were developed to test four foraging strategies: maximization of forage biomass intake, equivalent to time minimization (TMin); probabilistic movement away from water (MaxDist); maximization of energy intake adjusted for distance from water (EMax-Dist) and energy intake maximization based on forage quality (EMax-Q). Animals began each day at the water source and then foraged independently until reaching their daily intake requirement.

If a 'start-eating' rule was satisfied, a single bite was taken from each position before progressing to the next position. The 'start-eating' rule for TMin, MaxDist and EMax-Dist allowed consumption if the current location held more biomass than a fraction (ET) of the environmental mean, for which the environmental mean was calculated globally, across the length of the piosphere gradient.

Animals moved from each position in the direction with highest mean available intake within their range of perception. MaxDist introduced probabilistic movement away from water. EMax-Dist goes someway to account for travel costs by dividing the intake rate at each position by the distance to water. Emax-Q used a 2nd order quadratic function to relate forage quality (digestibility) to forage biomass for substitution in the 'start-eating' and movement rules. Simulations were run for each version of the model on two types of landscape, one with a point water source in a square grid and another linear water source in a rectangular grid. The linear system presents a constant available foraging area at any position, in contrast to the increasing area with distance from water for the square grid.

All versions of Adler & Hall's model (*subm.*) produced patterns in grass biomass that were strongest near water and decreased with increasing distance from water. For the square grid, TMin and MaxDist gave the most recognizable piosphere responses, while EMax-Dist and EMax-Q curves indicated abrupt increases to background vegetation levels beyond the range of animal foraging (Fig. 1.7a).

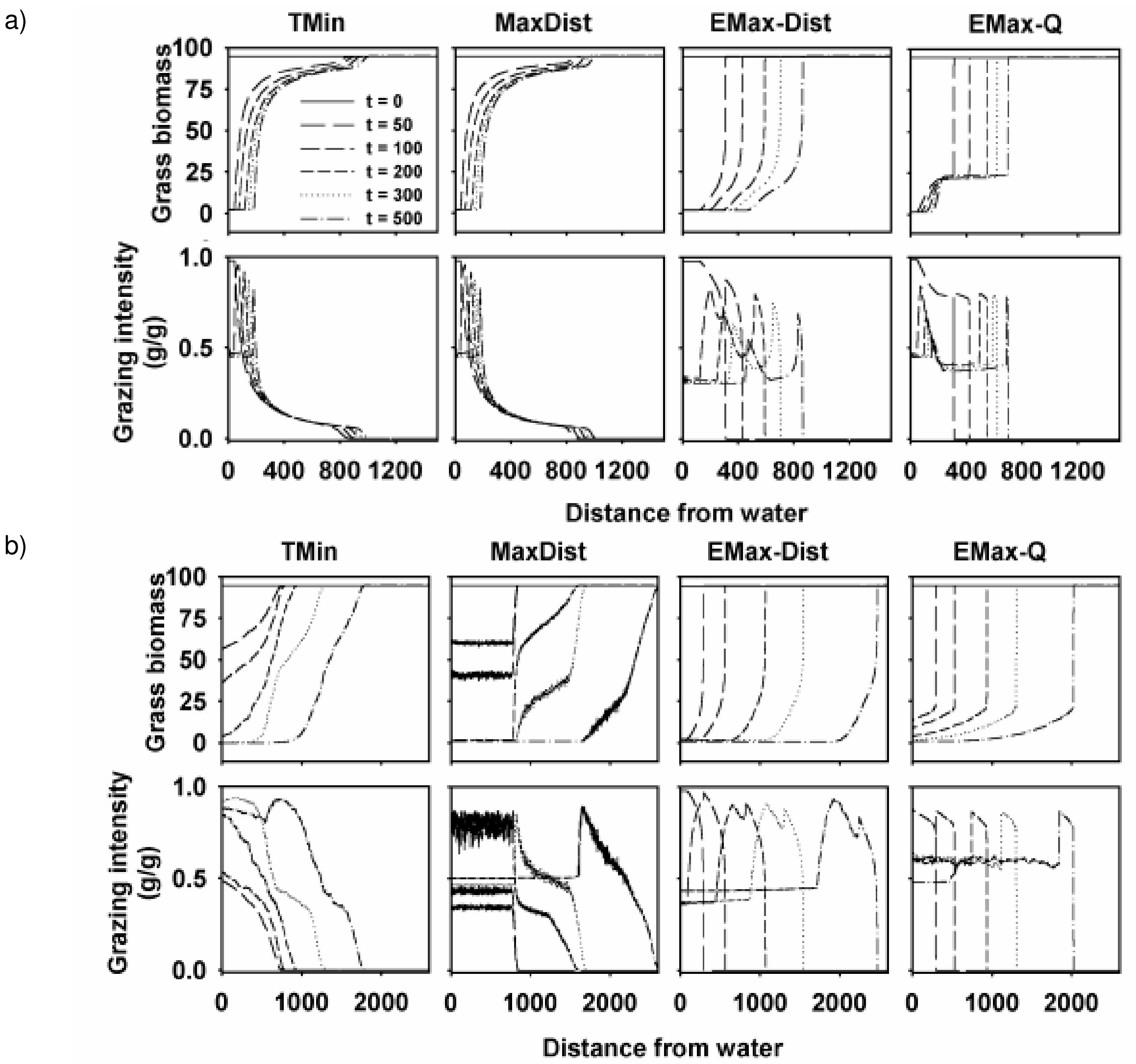


Fig. 1.7: Simulated temporal changes in patterns of grass biomass and utilisation (grazing intensity) under different foraging models run on a landscape with a) a point water source, and b) a linear water source. Lines correspond to patterns at different days (t = 0, 50…500) during the simulation. Results for the MaxDist model at doubled time intervals (t = 0, 100...1000) because the patterns were much slower to develop. Utilisation was calculated for the 50 day period preceding each output time for all models. ET=0.2 for purposes of model comparison. (Adler & Hall *subm.*).

In the linear landscape, responses for all versions of the model were abrupt beyond the range of animal foraging (Fig. 1.7b). All responses showed an increase in the extent of the severely degraded sacrifice zone over time. Utilisation initially decreased with distance from water and then developed a narrow peak at an intermediate distance that shifted away from water over time. So, intermediate peaks develop only after forage abundance nearest to the water source had been decreased to very low levels. Larger sacrifice zones and broader utilisation peaks were seen for the linear system than for the point water source.

Adler & Hall (*subm.*) were able to moderate the strength of the piosphere response in their TMin model for both landscapes by manipulation of ET (Fig. 1.8). Effective suppression of the gradient formation was achieved for ET equal to 1 which meant that only sites with biomass in excess of the environmental mean could be utilized. Lowering ET produced utilisation patterns with increasing degradation of grass biomass nearest water.

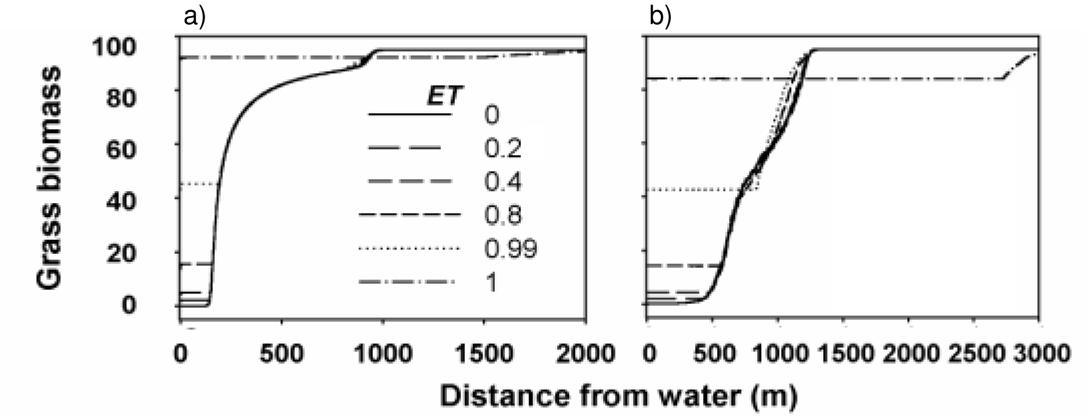


Fig. 1.8: The influence of ET on simulated grass abundance across a distance from water gradient, using using the TMin model on a landscape with a) a point water source, and b) a linear water source. For each simulation, grass biomass is shown at day 300. (Adler & Hall *subm.*).

Adler & Hall's model (*subm.*) is the most comprehensive systems model of piosphere development reported outside this thesis. They do not assume a utilisation gradient but integrate animal foraging behaviour with vegetation dynamics to evolve the piosphere pattern without a predetermined distribution of animal spatial foraging. However, the strength and shape of the responses may be attributable to assumptions in their model. Their 'start-eating' rule is a derivative of the Marginal Value Theorem (Charnov 1976), that predicts that animals should move to more profitable sites once resources at the current location have been depleted to the environmental mean (G*). This defines the theoretical giving up density (GUD) for the resource. An extension of this is Ideal Free theory (Fretwell & Lucas 1970) which predicts that herbivore densities should reflect resource distribution in a heterogeneous environment. Although Adler & Hall (*subm.*) assume that animals have perfect ("ideal") knowledge of resource profitability and are "free" to move between resource sites, using levels of ET below 1 is a manipulation of Marginal Value Theorem assumptions.

With ET=1, animals remove a single bite from locations with resource levels above G*. The model does not include energy expenditure nor does it limit available foraging time, so they are able to move freely between sites without constraint, until daily intake requirements are met. Utilisation patterns are consequently diffused (*not shown*). Reducing ET below 1 improves the profitability of all sites relative to G*, and the animals do not need to travel as far from water to find a comparatively resource-rich location. Further reducing ET emphasizes local profitability and the sacrifice zone is reduced to lower resource levels (Fig. 1.8). Because animals are held local to water, the majority of foraging activity occurs to extend the sacrifice zone, and the rise beyond this to background resource levels is artificially abrupt.

The model fails to capture the essential control on animal spatial foraging behaviour exerted by dry season conditions. Arditi & Dacorogna (1988) described how food patchiness could be a function of the critical food density equal to the animal GUD. Increasing the GUD tends towards the continuous food supply that may underlie a patchy distribution. Using a fraction of G* will effectively increase the size of patch, and reduce inter-patch distance, in spatially heterogeneous distributions of resources.

Adler & Hall (*subm.*) are correct to conclude that the response shapes in their results "indicate that other factors not included in the models have important influences on animal movement". It is reasonable to speculate that these factors include time and energy. Animal movement is moderated by energy travel costs, which must restrict the distances travelled when resources are dispersed, (*e.g.*, for increasing ET). Thus energetic constraints would act in parallel with limitations on the available foraging time to compromise daily intake for insufficient local resources. Simply put, animals do not have time to fully exploit their environment, whilst any additional energy expended during travel needs to be offset by equivalent energy intake.

Further discussion of forage digestibility, energy intake maximization, travel costs and spatial foraging strategies and other issues relating to Adler & Hall's work (*subm.*), and a comparative study, also contrasting a square grid with a linear system, can be found in Chapter 3.

1.2.12 A grid-based model of a single piosphere

Jeltsch *et al.* (1997) considered the question of piosphere reversibility and spread using a grid-based simulation model of 2 separate borehole sites in the Kalahari thornveld. They succeeded in generating similar variability in piosphere size, as determined by changes in grazing pressure, to that observed by Perkins (Perkins *&* Thomas 1993a). Fundamental piosphere responses are recognizable in their model's output for herbaceous and woody cover. While this exercise provides invaluable insight into the generation and maintenance of piosphere responses in vegetation cover, the rule-based algorithms comprising the model do not extend to include foraging behaviour. This means that the grazing pressure was constantly levied according to location along the extent of a preconceived, exponential grazing gradient. Reduction of phytomass in random grid cells conforms to this grazing pressure. Perhaps then, accumulated depletion is likely to give rise to a herbaceous layer that reflects a deterministic gradient. Possibly more impressive is the model's simulation of bush encroachment. The location and depth of bush encroached zones in the near vicinity of the "virtual borehole" are similar to those measured by Perkins (1991), and were found to be stable for simulation times in excess of a century after removal of grazing pressure. The bush dynamics are a product of increasing the grazing pressure upon nearing the water point, leading to extinction of herbaceous cover within local grid cells, and subsequent colonization of those grid cells by a woody species. Perkins (1991) carried out his experiments in the eastern Kalahari, where precipitation levels (~450mm/yr) might be expected to generate rooting patterns that seek to partition the water resource (Mordelet *et al.* 1997). Deep surface sands proffer a low storage capacity for infiltration (Mazor 1982) which allow shallow herbaceous roots access before percolation to the deeper placed roots of the woody vegetation. It is reasonable, therefore, that the foundation for bush encroachment is considered to be the depletion of grasses by the high herbivore utilisation intensity near the borehole. Fire (included in the model as a function of fuel load) was previously identified as having an important influence on the model's results (Jeltsch *et al*. 1996). Perkins (1991) originally identified the exclusion of fire by the continuous grazing of the herbaceous layer, which reduces the available fuel load, along with seedling establishment following favorable rainfall patterns, as cofactors in the promotion of the woody layer (Perkins 1991).

1.2.13 Grid-based models of animal densities

Another Kalahari-based model (Starfield *et al*. 1982) moves 3 species of wildlife between blocks along a section of river according to an index of attractiveness that captures diet preferences and water dependence, including drought tolerance. The model was successful in predicting basic animal movements and population dynamics in response to water location and accumulated defoliation in blocks hosting a watering point, but is not configured to model piosphere patterns. The *Paddock* utility in RANGEPACK (Stafford Smith 1988, Stafford Smith *&* Foran 1990, Cridland *&* Stafford Smith 1993) provides a user interface for the specification of paddock characteristics, such as watering point location, fencelines, and wind direction (an influence on sheep movement). The exponential decay model is used to impose a grazing gradient, the slope of which is determined by watering point salinity and a vegetation preference index, also influenced by watering point salinity, thereby introducing an element of animal physiology. The model can be used to test sketched paddock designs against predicted spatial impacts for multiple watering point systems, and is being developed to accept real paddock data via GIS input.

1.2.14 Modelling the physiology of foraging behaviour

Mechanistic models move away from the grazing gradient approach towards predictions of animal movement whilst accounting for physiological constraints. To model animal movement with respect to water requirements, the balance between acquirement via drinking and dietary moisture content, and losses via respiration, sweat, urine, and fæces need to be considered. Loza *et al.* (1992) include all of these factors in a physiological submodel, and specify the location of a watering point and shade in a landscape submodel. An hourly iteration interval sees animals making daytime decisions conditional on their physiological status, derived from thirst, respiration and hunger indices. Animals are mobilised towards water or shade according to the strength of the corresponding index, and if sufficiently hungry, will forage *en route*. A priority is set for drinking, over shade, over eating. During winter, animals were predicted to spend roughly a half of each day near water. During warmer months animals were predicted to suffer higher water loss, spend longer drinking, and spend more time near shade. Increasing the distance between water and shade reduced the time spent near water in favour of travelling to shade after drinking requirements had been satisfied. The representation of the landscape is course. Water and shade are located in, and separated by, adjacent kilometre-wide blocks with movement in 0.5 km units. Forage growth is not dynamic, daily growth being input as a value independent of consumption. Hence, impacts are not recorded.

1.2.15 Distance to water versus animal energy expenditure

SAVANNA (Coughenour 1993) does not simulate animal water balance but does take account of energy expenditure in travel undertaken to satisfy water requirements. The iteration interval is a week. Animals are distributed across the grid-based landscape in relation to an index of habitat suitability, assessed in terms of distance to water along with forage abundance and tree cover. Watering points may either be seasonal wells, permanent wells or perennial streams, each classifiable as either a mineral or fresh quality. The level of seasonal wells are dependent on the previous three months' rainfall, whilst loss from permanent wells is dependent on the previous 12 months' rainfall. Discharge rates and distance to water are input as maps. Animals that cannot be supported at current discharge rates disperse to other areas containing excess water. A maximum animal density may be set for each grid cell. Plant growth is related to soil moisture and transpiration rate. Trees are classified into size classes. Grazing and browsing impacts are registered on the corresponding phytomass in each cell. Whilst, the model has been successfully applied to predicting large-scale vegetation dynamics and animal distributions (Kiker 1998), an assessment of the model's capacity to simulate piosphere dynamics has yet to be carried out.

1.2.16 Piospheres and the socio-economics of livestock production

An additional dynamic component important to sustainable rangeland management arises from market forces. Piosphere dynamics in the Kalahari are inextricably linked with socio-economic (Perkins 1991) and political factors (Perkins 1996). A benefit function in ORIA (Optimal Rangeland Integrated Assessment model, Duraiappah & Perkins 1999) is used to encapsulate the income from livestock sales, the cost of shipment from the cattlepost to the abattoir, the gain of milk, draught power, hides and prestige by retaining animals and the loss of these benefits by selling animals. The analytical model also includes the cost of restocking, the provision of supplementary food, labour costs and effort. Borehole density for the modelled region is limited within bounds to avoid overlap of neighbouring piospheres. The cost of borehole establishment and maintenance are also charged. Additional boreholes are drilled if the current quantity of boreholes cannot support the current head of livestock. Stock numbers fluctuate with available forage. Vegetation dynamics are modelled for grass and browse within 2 concentric zones surrounding the boreholes, and a grazing reserve beyond the outer annuli. The level of bush encroachment is assumed to be an exponential function of distance from a borehole once grass levels fall below a threshold. Forage intake is balanced against energetic requirements for maintenance and travel. Vegetation is trampled in proportion to animal density and affects grass more than browse. Substitution of herbaceous forage with browse is constrained to reflect digestive constraints in cattle. The model seeks to maximise the benefit function net costs limiting sales to levels that do not result in a smaller herd size than the initial herd. The model manages to simulate various aspects of Kalahari piospheres; including, temporal dynamics such as bush encroachment, spatial effects such as essential winter grazing being limited to the outlying grazing reserve, and animal behaviour such as mixed diets during summer. It also provides a test of optimal herd sizes and national agricultural policy, finding in support of an 8 km spacing of boreholes. Ecologically sustainable stocking rates (carrying capacity) were found in excess of economically sustainable stocking rates, dependent on cattle prices and borehole costs. Losses from trampling were found to be large enough to justify investment in more boreholes to diffuse herd intensity.

1.2.17 Miscellaneous models

Aspects of other models lend themselves to solving some of the problems envisaged during development of a comprehensive piosphere model. A few examples are parsimoniously given here. Fryxell (1998) has generated a central-place foraging model of beaver resource depletion that effectively generates a piosphere pattern. The model accounts for the effects of forage abundance and nutritional quality on beaver forage preference and subsequent handling and retention times. The pitfall with beaver foraging behaviour, when comparing it to *e.g.*, livestock, is that beavers restart their foraging excursions from a central position on each occasion. Each food item is located relative to the central point rather than with respect to the previous food item, lending itself well to the Markovian Chain approach adopted, but requiring modification if to be applied in a piosphere modelling context. Pennycuick (1979) provided a useful allometric energetics model of animal mobility to calculate the foraging radius, the determinant of piosphere extent and the dry season (home) range of the free-ranging animal. Effective and economical artificial water provision is partly dependent on the type and dimensions of the water container (Zambatis 1985), and this could be included in bioeconomic system models of watering points. Evaporation is related to surface area, therefore, water loss from rectangular troughs is proportional to the length of their perimeter, whilst water loss from circular pans increases exponentially with their diameter. Insufficiently sized pans (<10 m diameter) tend to become mud wallows. This deters drinking. Sufficiently sized pans (>25 m diameter) lose 16.7 times more water to evaporation (919.8 m^3 *per annum*) than that lost from a 15 m trough (55.1 m^3 *per annum*) holding 6300 litres, deemed a minimal capacity for daily wildlife water provision.

1.2.18 Conclusions and gaps in knowledge

The location of animal drinking water has been identified as an important factor in determining patterns of rangeland use, and yet models of the piosphere response are scarce. Ecosystem modelling efforts tend to concentrate on the prediction of animal distributions, as a simple function of distance from water. Although animal movement may be based on simple rules, complexity is evident in the piosphere response and the consequences that this will have on animal utilisation of rangeland. Animal distribution models that do account for water location fail to account for piosphere dynamics, confining grazing impacts to within appropriate limits. Models that do simulate spatial impacts have not investigated the significance of the many other factors that may be contributing to the grazing pattern, including animal response, and assume a gradient of grazing intensity to be a sufficient predictor of piosphere generation and dynamics. The advantages of including an economics component have been recently demonstrated, although the structuring of this will vary with application. Animal effects omitted from mechanistic modelling efforts include trampling, defecation and urination.

Hydrology has been ignored as a factor in causing spatial vegetation growth patterns around watering points. Natural waterholes are points of collection for rainwater and retain water longer than at equivalent soil depths in the surround. Slow release of leaked water from natural pans, and even artificial, concrete-lined pans (by way of cracks in their bases) will bolster local soil water content. In contrast, the pumping of boreholes causes an inverted cone in the aquifer, a 'drawdown' of the water table, which expands with increased use. The withdrawal of groundwater reduces pore-water pressure and collapse of the soil structure, leading to subsidence (Hsi *et al.* 1994). No work has been reported that relates this phenomenon to piosphere dynamics around pumped sites. Drawdown of groundwater also occurs at much reduced hydraulic potentials than those generated by pumping when evapotranspiration exceeds precipitation (Hosty & Mulqueen 1996). The recharge of subterranean water reserves also requires consideration. For the Kalahari in particular, each year, the amount of rainfall reaching the water table has been thought negligible due to impedance by surface sands, causing enough delay for eventual loss to evapotranspiration during winter. This widely accepted sequence of events does not account for the levels of recharge activity subsequently measured in Kalahari groundwater (Mazor 1982), implying the need for a re-evaluation of water flow in these soils.

It is impossible to predict whether increasing the number, and detail, of mechanisms simulated in a model of piosphere dynamics will improve its performance. However, as we improve our comprehension of the factors that generate piospheres (summarized in Fig. 1.9), it will become possible to evaluate their relative influences on the piosphere response, potentially via the use of models. Perhaps then we may expect improvements in our models of rangeland use, and elicitation of the role of gradients in rangeland degradation and utilisation.

1.3 This thesis

1.3.1 Problem statement

Piospheres are examples of the spatial impacts animals have on their environment. They are a result of the constraint in foraging area when animals approach and retreat from a focus in the landscape. In grazing systems, the effect is to concentrate the impact of herbivory, trampling, defecation and urination. The consequences for the animals are via detrimental modifications of their resource base; a reduction in the density and production of forage (Andrew & Lange 1986b, Thrash *et al*. 1991 and 1993), changes in the species composition of forage vegetation (Skarpe 1986), bush encroachment (Tolsma *et al*. 1987), and reduction in the nutrient content of their diet (Tolsma *et al*. 1987).

The problem may be summarised as follows,

- The large scale, landscape effect of water provision is a topic under discussion presently in southern Africa.
- At the scale of the individual site, cover and compositional changes have been measured for vegetation and nutrient analysis has been carried out for soil.
- The findings at sites with compositional changes have led some workers to expect changes in forage quality, presently gauged in this context as palatability.
- Site-to-site differences are apparent but lack of a comparative study has meant little is known about the factors that determine piosphere dynamics.

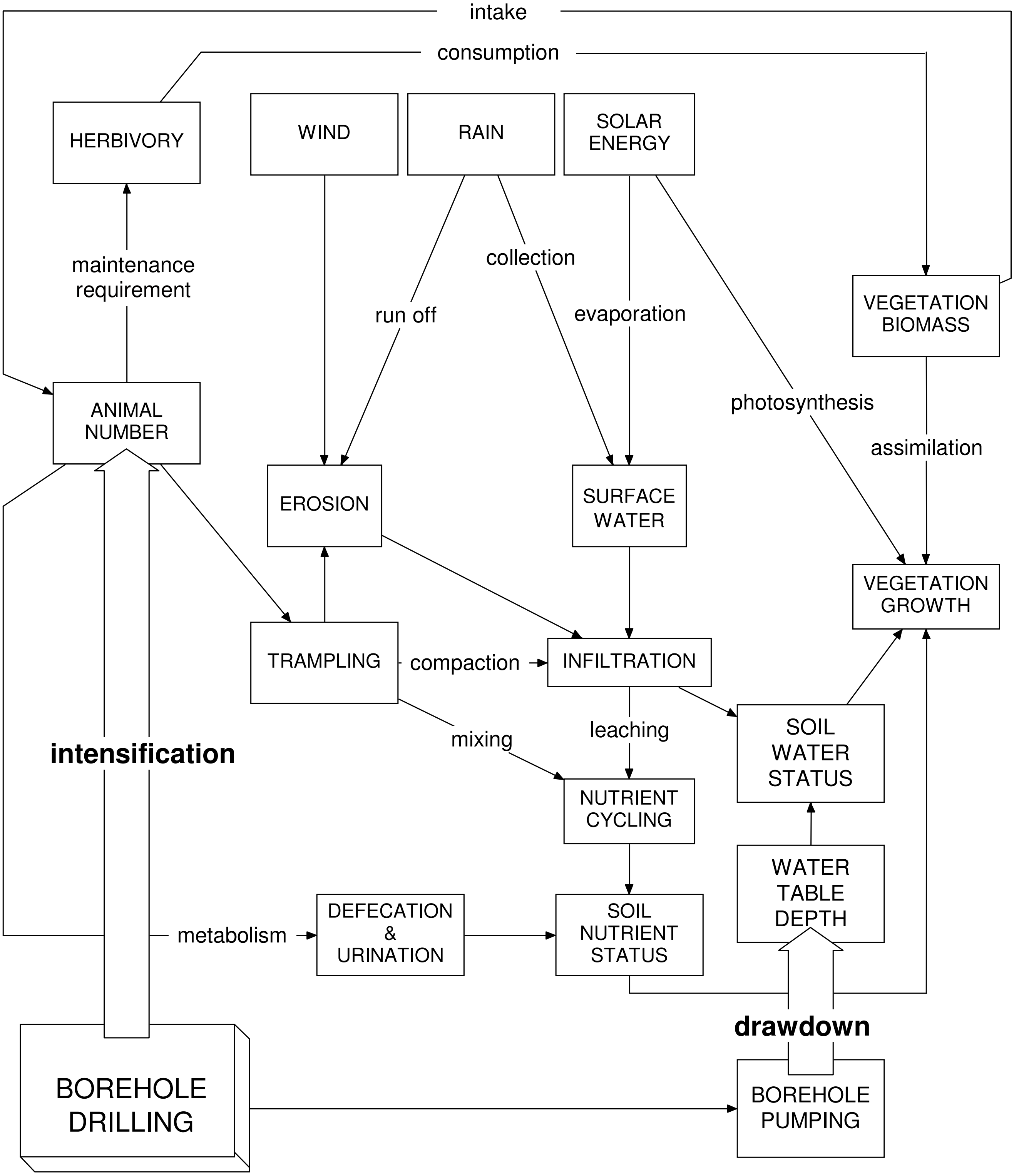


Fig. 1.9: Underlying processes and their interactions contributing to land modification in the vicinity of a borehole causing animal congregation. For comparison, see Weir (1971), Jarman (1972) and Goudie & Thomas (1985) for an account of how naturally occurring pans may evolve through animal action (including removal of mud), wind erosion and stream flow.

- Site specificity of the effect, via the influence of differing involvement of biotic and environmental factors, make piosphere dynamics complex.
- Application of the diversity of responses to the landscape level has lead to different approaches to environmental impacts.
- Clarification is required of the fundamental components of piosphere systems and their interactions in determining the system dynamics.
- Modelling approaches have managed to simulate some aspects of piosphere dynamics, without revealing much information about the mechanisms underlying change.

1.3.2 Research questions and objectives

The gradient of impact can be detected by field measurements and may be mathematically described using a logistic equation, but piosphere dynamics are not simply an academic issue. Scientists and managers alike have measured rangeland in terms of the piosphere unit. Examples are given from southern Africa to demonstrate how piospheres are establishing a pivotal role at the very hub of livestock and wildlife management. Nonetheless, animal behavioural studies are often confounded by environmental complexity, but organisation of certain factors with respect to some known entity (the independent variable) facilitates our posing of scientific questions regarding animal responses to their environment (Martin & Bateson 1993). Thus, the organisation of resources into ecological gradients provides an opportunity to test our understanding of large mammalian herbivore ecology. A model will help us understand the dynamics of the processes interacting in the formation and development of piospheres and their role in this ecology.

The organisation of impacts into a gradient provides a useful tool with which to investigate the generation of spatial heterogeneity in the habitat, the response of animals to that spatial heterogeneity of their resources, and the response of animals to the utilisation gradient itself. Better understanding of dynamic processes that generate spatial heterogeneity, spatial pattern and the consequences that utilisation gradients have for animal foraging behaviour will contribute to the improved management of spatially heterogeneous rangeland.

Questions about animal spatial foraging must involve consideration of spatial scale because animals perceive the environment at different scales. Therefore, a primary objective of this thesis must be to identify an appropriate methodological scale for the study of behavioural response to resource heterogeneity by a specific animal, and to interpret this response in the energetic terms of contemporary Optimal Foraging Theory. Such findings can then be used to quantify the animal response to resource gradients for the individual and the population.

Specific research questions and objectives are given in more detail for the experiments in each chapter. Here follow the key questions posed in this thesis which relate to the utilisation of spatially distributed resources by free-foraging animals,

1. Do animals respond to the spatial heterogeneity of their resources? If so, then what is the operational scale of this response?
2. How does resource spatial heterogeneity become organised into a utilisation gradient?
    i. What is the role of water dependency in dictating foraging range during the dry season?
    ii. Are the impacts distributed actively as a function of animal foraging patterns, or alternatively, are the impacts distributed passively in relation to landscape geometry?
        a. How can the processes that lead to the spatial distribution of impacts into a utilisation gradient be characterised?
    iii. How do the assumptions about energy balance in Optimal Foraging Theory influence the spatial distribution of impacts?
        a. Do travel costs affect the utilisation gradient? If so, then is there an optimal distance along the utilisation gradient at which animals forage to maximise nutritional intake net of the costs of travel? *i.e.*, is there a trade-off in energy gain and energy expenditure?
3. Does it matter that animal foraging range during the dry season is constrained by water dependency? *i.e.*, what is the animal response to the utilisation gradient? This is better stated as,

i. Do utilisation gradients affect animal intake? If so, then are there consequences for animal reproduction and survival? Is there a subsequent effect on population size?
    a. Is it possible to quantify the animal response to the utilisation gradient? Can its effect be detected in the animal functional response?
ii. Do dry season conditions for foraging pose animals with selection pressures to mitigate the constraints on their foraging range?

1.3.3 Thesis structure

The next chapter, Chapter 2 deals with animal response to resource heterogeneity. Spatial resources are characterised in terms of animal utilisation patterns and the scale of animal assessment is identified.

Chapter 3 considers the organisation of spatial impacts into a utilisation gradient. The response of animals to the gradient is investigated in terms of their foraging range and this is put into the context of their water requirements and energy balance.

Energy intake is further investigated for a resource gradient in Chapter 4, where constraints on energy gain from the gradient are identified.

The consequences of these constraints on individual intake and animal population dynamics are further considered in Chapter 5, in addition to characterisation of the utilisation gradient and its effects with reference to modern ecological theory.

Chapter 6 presents a general discussion of experimental findings, considers the evolutionary importance of utilisation gradients, highlights future research opportunities, and concludes with a summary of contributions made by this thesis. Appendices are numbered sequentially and are included with the bibliography at the end of the thesis.

1.3.4 Experiment locations

Semi-arid zones are described as receiving 300-600 mm annual rainfall (FAO 1987), although savanna, the characteristic wooded C4 grassland associated with such places, particularly in southern Africa, is prevalent under 50-1800 mm (Huntley 1982). It is therefore appropriate to refer to “arid” and “moist” savannas for areas typically receiving less and more than 650 mm rainfall *per annum*, respectively (Huntley 1982). A high annual and seasonal variability in rainfall dictate the nature of savanna, determining the species composition (O’Connor 1985) and wide fluctuations in the production of the vegetation (Ellis & Swift 1988, Ellis *et al.* 1993, Stafford Smith & Pickup 1993). This variability gives rise to several subtypes; steppe, thorn savanna, tree savanna, parkland, savanna woodland, woodland, thicket, dry forest, bushveld, etc. (Huntley 1982). To provide consistency across studies Acocks (1953) is the most enduring and, fortunately, the most commonly used reference when classifying vegetation types in southern Africa.

The experimental sites used in this thesis were chosen primarily for their availability, as part of an existing program between the universities of Edinburgh and Fort Hare, but were also favoured from other potential sites for their suitability for each experiment, and their safety from repossession by land reform in South Africa.

The Fort Hare thornveld differed markedly between the two sites chosen and this reflected the different research questions being asked. A densely vegetated, highly variable, undulating paddock was chosen for the first experiment that investigated diet selectivity and foraging behaviour in browsing animals within heterogeneous environments. The second experiment required a more homogeneous vegetation composition to allow observations to be made for a single browse species. The second experiment location was also selected as it was quite level and it could accommodate a long, thin paddock.

Vegetation composition would be expected to confer site specificity on the experimental findings. However, observations in the first experiment were made across a wide range of plant species and animal foraging activities were largely interpreted as broad scale spatial patterns. Therefore, equivalent observations would be expected for similarly heterogeneous savanna, independent of composition. In the second experiment, observations were made at a small spatial scale allowing inferences to be made about the mechanisms underlying the rate of animal feeding. These findings would be general to plant species exhibiting a similar morphology because they would present the animal with similar diet decisions. Furthermore, the capacity for selection and handling of plant material at this scale is related to animal body mass. Thus, animal species of a similar size would be expected to be subject to similar extrinsic conditions. This is further explained below and in the relevant chapters.

1.3.5 The model animal - the domestic goat (*Capra hircus*)

A large flock of Nguni and Boer goats was maintained on the study site at the University of Fort Hare, South Africa. Goats are popular domestic livestock in southern Africa typically kept with cattle and traction stock such as donkeys and oxen. Their body size facilitates manhandling for experimental sampling and weighing. A comparatively small body size for a large mammalian herbivore can be shown to suit them for a primarily browsing lifestyle, using allometric relationships between body size and mouth architecture (Illius & Gordon 1987). However, goats are notorious mixed feeders, able to easily switch between grazing and browsing, and opportunistic foragers of more unconventional fodder (*e.g.*, linen).

When goats are not explicitly referred to in this thesis, the use of the term "animal" is used to refer to large mammalian herbivores in general (examples are given here for W>10 kg). These are the species members of the Bovidae family in the taxonomic suborder Ruminantia, order Artiodactyla (even-toed ungulates), with special reference to livestock and wildlife in the semi-arid regions of the globe, including; subequatorial Africa, Rajasthan, the Middle East, central Australia and equatorial USA. During the course of study, exploratory visits were made to South Africa, Zimbabwe and Botswana, with subsequent field experiments located in South Africa. Model parameters were sourced from sites in Zimbabwe, Botswana, Australia and South Africa.

CHAPTER 2 - UTILISATION OF RESOURCES IN A SPATIALLY HETEROGENEOUS LANDSCAPE

This work is unpublished to date, but was disseminated in part as a poster presentation to the International Rangelands Congress (IRC) 2001 held in Pretoria, South Africa (see Appendix 5).

Abstract

- Heterogeneous landscapes pose animals with foraging decisions to be made across a range of spatial scales.
- Our comprehension of the mechanisms underlying these foraging decisions will remain limited to large-scale processes until it is possible to identify the correct scale at which to investigate the mechanisms operating at finer spatial scales.
- Application of optimal foraging theory would suggest that animals adjust their foraging behaviour in response to the spatial dynamics of their environment, and that observation of their foraging behaviour would provide us with a method by which to associate activity with spatial impact.
- Trials were carried out in a paddock at the University of Fort Hare, South Africa, during which the foraging activities of Nguni and Boer goats were recorded.
- Duration of browsing activity was found to be correlated with measures of spatial impact.
- This relationship was used to investigate temporal adaptation and spatial selectivity by the goats in response to the heterogeneity of their environment.
- Large-scale plant distributions were grouped into phytosociological communities.
- Accumulation of defoliation impacts in one area was followed by utilisation of low impact areas.
- The selection of these areas was found to vary daily and to depend not on the plant community, but on the individual plant species.
- It is concluded that goat foraging behaviour operates at a small scale, that is, the search path.

2.1 Objectives

1. To identify the spatial scale at which animals assess the forage resources in their habitat.
2. To test the response of animals to the heterogeneity of their resources and to characterize that response.
3. To investigate the role of travel costs in determining the utilisation by animals of their resources.

2.2 Introduction

Highly spatially variable environments pose herbivorous animals with diet selection decisions that need to account for the patchy nature of their food resource (Ford 1983), eliciting a response from each animal species according to the degree to which they are affected by this resource fragmentation (Hester *et al.* 1999). Heterogeneity introduces complexity into decision making at a range of different scales (Senft *et al.* 1987), suggesting the need for (evolutionary) adaptations that optimize foraging behaviour (Pyke 1984) and which also unite optimal foraging with animal dispersal (Morris 1992). Given that an animal's energy intake fuels its requirements for basal metabolism, activity and thermoregulation, utilisation gradients would be predicted for situations for which there exists an incremental loss in the net trade-off between nutrient intake and energy expenditure (*e.g.*, the *piosphere*, Lange 1969). The corollary is that animals assay the energy balance underlying travel and intake against the profitability of their resource (Bailey *et al.* 1998). The scale at which this assessment is operational, the influence it has on animal foraging behaviour and the consequence it has for landscape utilisation are not clear. The landscape components that may act as cues for animal behaviour can be found: locally within plants, through whole phytosociological plant communities and up to the landscape and regional level (Senft *et al.* 1987). However, organisms perceive their environment at differing scales (Kotliar & Weins 1990, With 1994, Levin & Pacala 1997). So, whilst mammalian herbivores prospect their environment for an optimal diet (Illius & Gordon 1993), species differ in the cues that they use to do so (Eztenhouser *et al.* 1998). This means that the experimenter should undertake a precursory investigation to identify the appropriate scale at which to study a spatial ecological process and apply a suitable measure of landscape heterogeneity operating at that scale (Dutilleul 1998a). A critical step in this procedure is to ensure that behavioural assessments are made in terms of animal function rather than with respect to resource organisation (Li & Reynolds 1995) thereby providing a method with which to quantify the animal's perceived heterogeneity of its environment (Wiens 1976, Bailey *et al.* 1996).

Within an animal's perception of its foraging range it is unclear what the animal's environmental unit of diet selection might be and whether it follows that clumped resources and patterns of resource utilisation should coincide in their spatial and temporal distribution. Primary decisions at the scale of landscape regions are thought to precede choices made to differentiate between local foraging options (Orians & Wittenberger 1991). Subsequently, an animal's preferential foraging in an area comprising a certain vegetation type may be attributed to regional soil properties, plant phenology or the presence of individual forage species (Fritz *et al.* 1996). It is an attractive proposition that free-ranging mammalian herbivores assess landscapes at diminishing scales: habitats within landscapes, phytosociological communities within habitats, and plants within plant communities. This hierarchy would conform to our own perceptions of landscape organisation, albeit community classifications are diverse and may have little functional basis other than providing a convenient classification of plant density (Klopfer 1969). Even so, as diet selection is partly the result of an interaction between forage abundance and quality (Illius *et al.* 1987), it is perhaps reasonable to define resource patchiness simply in terms of heterogeneity in plant density (Cid & Brizuela 1998).

At the small scale, herbivore selectivity has an immediate consequence for the survival of individual plants and thus the local population dynamics of plant species (Brown & Stuth 1993). Whilst it is unclear what defines a plant community and its boundary, the term 'patch' commonly appears in the literature. Patches have been used to describe the recognisable areas of animal impact that result from localised defoliation impacts (*e.g.*, Morris *et al.* 1999, Illius *et al*. 2002), as well as the precursory areas of attraction that focus the animal activity resulting in those impacts (*e.g.*, Ritchie & Olff 1999, Wilmhurst *et al*. 2000). Patch choice is well documented in a variety of rangeland types (Weber *et al*. 1998), and attempts have been made to quantify spatial pattern generation (*e.g.*, Wallis De Vries *et al.* 1998), and to describe the spatial pattern itself (*e.g.*, Eztenhouser *et al*. 1998, Ritchie 1998, Xin *et al.* 1999). Such attempts to measure spatial pattern are complicated by modification of patch properties, (*e.g.*, patch size) by cumulative local impact and plant regrowth. Ultimately, the impacts of herbivory on heterogeneously distributed resources over time lead to temporal heterogeneity in herbivore resource use (Owen-Smith 1982, Weber *et al*. 1998). This temporal variation in selectivity is an animal response to accumulated defoliation that theoretically leads to an Ideal Free Distribution (Fretwell & Lucas 1970) of both forage resources and foraging activity (Farnsworth & Beecham 1999). The spatial pattern dynamics arising from preferential use of certain patches modify vegetation structure, animal utilisation of these areas and consequent nutrient cycling, and this has the potential to influence subsequent herbivore-vegetation interactions and ecosystem dynamics (Detling 1998).

Ideal Free Theory assumes that animals have ideal knowledge of the location and profitability of their forage resources and unlimited freedom to access those resources. Constraints on animal knowledge (Ranta *et al.* 1999) and perception (Gray & Kennedy 1994) would be expected to cause deviations from an Ideal Free Distribution of animals (*i.e.*, not "ideal"), as would increases in distance travelled and the associated travel costs (Tyler & Hargrove 1997), and the presence of competitive influences on animal movement (Palmqvist *et al.* 2000), such as landscape topography and the location of shade or drinking water (*i.e.*, not "free"). These inconsistencies with predicting animal distribution suggest a need for further investigation into quantifying the match between animal foraging activity and their forage resources in real world scenarios. In reality, animals are indeed constrained by restricted knowledge and challenged by the need to balance daily energy expenditure with energy gained from acquiring food.

Successful prediction of animal utilisation patterns in response to dynamic vegetation resources located within the environmental matrix of large-scale influences should lead to the incorporation of spatial heterogeneity into the management plans for livestock and wildlife. This would provide the potential for improved rangeland management. Although in some cases an alternative would be to eliminate spatial complexity (*e.g.*, Morris *et al.* 1999). Whichever approach, empirical characterization of spatial structure is a necessary precursor to applying spatial ecological theory (Li & Reynolds 1995, Steinberg & Kareiva 1997). Characterization of the spatial composition of a landscape is prone to subjective interpretation by failing to recognize the appropriate scale at which the functional heterogeneity of a spatial process applies (Li & Reynolds 1995) and that the organization of this spatial structure is apparent across a multiplicity of measurement scales (Brown & Allen 1989). In addition, the sampling effort to characterize a landscape in even the simplest detail often precludes satisfactory description of the spatial elements of the study system.

2.2.1 Specific research questions

An objective estimate of environmental heterogeneity might be obtained by extrapolation from patterns of animal foraging behaviour and the consequent defoliation impacts levied on their food resource. However, human and animal assessments of patchiness may vary (Wiens 1976). For example, dependent on the threshold that determines the investment of animal foraging effort, our assessed homogeneity may give rise to heterogeneous animal impacts (Arditi & Dacorogna 1988). If the decision to leave a patch differs considerably between patches (*i.e.*, does not conform to the Marginal Value Theorem, Charnov 1976) and differs from our expectation of animal utilisation across patches, then the patchiness of animal activity will not be found to be in response to the patchiness of their food. This leads us to ask whether the distribution of animal activity is in fact related to the spatial and temporal heterogeneity of the vegetation, and across what scales this coupling may apply. The hypothesis tested by the experiment described in this chapter is that there are 'hotspots' of high forage potential (a function of forage quantity and quality) which are favoured by animals. Following a season of growth, and as impacts accumulate in these areas of high initial (instantaneous) profitability, one can expect that the commensurate reduction in local profitability would cause choice of these areas to be succeeded by preference for areas offering lower initial profitability. Because patch profitability is net of the costs of travel, and travel costs accumulate with distance climbed on a slope (Lachica *et al.* 1999), it follows that a gradient in profitability would be expected for a hillside (of equivalent resources). Animals would be expected to utilize resources according to their location on the slope, dictating the sequence of utilisation by navigating 'least-effort' pathways (Ganskopp *et al.* 2000). This implies animal assessment of the heterogeneity of their resource. If foraging patterns are non-random, animals will impact their resources in response to the heterogeneity of the landscape. The methodology described in this experiment used previously identified, appropriate analysis types (Turner *et al.* 1991), as recommended for comprehensive characterization of a spatial landscape (Bailey *et al.* 1996), to detect and quantify the environmental heterogeneity of a landscape, as indicated by observations of animal foraging behaviour.

2.3 Methods

2.3.1 Experimental paddock

Observations were made during the dry season between 08/06/98 and 21/07/98 in a 19.8 ha section of the Lovedale Camp, on the research farm belonging to the University of Fort Hare, in the eastern Cape, South Africa (32^{o}47'S, 26^{o}51'E). The long-term (1970-1996) mean annual rainfall is 620 mm of which two-thirds typically falls between October and April. Only 347 mm fell during 1997/8, the year preceding the experiment.

The paddock was situated NW to SE across the undulating south escarpment of Sandile's Kop, an approximately 150 m-high outcrop (649 m a.s.l.). The slope of the scarp was steepest at its NW end (20-40^o) and shallowest at its SE end (5-20^o). Loam soils derived from underlying shale were punctuated by a dolerite dyke which ran the length of the paddock, parallel to the slope, and a drainage channel which cut the SE end of the paddock, perpendicular to the slope.

2.3.2 Vegetation

The vegetation type has been described as False Thornveld of the Eastern Cape (Acocks 1953). The paddock's species composition was surveyed using a macroplot scheme where an initial random point was identified as the start of a random walk (bearings were made using a prismatic compass and distances measured with a tape measure). At each point a 2 m x 2 m quadrat was blindly placed and its location recorded using a Trimble Pathfinder Basic remote receiver as part of a Global Positioning System (GPS). Species were recorded by ranking them according to their estimated contribution to the total aboveground biomass captured within the quadrat area, extended vertically to include shrubs / small trees as well as herbaceous cover. So far this follows the Dry-Weight-Ranking method (DWR, 't Mannetje and Haydock 1963) except that all species were recorded (scored 1, 2, 3 etc.), rather than just the top-ranking three species (assumed to contribute 70%, 20%, and 10% to the total biomass, respectively) as is usual for the DWR. The next quadrat location was reached by taking a random bearing and travelling a random distance. In total, 53 2 m x 2 m quadrats were randomly located throughout the paddock (Appendix 1) which exceeds the minimum recommendation of 50 quadrats when applying the DWR to dry rangeland (*e.g.*, Friedel *et al.* 1988).

A large number of woody species were present including *Acacia karroo* (AKAR), *Buddleja saligna* (BSAL), *Cassine* spp. (CASS), *Coddia rudis* (CRUD), *Diospyros lycioides* (subsp. *lycioides*, DLYC), *Euphorbia* spp. (EUPH), *Euryops* spp. (EURY), *Grewia occidentalis* (GOCC), *Hippobromus pauciflorus* (HPAC), *Jasminum angulare* (JANG), *Leucas capensis* (LCAP), *Lippia javanica* (LJAV), *Lycium ferrocissimum* (LFER), *Lycium* spp. (LYCI), *Maytenus heterophylla* (MHET), *Maytenus polyacantha* (MPOL), *Olea europaea* subsp. *africana* (OEUR), *Plumbago auriculata* (PAUR), *Phyllanthus verrucosus* (PVER), *Protasparagus* spp. (PROT), *Rhigozum obovatum* (ROBO), *Rhus longispina* (RLON), *Rhus refracta* (RREF), *Scutia myrtina* (SMYR), *Agave* spp. (Sisal, SISA), *Tecomaria capensis* (TCAP), *Zanthoxylum capensis* (ZCAP) and *Ziziphus mucronata* (ZMUC). Grasses present included, *Aristida congesta* (ACON), *Cymbopogon plurinodes* (CPLU), *Cynodon dactylon* (CDAC), *Digitaria eriantha* (DERI), *Eragrostis capensis* (ECAP), *Eragrostis chloromelas* (ECHL), *Eragrostis curvula* (ECUR), *Eustachys muticus* (EMUT), *Microchloa caffra* (MCAF), *Panicum maximum* (PMAX), *Sporobolus africana* (SAFR), *Sporobolus fimbriatus* (SFIM) and *Themeda triandra* (TTRI). Succulents present were mainly *Aloe* spp. (ALOE), in particular, *Aloe ferox* (AFER), but also *Opuntia ficus-indica* (OFIC). Forbs and Karoo bushes (KARO) and *Cyperaceae* (Sedge, SEDG) were also present. To ensure that vegetation foliage was abundant and avoid influences from recent foraging history, the paddock had remained unused by animals throughout the winter and during the previous summer growth season.

2.3.3 Plant communities

Phytosociological communities were identified from patterns of bush canopy cover visible in an existing 1:5000 aerial orthophotograph in combination with an expert's (Peter Scogings, UFH and University of Zululand) prior knowledge of the vegetation distribution. An orthophotograph was preferred because it has the spectral qualities of a photograph but the spatial attributes of a map, and is therefore more accurate than a standard photograph when deriving areal estimates. Distinct areas were initially identified from the orthophotograph on the basis of patterns of canopy cover. These areas were broadly categorised into numbered classes and lettered subtypes, as; "0 (a-f): open grass", "1 (a-e): sparse bush", "2 (a-c): medium bush", "3 (a-g): thick bush (associated with dolerite)", "4: thick bush (in drainage line)", "5 (a): eroded, with some bush", "5 (b-c): eroded, with moderate bush", "5 (d-e): eroded, with thick bush", etc.. A subsequent aerial photograph (Fig. 2.1a) was obtained using a Kodak DCS 420 Color Infra Red digital camera mounted on a Piper Cherokee 140 aircraft, flying at approximately 2600 m. The resulting image size was 1524 x 1012 pixels, comprising three bands: near infrared (0.7 - 0.8 μm), red (0.6-0.7 μm) and green (0.5-0.6 μm). A remote sensing cluster analysis technique was used to process the 3-band colour composite image and identify a minimal set of classes with which each pixel could be associated based on its spectral features. The areas from the orthophotograph were compared with the predictions of the cluster analysis and the survey of the paddock's species composition. From these sources it was possible to identify six main community types; ACACIA, OLIVE, ERODED, RIVERINE, ALOE and ZIZIPHUS (Fig. 2.1b), some comprising several distinct subtypes, *e.g.*, ACACIA A, ACACIA B, *etc*.. In total, 27 subtypes were identified.

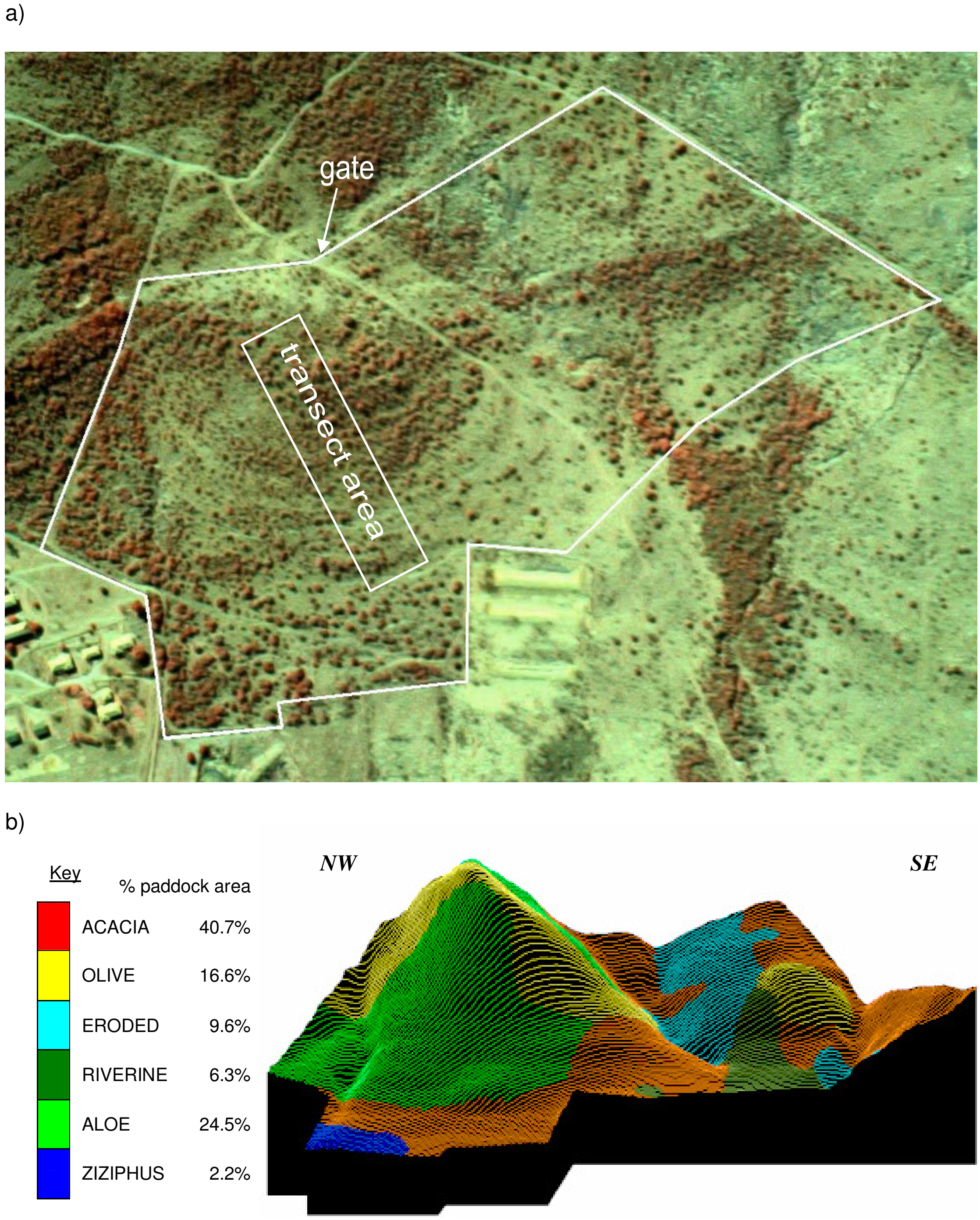


Fig. 2.1: The experimental paddock a) marked on an aerial photograph using an infrared camera, which contributed towards b) a digital elevation model constructed from a contour plot used in conjunction with a map of plant communities showing the community types present and the percentage contribution to the paddock area.

For the whole paddock, plant community categories were amalgamated at two levels to test the role of scale in community preference. The effect was to allow comparisons to be made between three category scales: A, B and C; the scenario including all community subtypes (*A*, N=24), and fusion of neighbouring communities of the same type (*B*, N=13), and combination of all communities of the same type (*C*, N=6). For there to be active preference for a community, the duration of foraging activity in that area must be disproportionately long enough to exclude the likelihood that the observed duration of feeding activity may have been the result of random animal foraging paths within a landscape comprising unequal community areas. Failure to account for community area may result in selectivity simply as a result of availability (Wilson *et al.* 1998). An ANOVA was used to investigate whether any bias occurred in the allocation of feeding time to each community per hectare and on a daily basis for each of these classifications. The null hypothesis was that the goats distributed their feeding effort evenly in the paddock such that feeding time was allocated equally to each unit area throughout the experiment, regardless of the location of unit areas within plant communities.

2.3.4 Animals

A mixed herd of approximately 120 Nguni and Boer goats was used from which 30 individuals were drawn at random and marked for identification. During the course of the 6 weeks of trials, the same herd was introduced into the paddock at the same entry point each day and allowed to range freely until collection, typically 6 hours later, in total accumulating an estimated 260 hours per individual. There was no drinking water provided in the paddock but the animals were watered in the morning before each trial. Although available foraging time was controlled by human intervention, feeding activity, which occupied approximately 66% of daylight hours (in agreement with allometric predictions of active foraging time, 62.9% for the mean weight of the herd 48.3kg, Mysterud 1998, and observations of daytime foraging in medium-sized ungulates, 35-60%, Owen-Smith 1988, and wild goats in particular, 64.7%, Nicholson &

Husband 1992 reported in Mysterud 1998), was minimal upon termination of each trial day.

On 14 days during this period, continuous animal locations for the marked individuals were recorded using a theodolite-single reflecting prism surveying technique in association with a Sokkisha RED1A electronic distance meter, and the GPS. Availability of animal positions for sampling via the theodolite-distance meter method was largely determined by the visibility of the reflecting prism through dense thickets. The GPS was substituted for the theodolite technique when it became available (after trial day 4) to increase the mean data collection rate (from 30 to 163 animal locations/day). Animals were sampled in as random a fashion as possible, given that it was not possible to fully randomise the sampling sequence as animal locations had to be reached with minimal disturbance to the herd. When the randomly selected animal had finished feeding and had moved away from a position, the location was recorded using the GPS, which also automatically logged the time of the recording. The next feeding animal was randomly selected and identified, and the process was repeated. There was a single GPS operator and several observers who worked as a team to announce the random number sequence, identify animals, and mark and record positions. Typically, the locations of 22 different animals were sampled throughout each GPS trial day. Sources of error in the recording of animal locations are discussed in Appendix 2.

2.3.5 Animal activity

Concurrent with the measurement of an animal location, the selection of grass and browse diet species was also recorded. The duration of feeding activity was taken as the interval between the times that were automatically associated with the GPS recordings. Each interval was considered a single feeding "event". This is based on the assumptions that feeding was consistent, and feeding by individuals was randomised, rather than being a synchronised herd activity, and that the previously recorded time was an unbiased estimate of the commencement of feeding by the next animal yet to be recorded. Using several observers made it possible to identify the next randomly-sampled animal sometimes already feeding, but sometimes while it was still travelling to the next feeding site. If animals spend equal times travelling and feeding then the interval between a random point in time and the cessation of feeding is an unbiased estimate of the mean time spent feeding. Although this assumption has not been tested it is assumed here that the mean time interval recorded is an acceptable measure of the mean duration of feeding events and that any bias is small. The median GPS activity duration, used to account for a positive skew to the distribution of GPS recording intervals, was substituted for the duration of all theodolite measurements, as the theodolite technique was too inconsistent to provide a valid estimate of feeding time. Where appropriate, analyses were carried out using total duration, the sum of individual measures of duration (Martin & Bateson 1993), for the activities to avoid autocorrelation problems. Log transformed activity duration values were used to stabilise variances in positively skewed data (Sokal & Rohlf 1995, Webster 1996).

In addition to the location data, the activities of all 30 experimental animals (including diet selection) were recorded at 5-minute intervals throughout the day. In total, 118 theodolite measurements, 1630 GPS measurements, 1748 observations of diet species and 19930 activity observations were collected. Social facilitation may lead to underestimation of variances associated with individual activity. Although such effects have been shown to be small (Rook 1998), animals in a group cannot be considered to be independent and the sample size is unity. Therefore, to correct for the use of individuals as replicates of activity duration (Rook 1999), the duration of each consumer activity (*i.e.*, browsing or grazing) was scaled to the proportion of the 30 experimental animals engaged in like behaviour. Sources of variation in the logged browsing durations associated with the GPS measurements were investigated using a residual maximum likelihood (REML) method in GENSTAT 5.3.2 (GENSTAT 5 Committee 1993) and GENSTAT 7.1 (GENSTAT 7 Committee 2003). For the earlier version of GENSTAT, the significance of fixed-effect Wald statistics was assessed using the method of Elston (1998) and tested at conservative degrees of freedom as discussed in Appendix 2.

A maximum likelihood estimate (MLE) of mixtures of normal distributions N(μ,σ) was obtained for the feeding activity durations using MLE (Derry *et al.* 1998). Fitting a mixture of normal distributions assumes that the observed data comprises two or more overlapping normal distributions with differing means (μ) and variances (σ^2) (Gibb & Ridout 1986). The additional parameter of the mixture is the proportion of each component in the distribution. The best-fit model was selected using Akaike's Information Criterion (AIC, Buckland *et al.* 1993).

2.3.6 Spatial analysis

The following geostatistical methods were used to analyse the point pattern distributions of browsing and grazing activity durations;

1. A nearest-neighbour index analysis (Li & Reynolds 1995) in ARCView (ESRI 1998) was used to test the distributions of browsing and grazing activity locations for complete spatial randomness (Hooge & Eichenlaub 1997). Comparisons were made against a random distribution in favour of a functional distribution model, *e.g.*, an Ideal Free Distribution that relates animal location to forage intake rate (Farnsworth 1996), as this would presuppose heterogeneity. The test returns R=1 for a random distribution, <1 indicates a tendency towards a clumped (clustered) pattern, and >1 indicates an organised (uniform) pattern.

2. A test was devised that attempted to detect an occurrence, or continuity, of cluster size that could be interpretative of a patch structure within the animal's assessment of its resource landscape. A quadrat analysis was carried out by a range of grids of increasing grid square size being superimposed over the activity duration data. The variation of measurements captured *within* each grid cell was compared to the overall variation *between* grid cells. This was the variance ratio (F-value) of an analysis of variance (ANOVA). Because the ANOVA degrees of freedom scaled with the square of grid cell size, it was not possible to infer a patch structure by comparing the significance of differences between the *within* and *between* grid cell variances across the range of grid cell sizes. Instead, it was possible to graph F-

values as a continuous variable, and inspect the response across the range of grid cell sizes. A fitted polynomial curve helped to make a visual best estimate of patch size where the variation ratio was maximal. Because this test lacked the explicit treatment of spatial heterogeneity maintained by the measures of semivariance below, it was best described as a test of “non-spatial heterogeneity”.

3. Moran's I statistic is a measure of autocorrelation (Ripley 1981), similar in interpretation to the Pearson's Product Moment correlation statistic for independent samples (Dutilleul 1998b), in that both statistics range between -1.0 and 1.0 depending on the degree and direction of correlation.
4. GS+ (Gamma Design 1999) was used to calculate the autocorrelation occurring for classes of distances separating each pair of sample points. Browsing and grazing activity duration associated with the recorded animal locations was analysed using this method and the results plotted against the distance classes as autocorrelograms. If spatial variation exhibits the same form in all directions it is said to be isotropic, in contrast to anisotropy where there is a strong directional influence in the distribution of a quantity (Jongman *et al.* 1995). Semivariogram analysis was used to look for anisotropy and trend in the measurements of browsing and grazing activity durations. The spatial semivariances (Cressie 1993) of the log transformed activity duration values were calculated, and commonly used variogram models were fitted using GENSTAT 5.3.2 (GENSTAT 5 Committee 1993).
5. Interpolated surfaces may be predicted most accurately with correct error estimation (the variogram model goodness of fit) by kriging (Webster 1996). Kriging uses the underlying spatial relationships in a data set as optimally given in the variogram model. Krigged surfaces were generated for both the browsing and grazing activity duration data.

2.3.7 Animal impacts

Defoliation impacts were assessed midway through the study period (Survey I), and repeated at the end (Survey II). A tape measure was used to lay 20, 50 m transects, spaced 10 m apart, parallel to the slope of the hill. The transect area was sited on a consistent 1:4 incline in order to investigate whether animals account for energy costs in their assessment of resource profitability (see transect area marked on Fig. 2.1). The transect area cut through four community subtypes; ACACIA/MIXED, ALOE, OLEA/ALOE and ALOE/OLEA (see Appendix 1). The transect termini were located using the GPS. The position of each individual shrub/tree making contact with the tape was recorded along with an assessment of defoliation damage (removal of total available browse material) up to 1.5 m in height, the typical maximum extent for goats (Steele 1996). Defoliation was scored using a 6-point scale, similar to the system of Walker (1976), as follows: 0=0%, 1=1-10%, 2=11-25%, 3=26-50%, 4=51-75% and 5=76-100%. The grass layer associated with each tree scored in this way was taken as the average of four pasture disk meter measurements (Danckwerts & Trollope 1980), each made a metre distance from the tree trunk along a cardinal bearing. The midpoints for the percentage defoliation categories were used to calculate the mean transect impacts for use in Generalized Linear Model (GLM) analysis carried out in GENSTAT 5.3.2 (GENSTAT 5 Committee 1993) and GENSTAT 7.1 (GENSTAT 7 Committee 2003) and an Olmstead-Tukey Corner Test of Association to account for outliers (Steel & Torrie 1980) carried out in Microsoft® Excel 97.

Bias in sampling was tested using a χ^2 test to compare the proportion of times an individual goat was sampled with respect to the sampling frequency for all animals on GPS trial days before and after Survey I. Wilcoxon's Signed Rank test (Wardlaw 1985) was used to check the consistency of the sampling procedure on GPS trial days before and after the first impact survey. Runs tests were used to check the randomisation of goat sampling sequences on GPS trial days (Sokal & Rohlf 1995).

2.4 Results

The goats were observed travelling through a large proportion of the paddock on a daily basis, tending to follow a roughly similar pathway each day to the one established on the first day of exposure to the paddock. Data was not collected on all days during the experiment period which lasted forty-four days, but after only the first day that the goats were introduced to the paddock, on which data was recorded, observations were made in over a third (n=9) of the total number of community subtypes eventually recorded by the end of the experiment period (n=25). Half of these communities were included in the data set four days after the goats were first exposed to the paddock, and observations had been recorded from all communities by the sixteenth day, a third of the way through the experiment period, by which time there had been seven out of the fourteen days of data collection (see Appendix 1). It was noticed how adaptation of the goat's foraging path from day-to-day included taking alternative routes up the hill, incrementally slicing higher up across the face of the slope, but sometimes circumnavigating the hill and gaining the higher ground near the gate via a more gradual slope at the NW end of the paddock (see Fig. 2.1).

2.4.1 Animal activity

Browsing accounted for 97.5% of the total feeding time recorded. The overall average time for a browsing event by an individual on each day was 38.7 seconds (median 23.53 seconds and standard deviation 59.9 seconds). The duration of a single browsing event ranged between 11.3 and 267.5 seconds. Average grazing activity persisted for 30.8 seconds per individual (standard deviation 46.0 seconds). Frequency distributions (Fig. 2.2a,c) for browsing activity duration (on all days) were positively skewed (skewness score from 1.38 to 4.18). The mean is not the most appropriate measure of a highly skewed distribution (indicated by the mean being much larger than the median and an inflated standard deviation). It is better to use the geometric mean, calculated as the back-transformed mean of the logarithmically transformed data, in conjunction with the interquartile range (H-spread or Q3-Q1) (Sokal & Rohlf 1995). The geometric means for browsing and grazing activities were 16.76 and 12.15 seconds, respectively. The interquartile ranges for browsing and grazing activities were 39.37 and 20.29 seconds, respectively.

The frequency distributions of the logged ($\log_{10}$) activity duration measurements were polymodal (Fig. 2.2b,d). The distributions mixture for browsing activity comprised 86.2% of N(μ=29.7 seconds, σ=0.6 seconds) and 13.8% of N(μ=1.0 second, σ=0.5 seconds), with AIC=8609.5. Grazing activity exhibited a weaker bimodality, its double normal distribution comprising 83.8% of N(μ=24.7 seconds, σ=0.5 seconds) and 16.2% of N(μ=1.0 second, σ=0.4 seconds), with AIC=346.0.

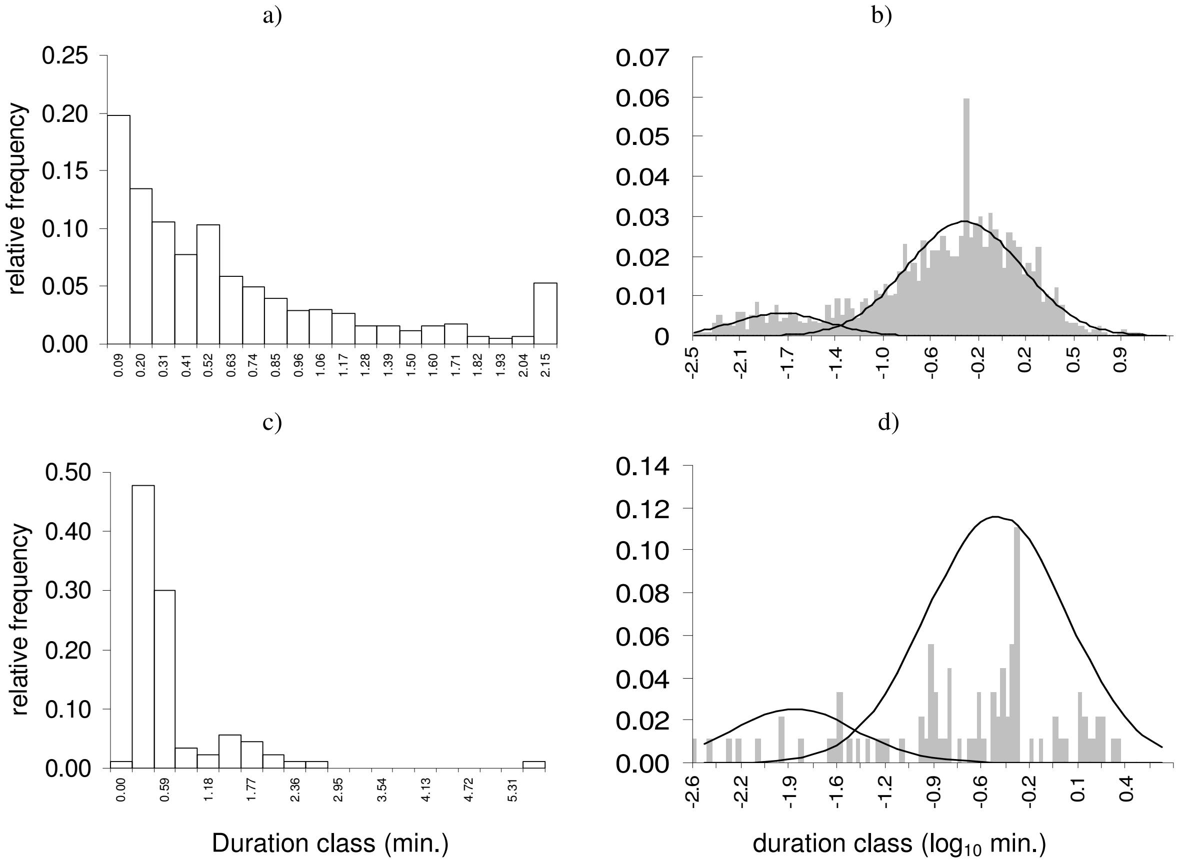


Fig. 2.2: Relative frequency distributions (a,c) and double normal distributions (b,d) fitted to the logged ($\log_{10}$) duration measurements of browsing (a,b) and grazing (c,d) activity.

2.4.2 Animal locations

Tests for bias in the selection of animals for observation showed that the sampling procedure was both balanced (*i.e.*, animals were selected equally, χ^2_{22}=19.35; P=0.621) and consistent across all GPS trial days (N=23, T=89.5, Z=-1.475; P=0.140). A median runs test found no trends in the sampling sequence on all GPS trial days bar two (day 5 χ^2_9=10.04, P=0.347; day 6 χ^2_9=9.68, P=0.377; day 7 χ^2_9=4.06, P=0.908; day 8, χ^2_9=23.32, P<0.01; day 9 χ^2_9=12.73, P=0.175; day 10 χ^2_9=4.26, P=0.893; day 11 χ^2_9=6.51, P=0.688; day 12 χ^2_9=5.58, P=0.781; day 13, χ^2_9=32.31, P<0.001; day 14 χ^2_9=15.69, P=0.074). An up-and-down runs test found no trends in the sampling sequence on all GPS trial days except day 10 (day 5 χ^2_5=3.09, P=0.686; day 6 χ^2_5=2.93, P=0.711; day 7 χ^2_5=6.21, P=0.286; day 8 χ^2_5=1.93, P=0.859; day 9 χ^2_5=3.49, P=0.625; day 10 χ^2_5=20.23, P<0.01; day 11 χ^2_5=2.41, P=0.789; day 12 χ^2_5=3.87, P=0.569; day 13 χ^2_5=3.85, P=0.572; day 14 χ^2_5=5.00, P=0.416). The trends in animal sampling sequences for these days gave rise to bias in the sampling of individuals on only one of these trial days (day 8, χ^2_{22}=33.50, P=0.055; day 13, χ^2_{21}=32.41, P=0.053; day 10, χ^2_{21}=66.45, P<0.001), equivalent to less than 10% of all locations that were recorded within the transect area.

2.4.3 Spatial impacts

The goats expanded the range for their foraging activity measured as the distance from the bottom end (lowest altitude) of the transect area slope (between 1 m and 174 m prior to Survey I, to 11 m and 196 m afterwards), giving a mean position further up the slope for Survey II both in terms of distance (means=60.5 m and 101.7 m, t_{96}=3.53, P<0.001) and altitude (means=540.9 m and 549.6 m, t_{96}=2.89, P<0.01). Goat locations within the transect area showed an increase in the maximum daily distance from the bottom of the slope (*distance*, m) with the accumulation of total browsing time (*browsing*, seconds) from each trial day (*distance* =1.73 *browsing* + 82.25, R^2=0.4, $F_{1,10}$=6.18, P<0.05). On average, this translates into 0.17 m horizontal distance gained, and 0.04 m vertical distance climbed ($F_{1,10}$=6.00, P<0.05), for each minute spent by an individual on the slope. The goats steadily increased their browsing activity within the transect area, given as minutes spent per individual, with each day elapsed since the beginning of the experiment (*browsing* = 0.02 *day* + 0.32, $R^2=0.6$, $F_{1,10}=10.96$, $P<0.01$).

Individual activity duration associated with each impact survey (leading up to Survey I, and then before Survey II) did not differ significantly (means=31.8 seconds and 53.7 seconds, $t_{96}=1.5$, $P=0.13$). Average impacts for each transect were 104% higher in Survey II than Survey I (paired $t_{19}=8.58$, $P<0.001$). A GLM analysis of the transect data (Appendix 3) showed that the selection of tree species within transects accounted for most of the variation in impact (35%) for either survey ($F_{14,383}=24.97$, $P<0.001$), and, that throughout the experiment, the level of that impact varied with the distance upslope ($F_{1,383}=19.07$, $P<0.001$). The overall amount of impact increased two-fold (2.3) during the experiment ($F_{1,383}=154.12$, $P<0.001$) changing in its distribution so that trees at the foot of the slope initially suffered a higher degree of impact than those further upslope ($F_{1,383}=20.58$, $P<0.001$, Fig. 2.3). This was due to selection of different tree species ($F_{14,383}=5.96$, $P<0.001$) prior to each survey. Grass standing biomass was found to decrease going upslope ($F_{19,383}=7.74$, $P<0.001$), and to be mostly associated with the open ALOE community (ACACIA/MIXED: $t_{369}=1.6$, $P=0.11$; ALOE: $t_{369}=3.45$, $P<0.001$; OLEA/ALOE: $t_{369}=1.88$, $P=0.06$; ALOE/OLEA: $t_{369}=0.63$, $P=0.53$) . Grass biomass did not differ between surveys ($F_{1,383}=0.19$, $P=0.66$).

Both browsing time and defoliation impact scores decreased with distance upslope prior to Survey I, and up to Survey II. The average minutes of browsing time accumulated for each transect before Survey I showed a good relationship with average defoliation impact scored for that transect during Survey I (*defoliation* = 0.40 *browsing* + 0.97, $R^2=0.32$, $F_{1,19}=8.27$, $P<0.05$). Extreme values precluded a significant regression of mean accumulated animal browsing activity and average impact score from Survey II ($F_{1,19}=0.04$, $P=0.84$). However, such values are favourably treated by the Olmstead-Tukey Corner Test of Association, which showed that defoliation impacts accumulated since Survey I were positively related with mean accumulated browsing duration (Quadrant sum=20.0, P<0.005). However, the relationship is weaker for Survey II than Survey I such that the overall average impact score was related to the average minutes of browsing time spent per browsing event at each transect distance by *defoliation* = 0.28 *browsing* + 1.63 (R^2=0.11, $F_{1,39}$=4.83, P<0.05; Fig. 2.4). From this regression, the average browsing event of 38.7 seconds approximates to 11-25% defoliation.

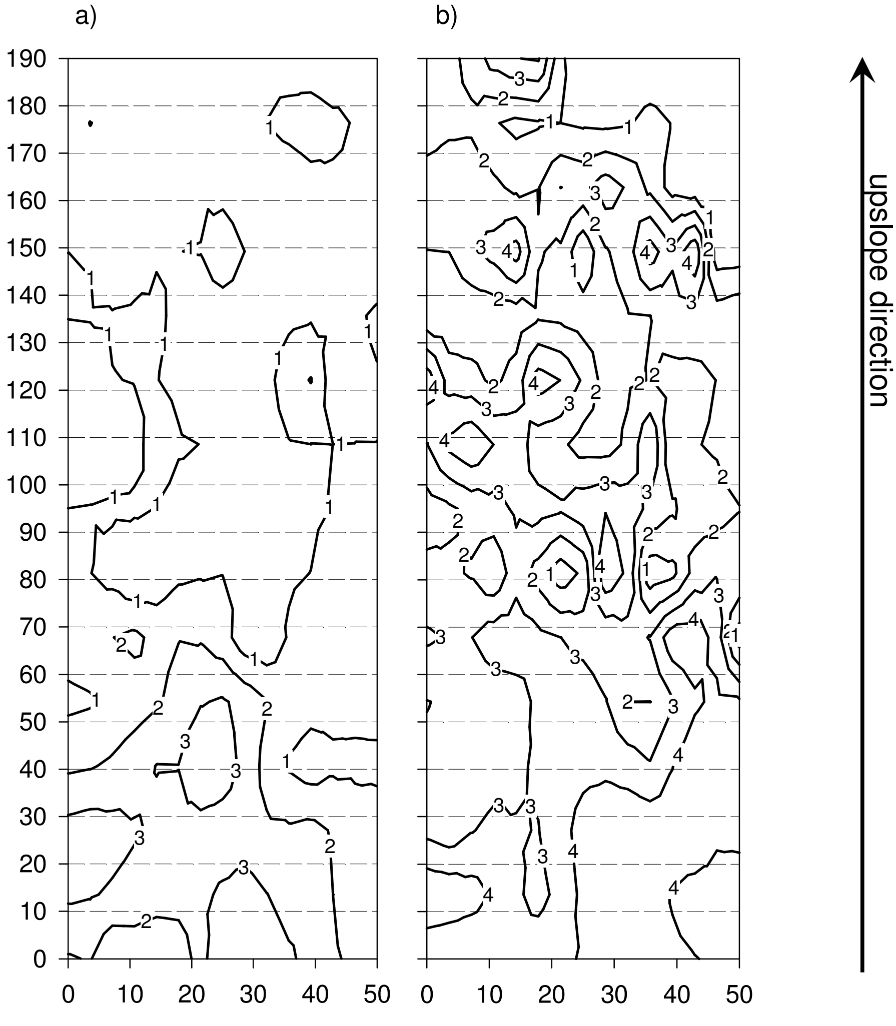


Fig. 2.3: Contour plot showing distribution of impact scores (contour labels), for defoliation by browsing, collected within the 200x50 m transect area (axes) during a) Survey I and b) Survey II. The position of the transect area in the paddock can be seen in Fig. 2.1, and relative to the community subtypes in Appendix 1. Defoliation was scored using a 6-point scale as follows: 0=0%, 1=1-10%, 2=11-25%, 3=26-50%, 4=51-75% and 5=76-100%.

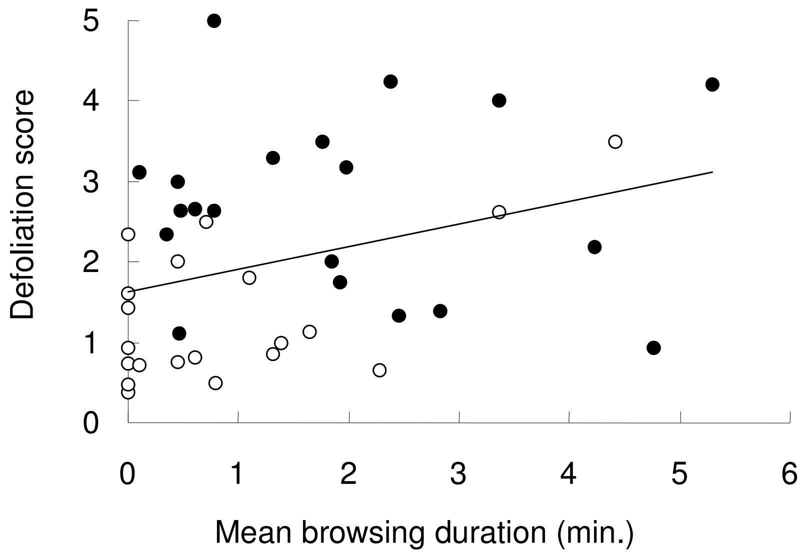


Fig. 2.4: Relationship between defoliation impacts and mean time spent browsing per transect by goats before Survey I (O) and before Survey II (●). The regression is for all the data (see text). Defoliation was scored using a 6-point scale as follows: 0=0%, 1=1-10%, 2=11-25%, 3=26-50%, 4=51-75% and 5=76-100%.

2.4.4 Community selection

The goats were observed to browse in densely wooded areas, and graze in open areas, and rest and graze in shaded areas. Most grazing (30.3%) occurred in the ZIZIPHUS community at the base of the hill, and in the open ALOE community near the gate at the top of the hill. Overall the goats allocated their browsing time to each community type as follows (proportion of total paddock area occupied by each community type in brackets): ACACIA 37.4% (0.40), OLIVE 21.3% (0.18), ERODED 11.0% (0.10), RIVERINE 4.4% (0.06), ALOE 24.6% (0.24) and ZIZIPHUS 1.3% (0.02). At this broadest scale of community category, browsing activity (hr.) summed for each community type was related to community area by *browsing* = 3.177 *area* + 0.024, R^2=0.95, $F_{1,5}$=69.15, P<0.01).

Selectivity for community type by the goats was only apparent for browsing at the finest scale (*i.e.*, no amalgamation, Table 2.1). However this was more an effect of avoidance of a few communities rather than differing use of communities for which feeding duration was recorded (Fig. 2.5). From day-to-day there was variation in the preference for all communities bar ACACIA (ACACIA χ^2_{11}=17.88 P>0.05, OLIVE χ^2_{11}=35.78 P<0.01, ERODED χ^2_{11}=66.62 P<0.01, RIVERINE χ^2_{11}=28.81 P<0.01, ALOE χ^2_{11}=43.07 P<0.01, ZIZIPHUS χ^2_{11}=99.36 P<0.01).

Category Scale	1		2	
	F	P	*F*	P
A	1.70 [26,323](54)	<0.05	1.15 [23,287]	0.295
B	1.32 [12,155]	0.215	0.75 [11,143]	0.693
C	1.58 [5,71]	0.181	1.30 [5,71]	0.278

Table 2.1: ANOVA results showing variation between preference for plant communities as a function of activity time investment. Degrees of freedom are included in square brackets following each F-value. 1) Selectivity was detectable for only community structure A between all communities (for which conservative denominator degrees of freedom are given in parentheses, see Appendix 2), including communities that were avoided and for which no feeding time was recorded. 2) No bias was apparent between communities when avoided communities were excluded.

Investigating the distribution of browsing activity using a REML analysis (Appendix 4) showed that feeding duration was determined by selection of the diet ($F_{21,461}$=2.24, Wald=46.96, P<0.001, conservative df=21,17) and that diet differed between communities ($F_{225,461}$=2.31, Wald=518.77, P<0.001, conservative df=225,13). Diet varied during the course of the experiment ($F_{155,461}$=5.90, Wald=914.83, P<0.001, conservative df=155,4) but not as a function of a shift in community selection ($F_{159,461}$=0.91, Wald=144.65, P=0.786).

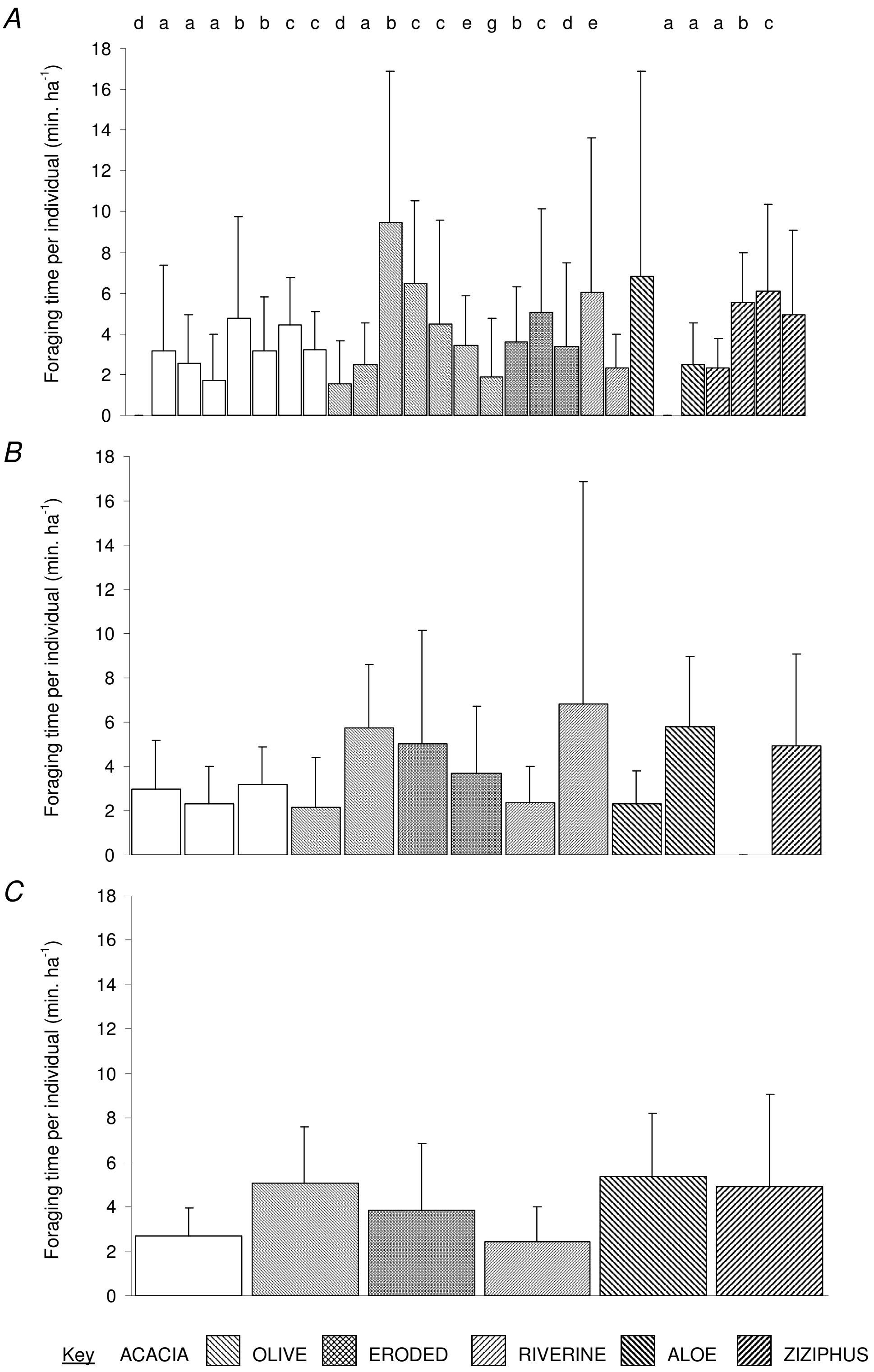


Fig. 2.5: Amalgamation of community subtypes (a … g) giving three category scales, A, B and C, across which to make comparisons of community preferences given by mean daily feeding time per hectare per goat. Error bars show upper 95% confidence limits. See Appendix 1 for details of community subtype classification.

2.4.5 Landscape utilisation

Foraging behaviour cannot be explained in terms of plant associations as communities. Rather, it has been illustrated that goat activity, and the subsequent impact, were distributed according to individual plants. It follows that the cumulative distribution of animal activities should reflect the heterogeneity of plant species distributions. An entirely random distribution of animal activity would not be expected to do so, and would imply that although goat activity was attenuated at chosen sites, foraging paths were not determined by plant distribution.

Nearest-neighbour index analysis of the distribution of browsing locations gave R=0.30, N=1146, |z|=45.26, P<0.001. The distribution of grazing locations gave R=0.08, N=77, |z|=15.43, P<0.001. The distribution of goat locations for both browsing and grazing activities showed a tendency towards clumping, thereby concentrating the duration of each activity within focal areas.

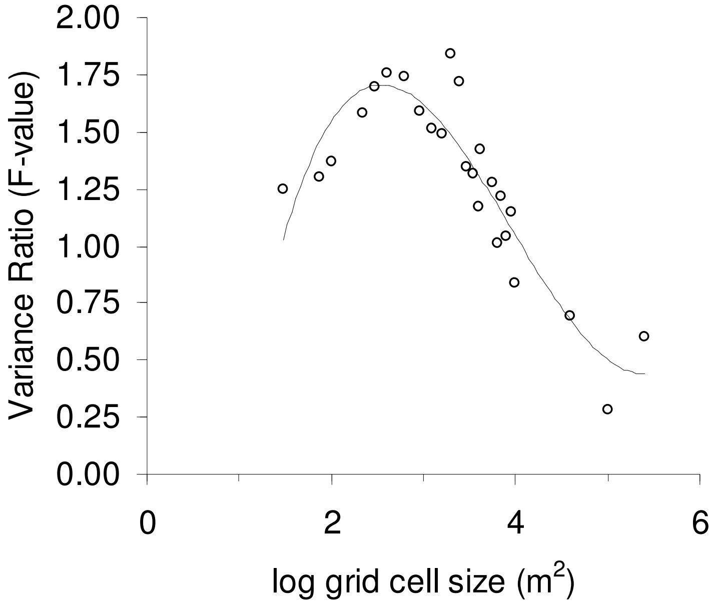


Fig. 2.6: F-values for ANOVA carried out on a range of grid cell sizes in a quadrat analysis of the browsing duration data. The fitted curve is a third order polynomial ($y = 0.112x^3 - 1.329x^2 + 4.590x - 3.211$, $R^2 = 0.85$, SE=0.16) used to help estimate the peak in variance ratio occurring for grid cell sizes from about 100 to 1000 m^2 (equivalent to patch sizes from 10 to 30 m).

The quadrat analysis of non-spatial heterogeneity in browsing activity duration measurements showed a peak in the response of the variance ratio across a range of grid cell sizes (Fig. 2.6). Fitting a polynomial line helped to visually estimate the range of grid cell sizes at which this peak occurred. In agreement with the Nearest-neighbour index analysis above, this peaked response in variance ratio implied a structure within the point pattern of browsing activity duration, and that measured locations were concentrated into clusters estimated between 100 to 1000 m^2. This further implied that animals may have been focussing their activity within [hypothetically circular] patches with radii of about 5 to 15 m, but it is not possible to relate this to, for example, the spatial distribution of tree canopies; the spatial pattern included the influences of gaps in the canopy as well as blocks of solid canopy. Detection of non-spatial heterogeneity in this range of grid scale does not provide comprehensive evidence of a patch structure – simply that the grid cells are sufficiently small to isolate regions of high and low activity duration. The ANOVA failed to detect non-spatial heterogeneity in grazing duration at all grid scales.

Analysis of the spatial data did not rely on the observations being independent of behavioural synchronicity. However, social cohesion within a herd could have given rise to clustered spatial patterns that would be best explained by group behaviour in goats, and recorded animal locations would simply describe the dispersion of individual animals about the herd centre. However, these measures of spatial pattern are unlikely to be surrogates of dispersion for the sampled individual goats within the herd. Firstly, the recorded point pattern results from all trial days, reducing the chance that each cluster arises from a single herd position on a given day by areas being revisited on subsequent days. Secondly, clustering of measurements is unlikely to be an artefact of experimental design as the sampling of individuals dispersed throughout the herd was continuous throughout each day, and all utilised areas were subject to the same sampling conditions. Also, the herd was observed to keep moving through the paddock when browsing was the dominant activity. A herd remaining in one location for some time would have introduced the possibility of enough measurements being made to affect a patch structure. Thirdly, the herd tended to be elongated, extending beyond the maximum patch dimension (30 m estimated by the quadrat analysis of non-spatial heterogeneity). Therefore, whilst social facilitation may have been an influence on some individual behaviour, it is unlikely to have significantly modified the recorded spatial patterns. Blackshaw *et al.* (2003) commented that although herding animals form 'mobs', their dispersion is "influenced greatly by availability of forage".

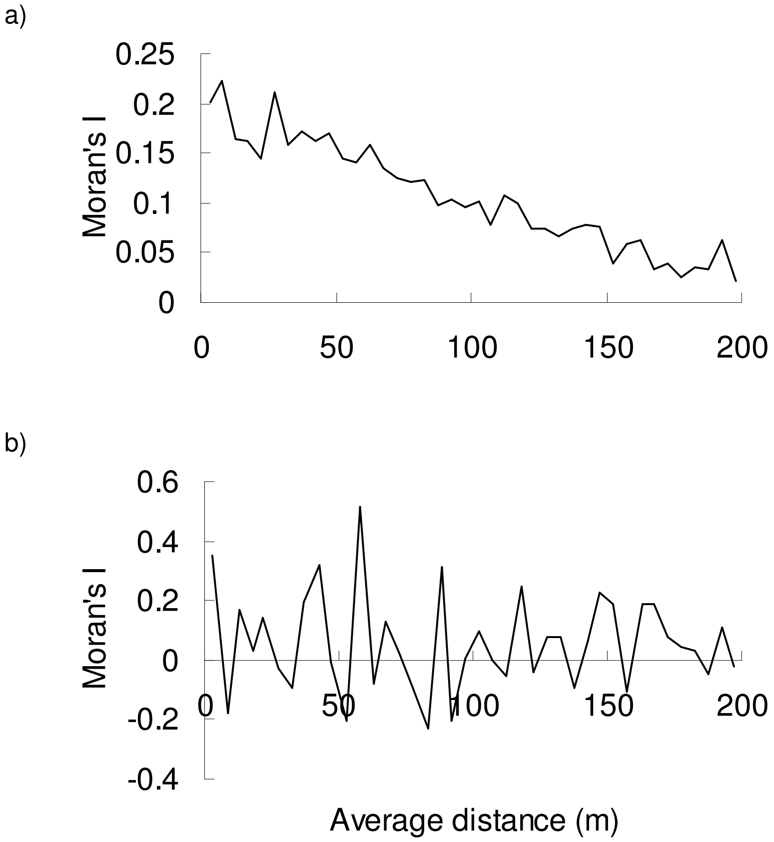


Fig. 2.7: Autocorrelograms for a) browsing and b) grazing activity duration observations.

An autocorrelogram of Moran's I statistic for grazing activity (Fig. 2.7) showed no spatial correlation, but browsing activity showed a gradual decline in autocorrelation to the extent of the data set defined by the paddock boundary (200m). Subsequent geostatistical analyses were also truncated at this distance.

The best fitting variogram model for both data sets was found to be the exponential form (Fig. 2.8) which best describes spatial data as, *abrupt changes occurring at all distances,* *with spacings between changes distributed according to the Poisson distribution* (Jongman *et al.* 1995), supporting the inferences made using Moran's I statistic of autocorrelation.

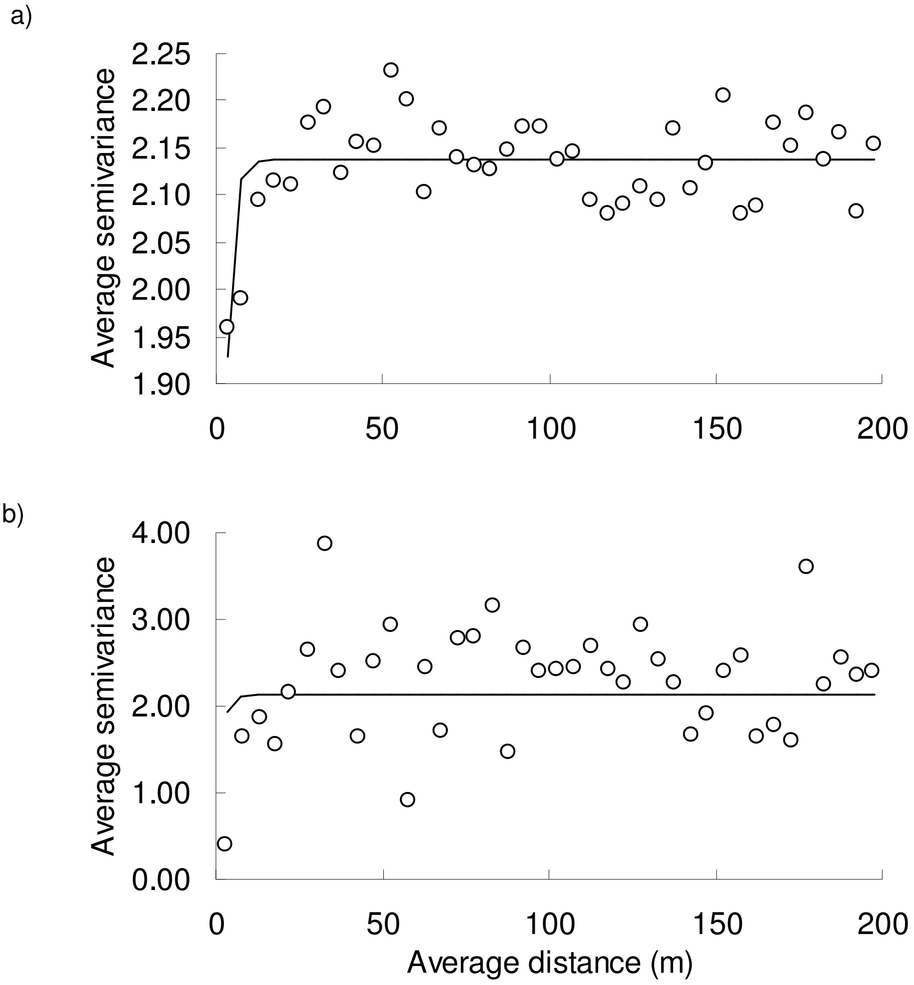


Fig. 2.8: Semivariogram of average semivariance (γ) against distance (h) for a) browsing and b) grazing activity duration observations. The model fitted in each is the exponential form,

Browsing $\gamma(h)=0.66+1.47[1-\exp(-h/1.80)]$ $R^2=0.33$

Grazing $\gamma(h)=0.66+1.70[1-\exp(-h/1.80)]$ $R^2=0.26$

Krigged surfaces for the whole paddock browsing and grazing activity duration data (Fig. 2.9) provide the best available visual representation of the spatial data. From the surfaces it is possible to see that browsing activity was noteably focused on the densely wooded slopes of the Kop (Fig. 2.1), avoiding the eroded portion of the escarpment and the riverine area. Grazing was mainly at the NW end of the paddock. However, no further information would result from subsequent extraction of statistics from those surfaces (*e.g.*, area covered by each duration class).

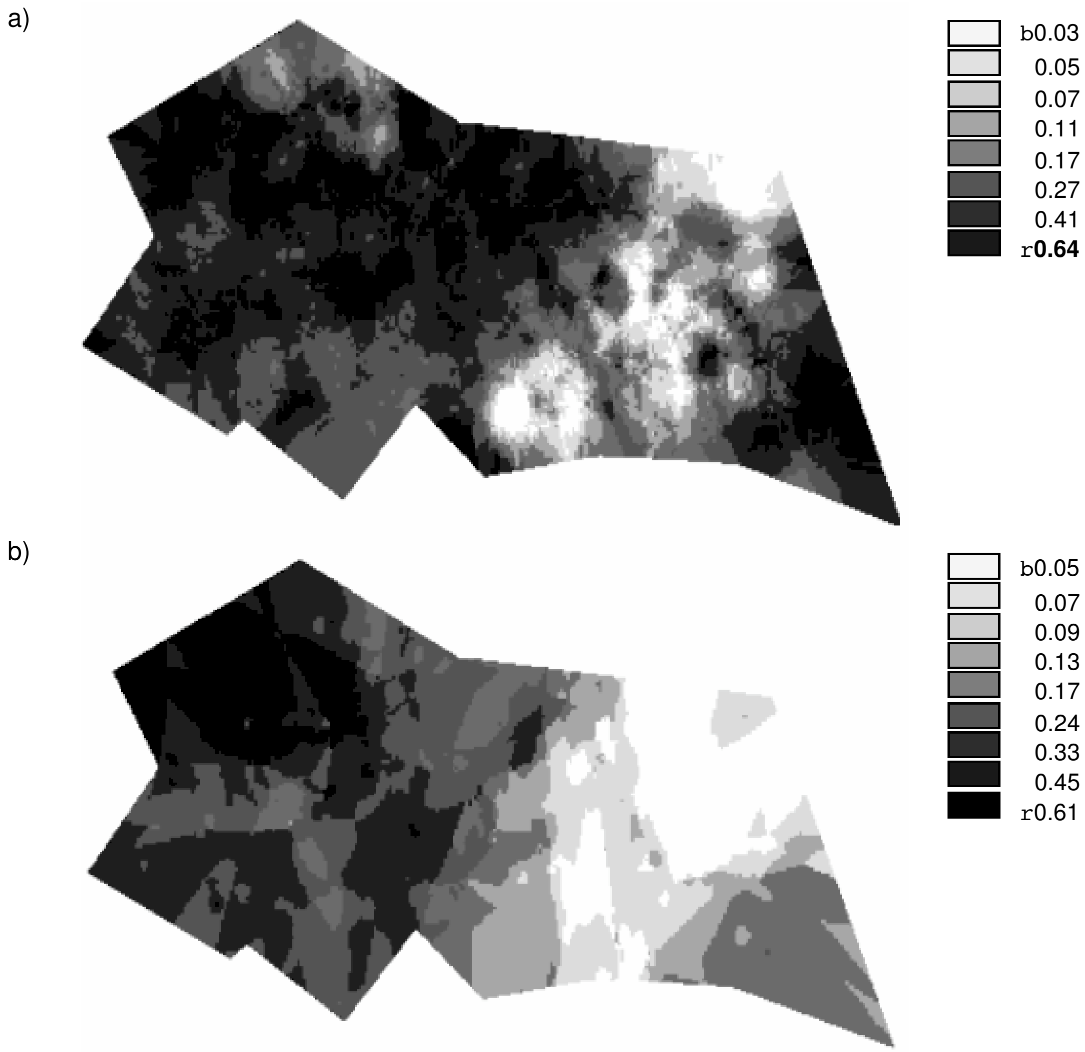


Fig. 2.9: Krigged interpolation of the log of goat activity duration showing the distribution of a) browsing (N=1308) and b) grazing (N=90) within an aerial view of the paddock. The classes of activity duration range from high (darkest) to neglible (lightest) in minutes per individual. See Fig. 2.1 and Fig. A1.1 for comparison with paddock structure, *e.g.*, distribution of vegetation types and location of gate.

2.5 Discussion

Perhaps it is anthropomorphic to expect animals to assess their resource base at different scales? The human brain might make decisions locally, but provides a contextual framework for them by using cues at a wider scale (*e.g.*, which restaurant to eat in before one looks at the menu). One might hypothesise that foraging herbivores make decisions locally from one tree to the next, and similarly use community level cues at a wider scale. In testing this hypothesis we must acknowledge that our community categorizations are highly artificial and is probably not at an analogous scale to that at which animals perceive communities. The appropriate scale for testing animal response to dynamic spatial resources is in question (*e.g.*, Etzenhouser *et al.* 1998). Characterization of resource distribution might typically necessitate exhaustive vegetation mapping. Fortunately, the methodology used to record animal foraging behaviour reported herein offers the added advantage of relative economy in comparison to extensive botanical surveys.

The goats were shown to initially concentrate their impacts on the lower slopes of Sandile's Kop. Subsequently, their attentions were focused on less impacted forage resources to be found higher up the slope, so that, at the end of the experiment, temporal change in foraging behaviour could be distinguished. As the duration of goat feeding activity was found to be a determinant of impact, and it requires higher energetic costs for a goat for reaching food items upslope (31.7 J/kg/m for vertical ascent compared to 3.35 J/kg/m for horizontal travel, Lachica *et al.* 1999), then the shift in foraging behaviour may be explained by application of Optimal Foraging Theory (OFT, Stephens & Krebs 1986). OFT hypothesises that mammalian herbivores select their diet on a basis that maximises their rate of net daily energy intake as a function of their body mass (Illius & Gordon 1987) and prey characteristics (Owen-Smith 1982). Goats increase their forage intake rate as a result of increased bite rates and increased bite sizes (Haschick & Kerley 1997).

It is evident that these processes define the operational scale at which goats assess their environment; individual trees were identified as a selection unit for diet rather than communities, which has also been found in moose (Åström *et al.* 1990). However, it was important to consider the roles of spatial learning and daily accumulated knowledge in the goat foraging decisions. Such information is used in subsequent foraging bouts (Bailey et al. 1989, Bailey 1995, Bailey & Sims 1998, Howery et al. 2000). The same goats were used throughout the experiment, but if they had insufficient experience of the paddock structure, it would not have been possible to make inferences about the scale of selection for unused areas of the paddock. However, as the rate the goats "explored" the paddock seemed high (see Section 2.4), these concerns were allayed.

It was concluded that goat foraging paths cannot be explained by community choice decisions being made concurrent with foraging activity, implying that goat foraging strategies in heterogeneous environments are opportunistic at the larger scale in the absence of principal selection *e.g.*, for location of drinking water. Foraging paths result from a string of encounters with food items, which must be partly connected by chance when forage is sparse. On this basis, it is reasonable that mechanisms of forage intake and animal metabolism are used as the foundation for models of foraging behaviour (Langvatn & Hanley 1996).

Random walk (*e.g.*, Stafford Smith 1990, Renshaw 1991) and diffusion models (*e.g.*, Blackwell 1997, Farnsworth & Beecham 1999) imply that a more stochastic mechanism underlies animal foraging behaviour. The stochastic element in determining foraging paths may account for the partial success enjoyed by random walk models. However, the findings presented here provide empirical support for Gross *et al.* (1995) who proposed that nearest-neighbour models best describe movement patterns “for many herbivores that typically consume visually apparent plants”. In so doing, there is the suggestion that it is the aggregation of individual plants that provides the correlation required to transform random walk models into successful animal foraging strategies, with the optimal degree of correlation inversely proportional to patch density (Zollner & Lima 1999). Indeed, goats have been observed to follow tortuous foraging paths through dense habitats but travel more directly and quicker between sparsely spaced bushes (Etzenhouser *et al.* 1998). Animals improve their foraging efficiency with alternative search patterns for different levels of the hierarchical patch system (Fauchald 1999); whilst the most effective non-systematic search paths are almost straight, an animal with a superior perceptual range is able to elicit similar foraging success from an exhaustive search strategy (Zollner & Lima 1999). So, good sight would be an advantage in sparsely vegetated areas, for the identification of patches in terms of forage species (Illius *et al.* 1999), but susceptible to impedance by physical barriers in denser areas (Etzenhouser *et al.* 1998). This mechanism does not preclude repetition of foraging patterns. Apparently habitual behaviour, could be reproduced on a daily basis in unchanging environments where herbivory impacts are moderate, and the same cues present themselves daily. In addition, there is some evidence that implicates learning and memory in reinforcement of visual cues, in goats (Illius *et al.* 1999) and other animals (Provenza 1995, Tear *et al.* 1997).

The selection of different areas in the paddock for browsing in contrast to grazing, evident from the krigged surfaces of activity durations, shows spatial utilisation of differing areas according to resource distribution. Positively skewed frequency distributions for browsing activity duration are in accordance with the model predictions of Weber *et al*. (1998) at a simulated mean defoliation severity of 25%, and under conditions of intermediate to high defoliation heterogeneity. In their model, increased heterogeneity generated bi- or trimodal frequency distributions of grazing pressure with high frequencies of extreme defoliation severities, and a predominance of lower defoliation intensities with a mean defoliation severity of 25%, which also agrees with the mean defoliation category for browsing from this study. The occurrence of double distributions for goat activity duration implies that two distinct processes are operating in both browsing and grazing. The activity duration distributions that are least present within each double normal distribution mixture may support suggestions of sampling or imperfect discrimination of diet species (Illius *et al.* 1999). Alternatively, in the case of grazing, more protracted periods were observed towards the termination of browsing activity on each trial day, with briefer grazing occurring interspersed with browsing activity throughout the day. Diurnal variation has also been found in sheep feeding on grass and clover (Penning *et al.* 1997).

Quantification of the spatial heterogeneity in point pattern data is limited to measurements of density and nearest-neighbour association (Li & Reynolds 1995) allowing comparisons to be made between distributions in order to investigate temporal sequence (*e.g.*, Haase 1995) and species interaction (*e.g.*, Coomes *et al.* 1999). However, these techniques only utilise locational data in order to derive small-scale information (Cressie 1993). Elucidation of complexity in the distribution of a quantity associated with each location across larger scales requires some form of geostatistical analysis in which variation in a quantity is quantified whilst maintaining the spatial information. The spatial concentration of activity would imply the existence of favoured sites within the paddock, and the longer activity periods in the more abundant normal distributions of each mixture would be expected to be associated with those sites. Geostatistics allows us to analyse these elements of a spatial data set concurrently. In accordance with Weber *et al.* (1998), the lack of evidence for detectable spatial heterogeneity in impacted sites precludes a quantitative characterisation of heterogeneous spatial pattern.

The definition of a patch as a region of the landscape selected for animal feeding behaviour and consequently receiving defoliation impacts is in question. No relationship linking goat diet choices to scales larger than individual trees was found. The range parameter of the semivariogram that otherwise might have provided some information about the concentration of feeding behaviour, *i.e.*, patch size, was too sensitive to the spatial extent across which the model was fitted. Thus, whilst kriging provided an illustrative view of spatial impact, the semivariogram showed no discontinuities that would have provided evidence of a patch structure. The values for Moran's I support the existence of locality effects where neighbouring locations received similar defoliation intensities. This shows that the goats did show selectivity, and that selectivity was controlled by a spatial component of the environment. However, it is not possible to state a specific scale at which this process operated. The linear decay in Moran's I shows that the correlation between defoliation impacts with spatial separation extends to the boundary of the paddock. Discontinuity in the decay would have given a range of patch sizes. Additional inference comes from the exponential semivariogram model. The implication is that concentration of animal foraging activity was evident, coupled with the correlation between these areas being detectable throughout the paddock. So, there is a structure to spatial impacts but, in this landscape, it could not be characterised as a patch structure. Similar distributions of activity duration were recorded on all days, therefore, it is unlikely that temporal selectivity may have sufficiently masked patch structure with the accumulation of intermediate levels of defoliation severity in locations between highly favoured sites.

Daily exposure to a paddock may be expected to generate goat behaviour different from that observed in less contrived circumstances. This experiment will have been subject to the effects of herd dynamics. Social facilitation has been shown to moderate feeding activity (*e.g.*, Rook & Penning 1991, Dumont & Boissy 1999), foraging rate (Provenza & Balph 1988 cited in Haschick & Kerley 1997) and distance travelled (O'Brian 1984), and, therefore, probably also influences travel paths. However, whilst foraging paths seem to be defined by individual plant frequency and distribution, other commitments will play a role in determining goat movements at the landscape scale. The distribution of impacts will be a function of both individual plant distribution and the location of more spatially restricted resources including drinking water (Orians & Wittenberger 1991). The long-term consequence is the generation of a utilisation gradient or piosphere. Some animals travel towards landscape focal points to appease requirements for nutrients (Murray 1995) and water (Walker 1979), despite local plant distributions. Other animals travel to water points to capitalise on local plant distributions (*e.g.*, giraffe, du Toit 1990) or for reasons independent of feeding optimality, for instance, reproductive strategy (*e.g.*, access to females in springbok, Ritter & Bednekoff 1995; intrasexual vigilance in male giraffe, Ginnett & Demment 1999).

2.6 Conclusions

- The goats did respond to the heterogeneity of their resources but their foraging behaviour is affected at the local scale.
- Consequently, impacts from herbivory are distributed such that they mirror the distribution of the resources at the plant species level.
- Browsing only results in the generation of spatially non-random impact patterns as an optimal response to what is locally there, on a plant-to-plant basis.
- The goats preferentially accessed resources with lower travel costs, before methodical utilisation of resources involving higher travel costs. Higher travel costs may be analogous to lower profitability.
- Open areas affording more grazing opportunities were utilised accordingly.
- Clumped resources in the landscape gave rise to the concentration of foraging activity, and the concentration of defoliation impacts.
- The spatial extent of these impacted regions may not have been quantifiable, but their visualisation was achievable using geostatistical methods.

CHAPTER 3 - THE ROLES OF ANIMAL WATERING BEHAVIOUR AND TRAVEL COSTS IN DETERMINING THE DISTRIBUTION OF SPATIAL IMPACTS

Abstract

- Animals exhibit a varying dependency for sources of drinking water.
- Livestock breeds differ in their water requirements and wildlife exhibit adaptations for water conservation.
- Lactation necessitates higher water intake.
- Daily foraging ranges may halve during the dry season, but animals are not distributed according to water requirements.
- The spatial extent of concentrated animal impacts about watering points is not a function of diet selection decisions made within the range of animal foraging.
- Spatial impacts are distributed according to available foraging area.
- There is no threshold distance for animal foraging range arising from a hypothesized conflict between daily energy intake and expenditure.
- Neither energy balance nor energy expenditure on travel costs are important factors in determining the extent of spatial impacts about water.
- Intake constraints and available foraging area combine to dictate the distribution of spatial impacts.
- Predictions of the distribution of spatial impacts are sensitive to the marginal value of forage resources.

3.1 Objectives

1. To investigate the association of water requirements and foraging range to resource utilisation at distance from water.
2. To investigate the influences of travel costs on animal foraging range.
3. To investigate the conditions for generation of the piosphere pattern.

3.2 Introduction

During the rainy season in water-limited regions (*e.g.*, summer in southern Africa) the drinking requirements of animals are met by the collection of water on land and leaf surfaces. Diminished incidence of these water sources during the dry season leads free-ranging animals to frequent localities where surface water persists naturally or where it is provided, (*e.g.*, at boreholes). During the dry season, wildlife may be observed freely moving between several watering points (*e.g.*, Funston *et al.* 1994), whereas livestock movements are dictated by management water provision (*e.g.*, Landsberg *et al.* 1997).

Conceptual models of the ecology of drinking water location hypothesise an isolated watering point located in a topographically consistent and uniform rangeland type (*e.g.*, Collinson 1983). The concentration of animal impacts towards a water point is because of a simple geometry that provides an exponential increase in available foraging area with increasing distance from water (Perkins 1996). The resulting herbivore densities about watering points give rise to the *piosphere*, a gradient of utilisation pressure that is greatest near the water and decreases as a function of distance from it (Thrash & Derry 1999). These spatial impacts of herbivory manifest a nonlinear response in herbaceous species composition, but are also detectable in range condition, grass production, biomass, understory cover, standing crop and basal cover (Thrash & Derry 1999). Pickup & Bastin (1997) showed that slight variation in paddock shape had no effect on animal distribution pattern other than in accordance with available foraging area. Their study did not go on to establish the geometric conditions necessary for piosphere generation.

Several questions can be asked of the interaction between animal watering and foraging behaviour. These behaviours are expected to conflict for the animals' time and energy resources. The most profitable area in which to forage, given a gradient of utilisation pressure, should be found farthest from the concentrated animal impacts near water, but this necessitates energy expenditure to return to the watering point to drink. There is the suggestion of the existence of some threshold distance where energy intake is in excess of energy expended, and net energy intake is maximal. It is also assumed that animals make decisions to resolve the conflict, account for energy travel costs, and actively select areas that offer the highest rate of net energy intake. These expectations follow from the findings presented in Chapter 2, namely that animals respond to the spatial heterogeneity of their forage resources, and travel costs are minimised when an alternative path is available, implying a strategy that maximises net energy intake.

The piosphere pattern is primarily generated by the impacts of sympatric species whilst their home ranges are constrained during the dry season. Where alternative watering points are accessible (*e.g.*, wildlife), animals may reduce forage biomass around a single watering point for several days (*e.g.*, 8 days, buffalo, Funston *et al.* 1994) before moving to another area. If alternative watering points are unavailable then grazing pressures ease through animal dispersal only at the onset of the wet rainy season, although cattle still tend to use ephemeral wet season pans (Nicholson 1985). Thus, each species present at a particular watering point generates spatial impacts according to its foraging behaviour, and the foraging distances of animals that generate a piosphere pattern determine the piosphere's extent. For less water-dependent animals, the time available between drinking bouts is longer, and the distance travelled may be further. Therefore, in a single animal species system, the piosphere extent is thought to be directly related to a species' water requirements, but there is no data to clarify the role in this of animal foraging behaviour and energy balance. The energetic conditions under which a piosphere is generated, and the limits on the foraging range of those animals, and ultimately the extent of the piosphere are not known.

3.3 Specific research questions

This chapter tests aspects of animal foraging behaviour in the generation of the spatial impacts that form the piosphere pattern. Firstly, the active selection of foraging areas at distance from water is studied in an attempt to explain the generation of piospheres. Secondly, the role of animal travel costs in determining the utilisation of forage resources at distance from water is investigated.

Specifically,

1. Are piospheres the result of animal foraging decisions? The "active" model predicts a distribution of spatial impacts independent of available foraging area. The null hypothesis is a "neutral" model that predicts piospheres result from a proportional depletion of resources per unit area towards water. This "neutral" model is defined by the (geometric) increase in available foraging area with the square of distance from water.

   (Hypothesis 1)

2. Because animals expend energy in travel from water to reach energetically profitable resources, during resource acquisition, and on return travel from there to water, is there a threshold distance at which animals optimally balance energy intake and expenditure between drinking events? (Hypothesis 2)

3. It is likely that travel costs have some influence on foraging efficiency. For example, heat production associated with travel in wild species of ruminant has been shown to limit diet selection and maximum energy retention as travel costs rise exponentially per gram of food and bite size declines in the resource supply during the Serengeti dry season (Murray 1991). The corollary of Hypothesis 2 is that animal travel costs dictate the threshold distance for animal foraging. Is this true, and is it reflected throughout the piosphere pattern? (Hypothesis 3)

These questions are tackled by adopting a representative model animal species. It is necessary to firstly establish the watering behaviour of this animal. The water requirements (water needed to maintain body fluids to prevent desiccation, due to losses to evaporation and urination), water intake (water consumed, largely as a function of need and availability), water utilisation (water losses to evaporation, urination and other metabolic processes) and effects of water deprivation all tell us about the animal's watering frequency, and therefore the animal's capacity for travel between watering events. To this end, a comprehensive literature review is presented to collect information about the watering behaviour of this animal. Lastly, three modelling approaches are used to consider the distances travelled by animals between watering events, and whether the energy costs of that travel limit the range of animal foraging behaviour. The final model looks explicitly at whether travel costs have any influence on piosphere development and extent, and seeks to test the existence of a threshold distance at which animals forage optimally.

3.4 Goat water requirements

Animals need to maintain a water balance within acceptable limits for homeostatic function. Lethal levels of water loss are reported for mammals at 20-36% of body weight (Adolph 1943 cited in Peters 1983). Body water is lost in urine, fæces and evaporation (in the sweat of larger animals, from nasal passages and in the breath of smaller animals whilst they pant to thermoregulate). In ruminants, water lost in fæces is approximately equal to that in urine because of the high-fiber content of their diet, which requires water to aid transport through the gastrointestinal tract. Cattle fæces contain 75-85% water while sheep and goat fæces have 60-65% water, depending on diet water content (BOA 1981).

Replenishment comes from drinking and differentially from the higher water content of some food, the relative importance of each source varies with animal feeding type and season. Water requirement to replace the loss is proportional to body weight (W, kg) raised to the power of 0.82 (MacFarlane & Howard 1972); a male goat of 53 kg is predicted to require 18.2 ml $kg^{-1}d^{-1}$ which equates to only 0.97 l d^{-1}. Thus, smaller animals have larger water requirements relative to their body size than larger animals (*i.e.*, $W^{0.82}/W = W^{-0.18}$). However, it should be noted that this general prediction is not reflected in the data associated with Fig. 1.1 (water consumption $\propto W^{1.237}$). Young individuals are known to consume more water in proportion to their body weight than mature [non-lactating] individuals of the same species (McDowell 1972, see Section 3.5, below). The reason may be that MacFarlane & Howard (1972) based their estimate of 0.82 on a narrower range of body sizes (40.3 - 520 kg) than that included in Fig. 1.1 (13 - 3000 kg), although 0.82 closely agrees with the range of exponents for water metabolism (0.80 - 0.85) found by Adolph (1943). Kay (1997) goes on to say that this greater need in small animals is how

167 million goats in Africa (8% of the total biomass of domestic ruminants) account for 11% of the water demand, whereas the 181 million cattle (70% of the biomass) require 65% of the water.

Water consumption is generally related to temperature (McDowell 1972), therefore, deviations from the allometric relationship largely arise from species adaptations to dehydration such that livestock (particularly exotics) tend to be more dependent on frequent access to supplementary water than wildlife (Table.3.1).

	W (kg)	Reported water requirements (ml kg^{-1} d^{-1})	Predicted water requirements (ml kg^{-1} d^{-1})
Hereford	200 – 250	46.2 - 64.2	53.9 - 64.8
Zebu	250 – 350	19.5 - 32.2	64.8 - 85.4
Buffalo	160 – 230	34.3 - 45.8	44.9 - 60.5
Eland	133	37.4 - 54.9	38.6
Wildebeest	157	29.9 - 48.1	44.2
Oryx	75 – 110	18.8 – 30.0	24.1 - 33.0
Thompson's gazelle	11 – 15	22.0 - 27.4	5.0 - 6.5
Grant's gazelle	20 – 30	20.8 - 38.6	8.2 - 11.4

Table 3.1. Reported (Taylor 1968) and predicted ($0.7W^{0.82}$) water requirements in ruminants across a range of body weights, W (kg). Reported values are for experimental animals exposed to heat stress between 20 - 40 °C.

Wildlife exhibits several key physical and behavioural adaptations to their physical environment. Rather than panting or sweating, a livestock strategy that loses water, wildlife tend to tolerate a raise in body temperature (Walker 1979), *e.g.*, Grant's and Thompson's gazelle only resort to panting at ambient temperatures above 40°C (Taylor 1972). This is made possible by a counter-current system of blood cooling, in which the heat from warm arterial blood on the way to the brain passes across to cooler venous blood in the nasal passages (Taylor 1972). Water is also conserved by minimal loss to waste products; dry fæces and concentrated urine. A typically light coat colour and increased surface area, for example, large ears, reflect solar radiation such that coat temperature may rise above air temperature causing a flow of heat away from the skin (Louw 1970). An uneven distribution of fat also avoids insulation of body heat. Behavioural adaptations include seeking shade and night feeding to take advantage of leaf dew and higher plant tissue moisture content (Eltringham 1984, Estes 1991). It is acknowledged that some of these adaptations may be by-products of other adaptations.

3.5 Goat water intake

Rate of water intake for the individual also scales allometrically with body size. For mammals ($0.01<W<2000$ kg),

$$\text{Water Intake} = 1.21\text{x}10^{-3}\ W^{0.88}\ \text{ml s}^{-1}$$

(Adolph 1943 cited in Peters 1983). This equates to 64.2 ml $\text{kg}^{-1}\ \text{d}^{-1}$ for a mature male goat of 53 kg and 67.6 ml $\text{kg}^{-1}\ \text{d}^{-1}$ for a corresponding mature female of 37 kg. It follows that younger animals consume more water in proportion to their body weight than mature, non-lactating individuals (McDowell 1972). However, the relationship underestimates water intake for adult non-lactating African livestock under ranching conditions (Table.3.2). It is worth noting that habitual intake of water in excess of base requirements has been observed in cattle (Phillips 1993).

	W (kg)	Reported water intake (ml $\text{kg}^{-1}\ \text{d}^{-1}$)	Predicted water intake (ml $\text{kg}^{-1}\ \text{d}^{-1}$)
Goats	30	66.7	57.5
Sheep	35	68.2	54.3
Zebu cattle	350	51.8	46.9
Camel	500	49.6	36.8

Table 3.2. Reported (King 1983 cited in Kay 1997) and predicted (eq.1) values (ml $\text{kg}^{-1}\ \text{d}^{-1}$) for water intake volumes for animals across a range of body weights, W (kg).

Type	W (kg)	Non-lactating female water intake (ml kg^{-1} d^{-1})	W (kg)	Lactating female water intake (ml kg^{-1} d^{-1})
Black Moroccan	~20	36 ± 4	33 ± 1	46 ± 5
Black Bedouin	17.7 ± 2.4	~85	20.6 ± 3.3	290
Swedish Domestic	~40	47.5 ± 2.5	42.8	137.7 ± 9.3

Table 3.3. The effect of reproductive period on goat water intake (ml kg^{-1} d^{-1}).

Reproduction demands additional water requirements for the individual. Water intake is 26% higher in pregnant Baladi goats (Hassan *et al.* 1989). Lactating animals have higher water needs due to the additional loss of water to milk production (Table.3.3) and are commonly used as experimental animals on this basis (Olsson *et al.* 1997a). In lactating black Bedouin goats, food consumption may be doubled and water intake (290 ml kg^{-1} d^{-1}) can be over three times that of non-lactating stock (85 ml kg^{-1} d^{-1}) (Matlz *et al.* 1982). Lactating black Moroccan goats consumed 46 ± 5 ml kg^{-1} d^{-1} whilst producing 21 ± 1 ml kg^{-1} d^{-1} of milk compared to 36 ± 4 ml kg^{-1} d^{-1} in non-lactating animals (Hossaini-Hilali *et al.* 1994). This is not simply in response to increased dry matter (DM) intake during lactation as indicated by a water/DM ratio of 1.7 in lactating goats and 1.3 in non-lactating goats (Hossaini-Hilali *et al.* 1993). Olsson *et al.* (1996) found that during periods of pregnancy and lactation in Swedish domestic goats, insensitivity to inhibitory signals arising from the oropharyngeal tract resulted in immoderate water intake. These drinking inhibitors transmitted by the ‘thirst center’ in the hypothalamus can also be overridden by warmth receptors that stimulate drinking in response to heat stress (Olsson *et al.* 1995). Water temperature more than 10^{o}C below ambient temperature tends to decrease water consumption in livestock (McDowell 1972) and provision of warm water (35^{o}C) in addition to cold water (15^{o}C) further stimulates water intake in heat–stressed lactating Swedish domestic goats (from 137.7 ± 9.3 ml kg^{-1} d^{-1} to 214.8 ± 37.4 ml kg^{-1} d^{-1}) such that associated reduction in milk secretion can be countered by increasing water intake (Olsson *et al.* 1997b). However, insatiable thirst for warm water may also bring about hyperhydration (Olsson & Hydbring 1996).

3.6 Goat water utilisation

One might expect the rate at which imbibed water is utilized, (expressed per unit time as total water turnover), to be comparatively low in species adapted to arid regions. Indigenous goats have a turnover rate as much as 11% lower than that of sheep at high temperatures (McDowell 1972).

However, this is in disagreement with Nicholson (1985) who ranks goats with higher turnover rates (81-208 ml kg^{-1} d^{-1}) than Zebu cattle (70-197 ml kg^{-1} d^{-1}) and indigenous sheep (74-200 ml kg^{-1} d^{-1}), with camels having the lowest turnover rate (37-74 ml $kg^{-1}d^{-1}$). Kay (1997) compares data from the same or similar sources finding low turnover rates in wildlife and indigenous breeds, and higher rates for exotics, with goats having a higher rate (94 ml kg^{-1} d^{-1}) than Zebu cattle (75 ml kg^{-1} d^{-1}), but a lower rate than western cattle (161 ml kg^{-1} d^{-1}) and sheep (102 ml kg^{-1} d^{-1}). Another source of data quotes values of 148-162 ml kg^{-1} d^{-1} for shorthorn cattle, 131-136 ml kg^{-1} d^{-1} for western cattle in Kenya, 88-90 ml kg^{-1} d^{-1} for western cattle on humid pastures, 135 ml kg^{-1} d^{-1} for Boran cattle in equatorial desert, 76 ml kg^{-1} d^{-1} for Boran cattle in arid equatorial grassland, 112 ml kg^{-1} d^{-1} for Zebu cattle on tropical pasture during the wet season, 87 ml kg^{-1} d^{-1} for unspecified indigenous cattle, 88-133 ml kg^{-1} d^{-1} for Merino sheep, 104 ml kg^{-1} d^{-1} for Romney sheep, and 52 ml kg^{-1} d^{-1} for goats in central Alaska during winter (MacFarlane & Howard 1972).

It can be seen from these gathered data how contradicting reports may result from water turnover rate varying markedly within and across breeds and species. Whilst temperature and diet have been shown to have an influence, there is evidence of a strong genetic control of water turnover rate. This is more clearly illustrated by a comparison carried out between a desert type of Zebu cattle (Baggara) with a lower water turnover rate of 73-90 ml kg^{-1} d^{-1}, giving a higher water retention and total body water, than in a riverine type (Butana) with a turnover rate of 79-129 ml kg^{-1} d^{-1} (Ahmed & El Hadi 1996). Desert-adapted goats and sheep have also been found to display superior water economy than non-desert types (*e.g.*, Shkolnik *et al.* 1972, Hassan *et al.* 1989).

An allometric scaling of total water turnover in mammals ($0.01<W<1000$ kg) is given by,

$$\text{Total Water Turnover} = 1.36\text{x}10^{-3}\ W^{0.86}\ \text{ml s}^{-1}$$

(Altman & Dittmer 1968 cited in Peters 1983). Again, for a mature male goat, expected daily total water turnover is 67.9 ml kg^{-1} d^{-1} and 70.3 ml kg^{-1} d^{-1} for a mature female goat. An alternative form gives,

$$\text{Total Water Turnover} = 1.42\text{x}10^{-3}\ W^{0.80}\ \text{ml s}^{-1}$$

(Eberhardt 1969 cited in Peters 1983), predicting daily total water turnover to be 54.7 ml kg^{-1} d^{-1} and 59.5 ml kg^{-1} d^{-1} for a mature male and female goat, respectively. Both allometrically-derived estimates are below the lower limit of Nicholson's range, and support McDowell's position. Hossaini-Hilali *et al.* (1994) found black Moroccan goats retained typical volumes of ingested water following rapid absorption, but lost 46% of excessive water after hyperhydration within 6 hours, also indicating a low water turnover rate.

Within species and breeds, young animals appear to have higher rates of turnover than adult animals, and adult female goats are reported to have a higher rate than adult males (Khan & Ghosh 1983).

Lactation increases turnover rate by 44% in both camels and Merino ewes (MacFarlane & Howard 1972).

3.7 Water deficiency in goats

The ruminant gastrointestinal tract that serves as a fermentation chamber for the microbial breakdown of their diet also doubles as a reservoir for water (Sneddon & Argenzio 1998). Water is required for fermentation of cellulosic carbohydrates and lignin, constituting 85-90% of the gut content (Sneddon & Argenzio 1998). But when an animal is dehydrated, 20-80% of this water can be reabsorbed to maintain body fluid homeostasis (Silanikove 1994).

Infrequency of watering decreases the volume drunk upon eventual exposure to water (*e.g.*, 50% reduction in Barmer goats, Khan *et al.* 1978), but also carries with it an associated weight loss, or loss of weight gain potential. Lactating and non-lactating black Moroccan goats deprived water for 48 hours lost 9% and 6% of their body weight, respectively, with 28% reduction in milk production and a slight decrease in food intake (Hossaini-Hilali *et al.* 1994). Depriving black Bedouin goats of water for four days caused 32% loss of body weight in lactating individuals and 23% loss of body weight in non-lactating goats (Maltz *et al.* 1982). Olsson *et al.* (1996) found similar rates of body weight loss as above in pregnant and lactating Swedish domestic goats deprived water for 30 hours in addition to reporting that "Catching sight of water was the most exciting procedure [for the goats] during these experiments". This emotional state in the goats, as quantified by measurement of plasma cortisol concentrations, was similar to the response in starved goats upon seeing food (Olsson *et al.* 1995) and in restrained goats (Eriksson *et al.* 1994 cited in Olsson *et al.* 1996).

Species	Recommended units of total dissolved salts in drinking water (%)
Camel	5.5
Goat	1.5
Sheep	1.3 – 2.0
Cattle	1.0 – 1.5
Donkey	1.0
Horse	0.9
Pig	0.9

Table 3.4. Tolerance of salty drinking water by different livestock. After Nicholson (1985).

Intake may be stemmed by contamination of water sources and by the presence of high levels of mineral salts (McDowell 1972) in excess of that recommended to avoid kidney damage from concentrated urine (Table.3.4).

3.8 Goat watering frequency

During the dry season, animal available foraging time is restricted to the interval between drinking events when they must return to a watering point to re-hydrate. Simply comparing daily water intake rate (64.2 ml kg^{-1} d^{-1}) with daily turnover rate (mean 61.3 ml kg^{-1} d^{-1}) implies a requirement to drink on a daily basis (every 25 hours). This is based on a mature male goat alone and so does not take into account lactation costs. However, to verify this estimate of watering frequency, total water intake at a single drinking event and subsequent water turnover rate is sufficient to calculate the interval to the next required drink.

The volume of total water intake was measured for a herd of 40 goats at the University of Fort Hare, South Africa, by recording the height of water in a trough immediately before and after the herd had drunk. Using the dimensions of the drinking trough it was possible to covert the difference between water surface heights into a volumetric measurement of the total amount of water removed by the herd, and therefore, into an estimate of consumption per head, ignoring individual variation from size, sex and reproductive status. On average, each goat drank 1.97 litres of water. The mean weight of the herd was 48.3 kg, hence the above estimate of mean daily turnover rate would suggest that this volume of water would be utilized in about 16 hours.

Assuming that there is sufficient herd cohesion (through, for example, social facilitation), for individuals with the highest water requirements in the group (*e.g.*, lactating females) to meet their requirements, the range 16-25 hours must be considered an overestimate of the interval between drinking events. On the other hand, water turnover rate estimates are likely based on the rate of disappearance of injected tritiated water, during short active feeding periods, and do not account for resting and sleep (*e.g.*, Maltz *et al.* 1982). Metabolism is probably less calorific when resting than during foraging bouts and nights are cooler and may also retard water turnover rate.

Other literature estimates state that cattle need watering between 2 and 5 times per day (BOA 1981), to every three or four days (Nicholson 1985). Deer visit water daily, day and night (Boroski & Mossman 1998). Sheep and goats need watering every one or two days (McDowell 1972, Adogla-Bessa & Aganga 2000) but show no signs of distress between three (Adogla-Bessa & Aganga 2000) and five days without water (Nicholson 1985), and Somali sheep and Galla goats need watering only once a week (Nicholson 1985). The minimum value reported here from the literature is in agreement with the above estimate of goat watering frequency. To allow for smaller animals and lactating females, it is assumed that goats return to water each day, defining the time that they have available to forage, and travel to areas of most profitable forage resources.

3.9 Literature estimates of goat foraging range

Little is known about short-term migratory behaviour to and from a watering point (compared to mass migrations, *e.g.*, Kalahari wildebeest). However, it is reasonable to assume that animals will seek to forage at the maximum possible distance away from water due to the near-water degradation of their resource base associated with such landscape foci. This will occur if the animals are sensitive to the level of impact (see Chapter 2), such that the impact is sufficient to be a constraint on required food intake. It is feasible that animals will select foraging orbits that coincide with a threshold in the tradeoff between nutrients and water. It is possible that there is some flexibility in this threshold. For example, cattle having to travel more than 0.25 km to water reduce their water intake to the minimum required for physiological function, with forfeit of habitual intake that is surplus to requirement (Phillips 1993).

Active foraging time is inversely (allometrically) related to the body weight of ruminants in North America and Europe, with an additional influence of animal feeding-type (Mysterud

1998). The slope is negative because it arises from the relationship between food quality and retention time. Rumination of low quality forage takes time; time which could otherwise be allocated to the throughput of new material. Consequently, goats, in temperate regions at least, are able to spend more of the available time actively foraging (43.8-75%) than larger animals (37.5-70.1%). This implies that if large distances are to be covered between preferred forage sources and drinking water, smaller animals may have more daytime available for trailing to the watering point once their nutritional requirements have been met. Food intake requirement varies across animals of different body size and condition. Also, the distance that an animal may travel whilst foraging between drinking events is determined by an optimal balance between intake and energy expenditure whilst sufficiently hydrated. It follows that for independently motivated individuals, foraging distances will differ according to their mass and reproductive status. Oestrus in cattle can cause ordinarily range-limited individuals to walk uncharacteristically large distances, such as 3.4 times their average daily range (Phillips 1993).

The areas occupied each day accumulate to converge on a maximum area covered (N>150 days, impala, Murray 1982; N>57 days, goats, O'Brian 1984). This maximum area is the animal home range, the total area covered by a free-foraging animal, and has been traditionally estimated using serial observations of animal distributions (*e.g.*, Prins 1989), or calculated as the area enclosed by animal sightings (*e.g.*, Brown 1966). Thus daily ranges may account for only a fraction of total range (*e.g.*, 9-43%, O'Brian 1984) and this may explain some of the discrepancy between various allometric relationships that have been proposed relating such estimates of home range size and body size (Reiss 1988). In an attempt to surmount this problem, a jack-knifing technique has been suggested as an appropriate preparation of trajectory data before its use in estimation of home range (Robertson *et al.* 1998). Alternatively, some daily ranges may tend towards the maximal foraging range. For example, goats in Norway have been noted to travel between 6 and 13 km during a single daily foraging excursion (J. Raats *pers. comm.*). These distances are similar to those recorded by Lachica *et al.* (1999) showing seasonal variation in the mean daily distances travelled by goats (dry season 8.6 km, wet season 11.4 km).

Social facilitation may modify the behaviour of individuals in contrast to more predictable foraging behaviour (Rook & Penning 1991, Rook & Huckle 1995). Coercion by larger animals may extend the natural foraging ranges of smaller animals, giving an intermediate range (Table.3.5), but these differences may simply arise from differences between body sizes (Harestad & Bunnell 1979). In the context of activities associated with the requirement to drink, the interactions between dominant individuals, age classes, and other cohorts, may determine when animals move towards water and the speed at which they do so.

Class	Area range (x 10^5 m^2)	Daily distance travelled (km)
Female herd	0.84 - 4.13	1.68 - 8.26
Male herd	1.60 - 5.40	3.20 - 10.8
Composite herd	1.03 - 2.72	2.06 - 5.44
Stayer female	0.15 - 1.08	0.30 - 2.16
Creche	0.26 - 0.65	0.52 - 1.30

Table 3.5. Daily range areas for social classes of feral goats and corresponding daily distances travelled. Social classes were defined as; Female herd: all adult females and juvenile animals; Male herd: males aged 3 years and older; Composite herd: all adult males, females and juveniles; Creche: juveniles in the absence of adults; Stayer female: lactating females separate from the female herd. Areas were measured using a scaled grid of 50 x 50m quadrats. Distances were calculated as Area x $50m^{-1}$ before unit conversion. Adapted from O'Brian (1984).

Wet season heat stress presents an animal with increased water loss as evaporation and as investment in thermoregulation, therefore, it is only the occurrence of ephemeral water sources during the wet season that permits animal dispersal. During this time sedentary animals (*i.e.*, non-migratory) may double their daily range (Fig. 3.1). Conversely, scarcity of food resources under extreme dry conditions (*e.g.*, drought) can force foragers beyond their wet season range (Redfern *et al.* 2003).

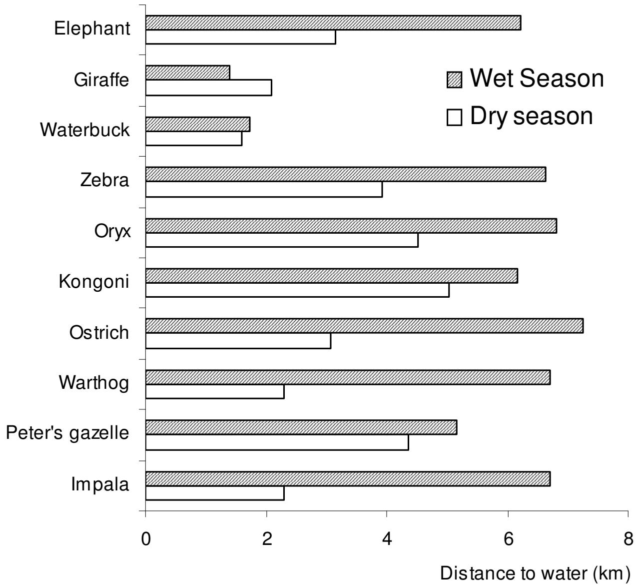


Fig. 3.1. Observed distance of wildlife to water showing extension of animal foraging range during the wet season (Data from Ayeni 1975).

In addition to these factors, protected wildlife tend to frequent more than one watering point (Young 1970). So, the maximum distance indigenous large herbivores have been observed from watering points in the dry season varies, for example, 10-15 km in Amboseli (Western 1975), 12-16 km in Kruger National Park (Van der Schijff 1957).

Cattle in central Australia have been observed moving up to only 4 km from water under favourable conditions, and extending these movements to 10 km in poor quality habitats and 20 km in highly degraded habitats (James *et al.* 1999). Nicholson (1985) suggests a 7 km foraging radius for cattle on every day between drinking events. Western (1975) observed goats up to 15 km from water during the dry season, and at 14 km from water for the same season, but during a drought year. On average goats and sheep were observed at 3.43 km from water (Western 1975). Cumming & Cumming (2003) similarly record goats and sheep at 3.4 km from water. James *et al.* (1999) liken the water requirements of goats to those of sheep, dispersing during the wet season, but constrained to within 3 km of a water source under dry conditions. The actual distance travelled between drinking events, in order to return to a watering point is, of course, double each of these distances from the watering point.

3.10 Model estimates of goat foraging range

Presented here are models to explore goat foraging range and the utilisation of resources with distance from water. This forms a test of the hypothesis that animals are faced with a conflict between requirements for nutrition and water. The first model is a simple logical working of some relevant allometric relationships for an animal's water intake and turnover used to calculate the time available for travel between drinking events, the rate of travel and, therefore, the distance travelled. The second model is adopted from the work of Colin Pennycuick (1979) to estimate the foraging range of an animal based on the energetic cost of locomotion. Finally, a mechanistic systems model of a heterogeneous semi-arid landscape was constructed that seeks to equate the balance between animal food intake and energy investment in maintenance and locomotion under the conditions of the piosphere.

3.11 Model 1 - foraging range from body size relations

Peters (1983) provides a useful working of data originally published by Buddenbrock (1934) which can be used to estimate distance travelled hourly by an animal travelling at its normal speed (Fig. 3.2). An animal's normal speed is less than its maximum velocity, and requires minimal travel costs. The allometric scaling of speed with body size predicts that a mature male goat weighing 53 kg travels at 0.76 m s^{-1}. In one hour, the goat will travel 2.74 km. Daily foraging time is assumed to be 10 hours. This period equates to ~66% of a 15-hour day length (see Chapter 2 Methods) although observations of grazing time partially reflect seasonal variations in day length (Illius & Gordon 1999). In 10 hours the goat may travel a maximum distance of 27.4 km, or 13.7 km each way, if the travel is in a straight path from water, and the animal returns by the same route.

This estimate for walking is comparatively fast because it is in the absence of foraging and, therefore, the resultant estimate of foraging range is in good agreement with James *et al.* (1999) for movement through highly degraded habitats.

Under highly controlled exerimental conditions, Shipley *et al.* (1996) found the maximum velocity for goats passing between successive plants arranged along the length of a runway to be 0.840 m s^{-1}. The mean velocity was 0.608 m s^{-1}. The velocity of goats used for the experiments presented in Chapter 4 of this thesis was measured whilst the animals foraged in a larger runway paddock. Application of the Shipley *et al.* (1996) model (see Equation 4.4 and Fig. 4.1) elicited a maximum velocity of 0.75 m s^{-1}, in good agreement with the allometrically-derived maximum velocity given above. The mean foraging velocity was 0.600 m s^{-1}, in good agreement with Shipley *et al.* (1996). An animal travelling at this mean velocity for the alloted foraging time will travel 21.6 km per day.

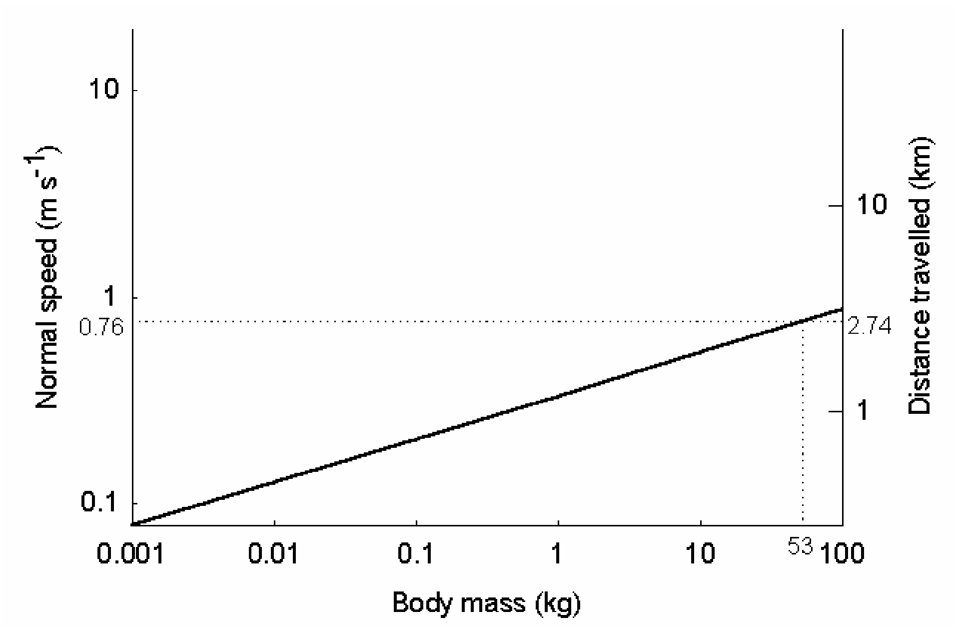


Fig. 3.2 The effect of body mass (W, in kg) on optimal speed of mammals ($V_{n(mammals)} = 0.33W^{0.21}$; Buddenbrock 1934). On the right-hand vertical axis, foraging radius is the distance an animal can cover in 1 hour at average speed. Intersections are marked for an animal of 53 kg body mass giving a normal speed of 0.76 m s^{-1}. For a foraging day length of 10 hours, this is equivalent to 27.4 km per day (Adapted from Peters 1983).

A slight adjustment can be made by comparing the rates of water intake and water utilisation, as above. A 53 kg animal will drink 3.44 l d^{-1} (Adolph 1943) which is utilized at a maximum rate of 3.57 l d^{-1} (Altman & Dittmer 1968), implying a time constraint on non-watering activity. Assuming that the effect of this constraint acts equally throughout the day, the available time for foraging is 3.44/3.57 x 10 hours = 9.6 hours. At a speed of 0.6 m s^{-1}, an animal can travel 20.7 km in this time.

3.12 Model 2 - foraging range from predicted energy balance

Pennycuick (1979) developed an elegant solution that can be used to calculate distance travelled from water (what he termed the "foraging radius"), based on energy balance between energy income (intake) and energy expenditure. The analytical model assumes no energy intake whilst moving, but this does not exclude handling on the hoof. For example, Pennycuick included an application of the model which estimated 10 km per day travel for wildebeest based on energy balance. Further calculation showed that 8% of wildebeest energy intake was expended on locomotion.

To explain the energy balance (with units energy/time) in Pennycuick's model, his working is shown here. Firstly, animal total instantaneous energy expenditure, E_{xz} can be written,

$$E_{xz} = E_m + E_f + E_{lz} \qquad 3.1$$

where E_m is the rate of energy expenditure on basal metabolism, E_f is the rate of energy expenditure on feeding (assumed zero whilst walking), and E_{lz} is the instantaneous rate of energy expenditure on locomotion. Surplus energy is simply the difference between energy intake and expenditure. E_{lz} is directly proportional to the velocity of the animal (V) and this can be substituted from Equation 3.1,

$$E_{xz} = E_m + kV \qquad 3.2$$

where k is the energy required to propel the animal with units energy/distance, *i.e.*, it is independent of speed. It is then possible to calculate the time (T) required to consume a threshold amount of energy (e) for locomotion and basal metabolism without net loss of body mass,

$$T = \frac{e}{E_{xz}} = \frac{e}{E_m + kV} \qquad 3.3$$

We are assuming that time T is the time between drinking events. Thus, Equation 3.3 equates to the distance travelled from water and back again. If the animal's foraging radius (r) is the outbound journey, then this distance is twice that ($2r$). Substituting for Equation 3.3 and rearranging gives,

$$r = \frac{eV}{2\left(E_m + kV\right)} \qquad 3.4$$

Pennycuick found literature values to use in Equation 3.4, which he then plotted against body mass. The linear relationship could then be simplified as the allometric body size relation, $r = 2000\ \mathrm{W}^{0.40}$, which predicts the foraging radius of a 53 kg goat to be 9.79 km ($2r = 19.58$ km) for an animal travelling at a speed of 0.84 m s^{-1}. $E_m = 90.62$ J s^{-1} and $k = 119.11$ J m^{-1}, so, rearranging Equation 3.4, $e = 4444.5$ J.

Pennycuick noted that there is an advantage in having a large foraging range. During the dry season, further travel reduces competition between sympatric species and, during the wet season, long distance travel is needed for migrations. But, information about the spatial distribution of resources is needed as a precursor before benefiting from this advantage. The flaw here is that Pennycuick only considers this information vital during the wet season, as dry season foraging can be reduced down to the progressive exhaustion of resources at increasing distances (*cf* shift in utilisation peak in Adler & Hall *subm.*, see Chapter 1, Section 1.2.11). Information cues along the migratory path may operate at a larger spatial scale than cues that prompt decisions about daily diet selection. This is understandable as migrations occur over a longer temporal scale, and a limited memory would need to be selective.

Nonetheless, the advantage of a large foraging range is clear. According to the allometric scaling of r with body size, the model makes predictions about selection pressures for increased foraging radius brought about by larger body size or a persistent fast gait, *e.g.*, animal proportions (mechanics) that maximise travel velocity. The latter would suggest a selection pressure for increased leg length, although stride properties at speed are strongly correlated with body size (Alexander *et al.* 1977), and so such adaptations would need to be independent of body size increases. Foraging velocity on the other hand is independent of body size as it is likely a result of perceptual, energetic and behavioural constraints (Shipley *et al.* 1996). Ideally a faster gait would be achieved at no greater net energy cost. However, during mammalian evolution, energy costs of locomotion have increased with body size (Taylor 1978), and relative to body size (*i.e.*, higher for larger animals relative to their mass, Underwood 1983). And, while locomotion costs are quite small compared to total maintenance (*e.g.*, the cost of walking for a 1000 kg animal is less than 15% of its daily metabolic costs), this implies a commensurate gain in energy intake for larger animals as a result of moving faster. Further discussion of these selection pressures can be found in Chapter 6, Section 6.8.

The next model attempts to readdress the importance of dry season foraging cues and explicitly accounts for the spatial heterogeneity of resource in optimal spatial foraging. Information is required for diet assessment and selection, and is stored for subsequent decisions.

3.13 Model 3 - foraging range from predictions of spatial foraging behaviour

In order to address the spatial aspects of foraging behaviour a non-spatial simulation model of a semi-arid grazing system was modified to introduce the capacity to include topography, soil nutrient distribution, surface water dynamics, plant distribution, drinking water location and animal spatial foraging behaviour. This model was based on the non-spatial representations of savanna dynamics and animal physiology developed by Illius *et al.* (1996b) as part of an earlier project. This earlier model calculated, from daily rainfall data, vegetation growth and its allocation to plant parts, the selection and intake of these by animals, the animal's consequent energy and protein balances, body growth, reproduction and mortality (Table 3.6).

Module	Inputs	Outputs	Source literature
Climate	Daily rainfall, wind speed, atmospheric pressure, radiation, temperature, relative humidity		Walker & Langridge 1996
Soil	Soil depth, cracking, fertility, root distribution	Daily run off, evaporation, infiltration, transpiration	
Vegetation	Daily growth (from transpiration)	Daily biomass fluxes	Poupon 1976, Rutherford 1984, Dye & Walker 1987
Animal	Daily plant parts abundance and bite sizes.	Daily diet selection, intake, biomass fluxes, mortality, reproduction, milk yield	Illius et al. 1998, Illius & Gordon 1999, Illius et al. 2000

Table 3.6. Key components of the models of soil water balance, plant phenology and animal metabolism used as the basis for the development of Model 3. See original sources for details of the relationships and discussion of the assumptions made.

3.13.1 Model description

The mathematical relationships used in the animal component of this model were described in Illius *et al.* (1998), Illius & Gordon (1999) and Illius *et al.* (2000). The components modelling the soil moisture balance and growth of vegetation were based a non-spatial model written by Walker & Langridge (1996). These models used inputs of daily weather conditions (*e.g.*, rainfall, wind speed, atmospheric pressure, radiation, temperature and relative humidity) and soil/plant properties (*e.g.*, depth, fertility and root distribution), and predicted the changes in soil moisture as a function of losses to deep drainage, evaporation and transpiration. Transpiration was translated into daily growth on a per unit area basis and this was partitioned according to the balance of woody plants and grasses.

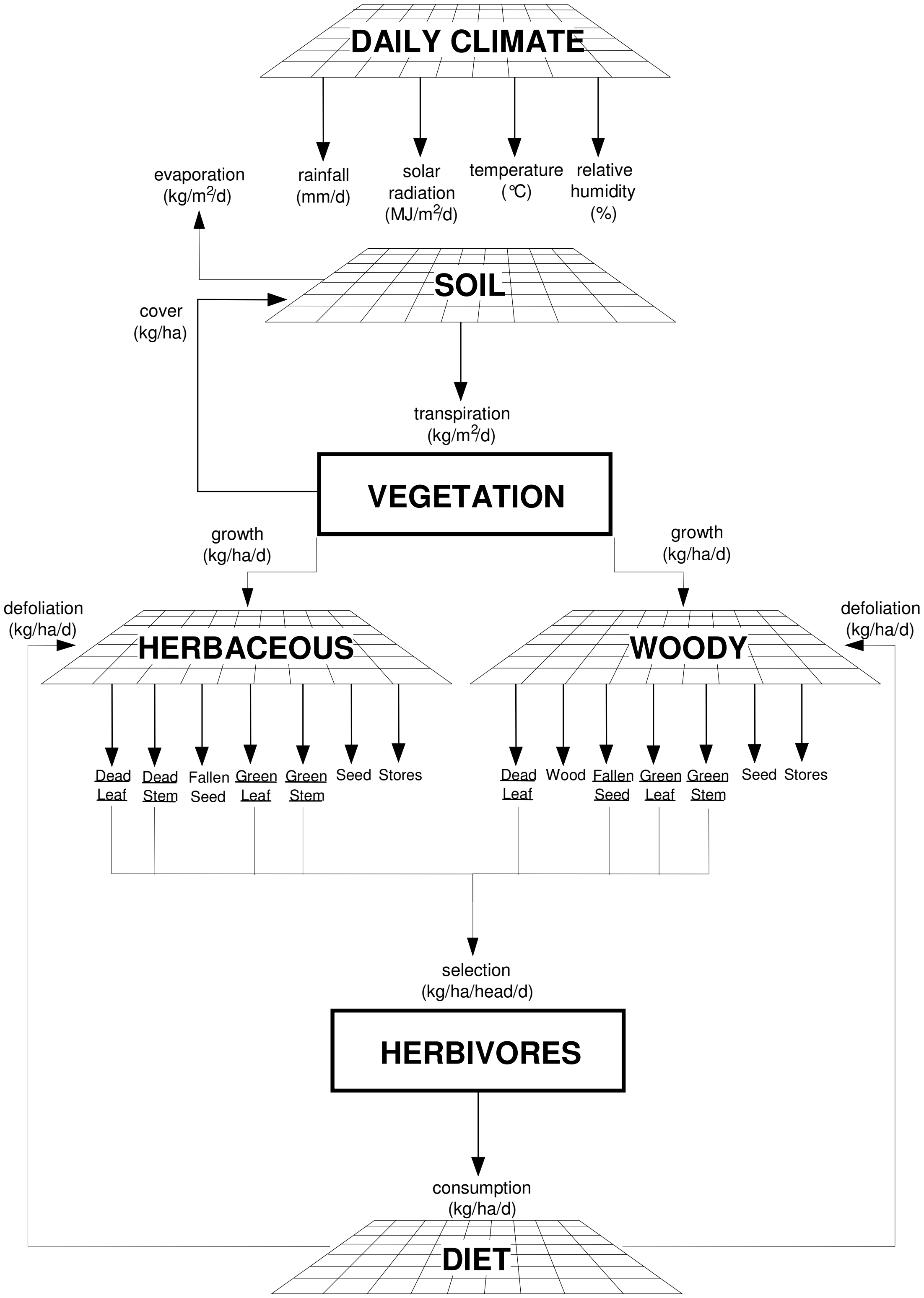
The phenology and allometric relations between the plant parts of these components (Poupon 1976, Rutherford 1984, Dye & Walker 1987) was used to predict the daily growth of green leaf, stem and seed (grasses) and green leaf, twig, wood and fruit (trees). Trees were assumed to have the same rain-use efficiency (the relationship between net carbon assimilation and transpiration) as grasses, in the absence of clear evidence to the contrary. Literature estimates of tissue senescence, decomposition and invertebrate herbivory were included in the prediction of tissue flow from net photosynthesis through to loss from the system. The state variables were, for grasses: carbohydrate stores, green leaf, dead leaf, green stem plus seed, dead stem, fallen seed; and for trees: carbohydrate stores, green leaf, fallen leaf, current season's twig, wood, fruit, fallen fruit.

Selection of these plant parts and their intake rates were calculated on the assumption that, each day, each species will select the diet that allows maximum daily energy intake, net of the energy costs of foraging. Daily intake for each vegetation component (grass: green and dead leaf and stem; browse: green leaf, shoot, fallen leaf, fallen fruit) was calculated according to the equations of Spalinger & Hobbs (1992), which used the abundance and potential bite size of these components. Selection between grass components was calculated from incisor breadth (based on Illius & Gordon 1987) and a limit, imposed by mouth size, on the ability to select the highest-digestibility component while rejecting those of lower digestibility. Daily potential intake, when abundance is not limiting, was calculated from equations summarising the digesta kinetics model of Illius & Gordon (1991, 1992) which showed good agreement between predicted intake of tropical grasses and that observed in a range of ruminant species. Actual intake was the lesser of that calculated subject to the constraints of food abundance, digestive capacity or ability to deposit protein and fat in animals of each age, sex and reproductive status.

Reproduction in females was determined by animal state (conception could take place if animals had >50% of the maximum fat mass for mature females of the species; pregnancy costs and lactation yield are calculated from body condition and nutrient intake). Mean body fat in each age class, sex and reproductive status was obtained daily from the calculated energy balance. Mortality occurs for animals on reaching zero fat mass.

The original contribution of this chapter concerns the re-implementation and extension of these former models into a spatially-explicit model and the exploration of spatial interactions that are not apparent from the earlier non-spatial models. The architecture of this new model (Fig. 3.3) is defined by the class structure outlined in Appendix 6; the merits of this particular object-oriented architecture are discussed in Derry (1998). The programming language was C++, initially compiled in Borland's Turbo C++ 3.1 (Borland 1991), and later using C++ Builder 4 (Borland 1999).

Fig. 3.3 (*overleaf*): Model structure and data flow. Grids were used within each model to model spatial processes such as climatic variation, landscape topography, surface water runoff, vegetation distribution and animal movement. The flow of energy for each iteration (arrows) passed data from the climate module to the soil module where daily transpiration was predicted before being converted into growth for each vegetation type and allocation to plant parts. Selecting the maximum energy intake rates of optimal mixtures of plant parts from the range of available forage components (underlined), predicted on an individual basis (per head), determined a foraging pathway for each animal herd. Herd consumption was levied on the selected forage plant parts. See text for details.


DAILY CLIMATE
evaporation (kg/m²/d)
rainfall (mm/d)
solar radiation (MJ/m²/d)
temperature (°C)
relative humidity (%)
SOIL
cover (kg/ha)
transpiration (kg/m²/d)
VEGETATION
growth (kg/ha/d)
growth (kg/ha/d)
defoliation (kg/ha/d)
HERBACEOUS
WOODY
defoliation (kg/ha/d)
Dead Leaf
Dead Stem
Fallen Seed
Green Leaf
Green Stem
Seed
Stores
Dead Leaf
Wood
Fallen Seed
Green Leaf
Green Stem
Seed
Stores
selection (kg/ha/head/d)
HERBIVORES
consumption (kg/ha/d)
DIET

3.13.2 Spatial extensions

The Climate, Soil and Vegetation modules were duplicated in each cell of a grid. This method was implemented as inheritance of the non-spatial *Climate*, *Soil* and *Plant* classes (Derry 1998) by extended hierarchies that incorporated spatial features (see Appendix 6), distributed across a grid. The result was that each spatial class contained a grid of equivalent dimensions (I columns by J rows, and each cell had co-ordinates (i,j), where $i \in \{1,\ldots,I\}$ and $j \in \{1,\ldots,J\}$), rather than the alternative of a single grid containing many spatial classes. The benefit was that during the introduction of spatial features (*e.g.*, cell altitude with which to generate a topographic landscape), module integrity was more easily maintained. For example, within grid communication such as runoff to neighbouring cells is a process occurring at the soil surface and was, therefore, coded for within the *Soil* module. Individual cells were referenced using the co-ordinate system, while whole grid data was collected by systematic contiguous sampling (*i.e.*, in sequence from top left corner, column-by-column).

Herbivore species were able to access the extent of the modelled area, therefore only one instance of each *Herbivore* class was required. However, a grid-based implementation of the existing diet selection object pointer method (see Derry 1998) was introduced by which selection of a spatially distributed diet and the associated herd movement could be predicted on a daily basis.

3.13.3 Scale issues

It is imperative to consider scale issues when modelling ecological systems (Wu & Hobbs 2002, Chave & Levin 2003). Many problems that may have hindered the development of this model were avoided by tracking most state variables in terms of density per unit area. Only the *Animal* module dealt in absolute values. For example, selected plant biomass was converted from a measure of dry matter density (kg DM/ha) to absolute biomass (kg DM) in order to calculate total herd consumption. Animal populations comprised age classes tallied by their total membership, but population dynamics were expressed in terms of animal density: animals per unit area (see Section 3.13.12).

Animal decisions are thought to conform to spatial scales; region, landscape and plant community (Senft *et al.* 1987). Bailey *et al*. (1996) extended this framework and proposed an attractive conceptual model of animal spatial foraging that involved selection down a hierarchy of six spatial (and temporal) scales; home range (1 month to 2 years), camp (1-4 weeks), feeding site (1-4 hours), patch (1-30 minutes), feeding station (5-100 seconds) and bite (1-2 seconds). Thus, selection at the habitat scale is a decision made prior to subsequent foraging decisions at smaller scales (Orians & Wittenberger 1991, Adler *et al.* 2001). The defining levels of this hierarchy are dictated by the size of the animal, because species of different size perceive the environment differently (Wiens 1976). This also defines the scale of patchiness for the animal's environment, and, it follows, the selectivity of their resource (Wallis De Vries *et al.* 1999). The sequence is attractive because it is not dissimilar to the sequence of decisions that we ourselves may follow in our own foraging excursions. Supermarket (5-10 minutes) → aisle (1-2 minutes) → shelf (1-30 seconds) → item category (1-5 seconds) → item (1-2 seconds). Or perhaps, restaurant (10-30 minutes) → table (5-10 minutes) → menu (1-10 minutes) → course choice (1-5 minutes) → dish choice (1-2 minutes). But, in other species, this remains a conceptual framework and there is little empirical evidence in its support. Animal diet selection can be influenced by the fine scale distribution of their food resources (Edwards *et al*. 1994, Turner 1999), but, it is much more difficult to establish selection at the scale of the habitat (feeding site *sensu* Bailey *et al.* 1996). One such example is provided by Fritz *et al.* (1996), who found selection of certain habitats (300 ha paddocks) by impala and kudu disproportionate to their availability (by area). However, they could only conclude that selection had been at the scale of individual species within those habitats, rather than, say, for habitat-defining plant communities. This is in accord with further evidence for random or nearest-neighbour search strategies with little or no active habitat selection (Turner *et al.* 1993, Gross *et al*. 1995, Forcadi *et al*. 1996 and Chapter 2). Because the animal herd moved from cell-to-cell, selection in the model was ultimately for the area represented by each grid cell (*see below*). But, the selectivity of animals for each cell was determined at the finer spatial scale of plant part density, with assessment of larger areas being based simply on mean accumulated resource profitability.

A daily iteration was chosen for the model. Although quicker processes are modelled (*e.g.*, animal movement between cells), energy fluxes were tallied at the end of each simulated day. Thus, a smaller temporal scale would not have enabled any more precision, whereas a longer iteration period (not just summation across days) would have denied investigation of daily foraging bouts (including animal digestive constraints, see below). The SAVANNA model (Coughenour 1993) employed a weekly time step, but the model aggregated daily rates and then merely reapportioned animal foraging days per grid cell according to a preference score. It is possible that a longer time step for the current model would have reduced simulation time.

3.13.4 Energy intake

Herbivores select their diets from a wide range of plants. The size of the animal typically determines their feeding behaviour (Illius & Gordon 1987). Buccal characteristics scale allometrically with body mass, the smaller animal having a narrower snout, which can be used to probe plant morphology (Gordon & Illius 1988). Therefore, depending on body size, the animal is able to select parts from within each plant. The reason for doing this is because plant parts differ in their nutritional value, which is related to a part's digestibility, a function of its nitrogen content (Illius *et al.* 1996a). Hence, upon maturation of plant parts, replacement of the nitrogen-rich cell contents by plant secondary thickening carries with it an associated reduction in digestibility (Illius *et al.* 1996a).

Digestibility is an important factor in energy intake. The digestible portion of consumed forage is that part that can be absorbed by the animal and is not excreted as fæces. Increased digestibility means less rumen fill, higher throughput and, therefore, more total intake by reduction of digestive constraints on intake (McDonald *et al.* 1977). The maximum intake of food was predicted with respect to its digestibility and animal size (Illius & Gordon 1991, 1992). Constant digestibility values for each plant part were included in the model. As the animals were able to select from a mixture of dietary components, the daily digestibility was an average of the plant part digestibilities weighted according to their contribution to daily intake (Fig. 3.4, see Section 3.13.12 for parameter values).

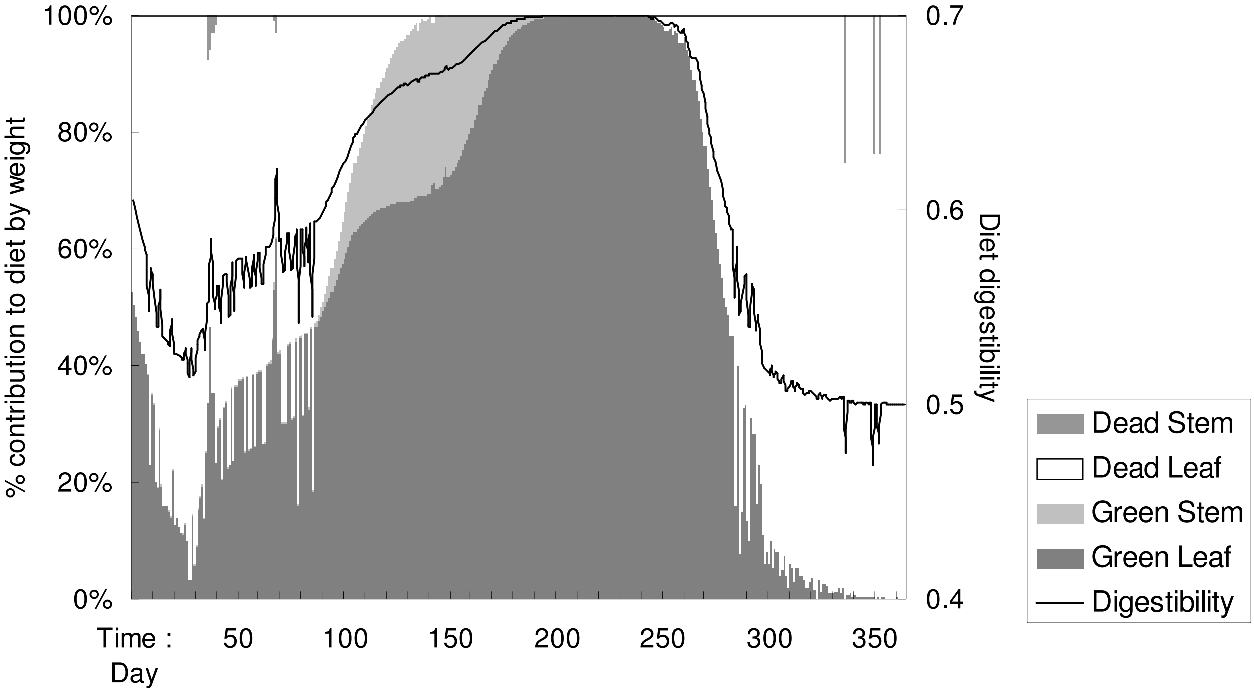


Fig. 3.4: Typical annual seasonal change in modelled herbaceous diet composition and the resulting digestibility for goats selecting parts of a perennial grass. *Dead stem* appears as the thin drop-down bars at the top of the figure.

3.13.5 Spatial foraging

Field observations and modelling exercises have shown that the maximization of daily energy gain is the rationale for optimal foraging strategies (Fryxell *et al.* 2001) and the primary determinant of animal movement patterns (Wilmshurst *et al.* 1999). Goats in particular have been shown to select diets that maximize their dry matter intake rate (Illius *et al.* 1999). Each day, animals foraged until either no available foraging time remained (this accounted for time for the return trip to water during the dry season), or daily intake requirement had been satisfied (see Section 3.13.11).

During the daily iteration, each cell of the *Herbivore* class spatial diet grid was populated with estimates of potential energy intake rate (E_{ij}^{R} , J s^{-1}) for the plant parts of each forage species present in that cell. This was predicted allometrically from the mass of a mature female animal. These intake rates were then processed using the extended contingency model of Farnsworth & Illius (1996, 1998, but also Fortin 2001), to account for simultaneous searching and handling of multiple prey items. The process involved separate addition of individual items to a mixture of plant components until the diet mix became handling-limited for the food item offering the highest profitability. Lower quality food items were discarded on the assumption that they would not increase the diet's energy intake rate, apart from a sufficiency to fill the animal's remaining gut capacity.

In this way optimal diets could be selected from each diet cell combining plant parts belonging to any number of forage species. As the spatial diet pointer grid was particular to each herbivore species, grids could differ between species according to animal size. Finally, actual intake was predicted by selection of a daily pathway that maximized energy intake. The complete optimal solution is akin to the Travelling Salesman Problem, however as it is unlikely that animals make decisions about movement in this way (Beecham & Farnsworth 1998), a stepwise sequential solution was favoured for realism.

Herd movements were driven by there being an available cell destination (see below). If a destination did not exist, the herd did not move. The herd moved when cued by sufficient depletion of forage resources at the current cell location. The theoretical giving up density, GUD, (*i.e.*, the resource density remaining when there is no profit in staying) is widely accepted as the point at which depletion of the current location depresses the resource to G*, the environmental (global) mean E_{ij}^{R} (a derivative of the Marginal Value Theorem, Charnov 1976). The central assumption here is that enough knowledge about the environment has been collected in order to make the comparison. In accordance with the IFD, typically animals are considered to have perfect knowledge of their environment, as if omniscient, or having permanent retention of encounters with resource profitability throughout their foraging range. Density-dependent interference effects were not included.

Before moving to a cell, the destination cell needed to be deemed profitable. For a cell to be profitable E_{ij}^{R} needed to be sufficient to account for the costs of travel to the cell, *i.e.*, commuting (E_{ij}^{C} , J), plus the costs of travel within the cell required to harvest the selected diet, *i.e.*, foraging (E_{ij}^{F} , J), at a potential energy intake rate above G*. This gave the cell net potential energy intake rate, e_{ij} (Equation 3.5).

$$e_{ij} = E_{ij}^{R} - E_{ij}^{C} - E_{ij}^{F} - \left(\sum_{i} \sum_{j} E_{ij}^{R} \right) \Big/ IJ \qquad 3.5$$

Time and energy foraging costs were calculated from the cell e_{ij} and the distance travelled whilst foraging, which was a function of bite size and bite density. Animals were assumed to commence foraging at the centre of each cell and forage towards the next destination. Therefore the distance commuted to a cell centre was assumed to be the actual distance between the cell centres less the distance travelled whilst foraging in the previous cell. Time and energy commuting costs were calculated from commuting distance using an estimate of herd velocity, which was weighted according to herd composition (O'Brian 1984).

Thus animal movement was not randomized. Random walk models (*e.g.*, Stafford Smith 1990, Renshaw 1991) and diffusion models (*e.g.*, Blackwell 1997, Farnsworth & Beecham 1999) imply that, in the absence of experimental evidence, a stochastic mechanism underlies animal foraging behaviour. However, recent empirical findings, including the fieldwork presented in Chapter 2, show that nearest-neighbour models may best describe movement patterns. In so doing, there is the suggestion that it is the aggregation of individual plants that provides the correlation required to transform random walk models into successful animal foraging strategies, with the optimal degree of correlation inversely proportional to patch density (Zollner & Lima 1999). Thus, browsing animals have been observed to follow tortuous foraging paths through dense habitats but travel more directly and quicker between sparsely spaced bushes (Etzenhouser *et al.* 1998). Animals improve their foraging efficiency with alternative search patterns for different levels of the hierarchical patch system (Fauchald 1999). Whilst the most effective non-systematic search paths are almost straight, an animal with a superior perceptual range is able to elicit similar foraging success from an exhaustive search strategy (Zollner & Lima 1999). So, good sight would be an advantage in sparsely vegetated areas, for the identification of patches in terms of forage species (Illius *et al.* 1999), but susceptible to impedance by physical barriers in denser areas (Etzenhouser *et al.* 1998). The model measures resource patchiness using the CV[1] for E_{ij}^{R} and assumes that vision is not impeded within the visual range.

3.13.6 Vision

Considering the difficulties in taking such measurements, it is not surprising that there is little empirical evidence for visual range in large herbivores. More has been achieved using visual cues in studies of spatial memory and foraging efficiency. Howery *et al.* (1999) found that artificial visual cues increased foraging activity and improved intake under fixed and variable forage arrangements. The arena that was used measured 1.58 acres (0.64 ha) which is equivalent to ~80 m maximum visual range. Laca & Ortega

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[1] coefficient of variation

(1996) also investigated the role of visual cues in spatial foraging by its effect on cattle intake rate, but their experimental range only reached 23 m. Spatial memory in sheep was tested in paddocks no larger than 45 m (Edwards *et al.* 1996) and 65 m (Edwards *et al.* 1997).

The positioning of the eyes on the head is paramount in deciding the animal's field of vision. This is how much can be seen without moving the head. For humans this is about 180^{o} laterally. For a horse it is about 215^{o} (Ramel 2004). A wide field of vision is characteristic of ungulates and may be an adaptation by prey animals to enable early detection of predators (Walls 1942 cited in Hutson 2000). As this is common in ungulates, it seems reasonable to base an estimate of visual range upon this characteristic. To minimize the constraints of this estimate it also seems reasonable to make this an optimistic estimate at the maximum known abilities of ungulate vision.

The location of ocular orbits on the side of the ungulate skull limits binocular vision, but enhances the animal’s field of view or peripheral vision. However, their monocular vision means they can see an object with only one eye, each eye having a field of view of almost 180^{o}. Therefore, by using both eyes, these animals almost have a 360^{o} field of view (Smythe 1975). In some herbivores there is some overlap in the field of view and these animals may have partial binocular vision (Sullivan 1999). Piggins and Phillips (1996) recorded a 306^{o} field of vision in sheep, where ears, horns and wool obstructed a greater panoramic vision. Estimates of field of vision in cattle range from 330^{o} (Phillips 1993) to nearly 360^{o} (University of California Cooperative Extension 1996).

Clark & Dukas (2003) presented this probabilistic detection function for predator vigilance in a foraging animal with field of vision θ,

$$f(\theta) = \delta_0 e^{-\theta / a} \qquad 3.6$$

where, δ_0 (m) is visual acuity or range, and a is attentional capacity, used in their model to impose limitations on perception and test the importance of cognitive constraints. This is not the purpose of the current model, so the equation was rearranged for δ_0, and $f(\theta)$ and a were set to their maximum values. Taking the midpoint between the two literature estimates for θ of 330^o and 360^o gives 345^o which, using the rearranged Equation 3.6, gives a visual range of ~400 m. This value for the animals' limit of perception was used in the model for animal assessment of their resource landscape. The effect of restricting visual range was compared with an equivalent simulation in which vision was unrestricted (see Fig. 3.11).

3.13.7 Assessment

With energy intake rate as fundamental, it was possible to incorporate visual range, the influence of prey species aggregation and nearest-neighbour selection into a vocabulary of animal assessment strategies for optimal landscape utilisation, across increasing scales, in fact, a Herbivore Assessment Lexicon (HAL) (see table 3.7).

To account for influences of patch density the spatial pointer grid was arbitrarily segmented into four directions of travel, such that each sector comprised D_d cells (where $d = 1,2,3,4$). Next, HAL calculated the mean e_{ij} that could be achieved by travel as far as the perceptual limits in each direction (p cells from current). These directional mean values do not acknowledge structural organisation of the landscape into a scale hierarchy of patches or super-patches (*sensu* Beecham & Farnsworth 1988). However, they do take into account the perceivable profitability for clumped resources at remote locations, beyond the scope of neighbouring cells, out to the limits of animal visual range. Taking the sum in these blocks would have given leverage to a larger collection of cells for non-central positions. Next, HAL compared the e_{ij} of the cells neighbouring the current position and having membership of the directional segment with maximum mean e_{ij}. If the search failed to find a profitable cell immediately proximate to the current location, then the search was expanded to the next nearest cells, and so on, until the limits of perception were reached.

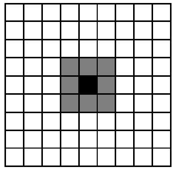
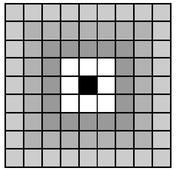
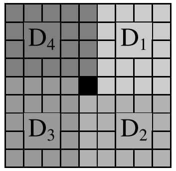
Range	Rule	Expression	Columns	Rows
Proximal 	Selection of the cell with maximum profitability from the 8 cells neighbouring the current cell location ■ (x,y)	Max e_{ij}	$i \in \{x-1,\ldots,x+1\}$	$j \in \{y-1,\ldots,y+1\}$
Remote 	Selection of the cell with maximum profitability from the range of cells at incremental offsets (α) from the current cell location ■ (x,y) out to the limit of perception (p cells from current).	Max e_{ij}	$i \in \{x-\alpha,\ldots,x+\alpha\}$ $\alpha \leq p$ $p \leq \text{Max}(x, I-x)$	$j \in \{y-\alpha,\ldots,y+\alpha\}$ $\alpha \leq p$ $p \leq \text{Max}(y, J-y)$
Directional  	Selection of the direction with maximum mean cell profitability, where each sector comprises D_d cells (where d=1,2,3,4) ranging from the current cell location ■ (x,y) out to the limits of perception (p cells from current).	$\text{Max}\left[\sum_i \sum_j e_{ij} \Big/ D_d\right]$	$d \in \{1,\ldots,4\}$ $i \in \{x-p,\ldots,x+p\}$ $p \leq \text{Max}(x, I-x)$	$d \in \{1,\ldots,4\}$ $j \in \{y-p,\ldots,y+p\}$ $p \leq \text{Max}(y, J-y)$

Table 3.7: Herbivore Assessment Lexicon (HAL) for animal foraging behaviour. See text for details.

It was therefore possible that the first cell visited might not be adjacent to the starting position for the day. Subsequent destinations also may not neighbour previous locations. For depleted landscapes where few profitable cells remained, the constraints on perceptual limit (range and direction) were relaxed, leading to an exhaustive grid-wide search, ranging out in incrementing annuli, from the current location in all directions[2].

3.13.8 Global and local G*

Optimality of foraging strategies was tested by modification of the assumptions made for G*, the environmental mean E_{ij}^{R}. As mentioned above, global G* was the mean potential energy intake rate calculated for the whole grid. Local G* was calculated as the mean E_{ij}^{R} of only the cells scanned during assessment as described in Section 3.13.7, above. This also included the cells visited along the foraging path.

Local G* should provide a more accurate estimate of the mean energy intake rate offered by the most available resources at the beginning of each day. During the dry season, animals that assess their environment globally would be expected to travel further from water to reach resource levels in excess of G*. Because local G* is estimated only from previous encounters, for an established utilisation gradient, this estimate would be expected to be lower than global G*.

The grids were initialized with low variation for the spatial distribution of vegetation (CV of only 1%), making starting conditions near identical. Consequently there is little difference between the local and global estimates of G* until the onset of the wet season which introduces more variation via plant growth (Fig. 3.5). Here, the locally derived measure of G* showed erratic fluctuations reflecting a series of encounters with

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[2] An alternative algorithm would have been to invoke a random or correlated random walk for exhausted grids. However, this would not be in keeping with the deterministic algorithm employed, which was purposely based on a nearest-neighbour rule in contrast to random walk models. Random walk models have enjoyed some success, but it was patch density that went some way towards determining animal foraging paths in the model, and it should have been the relaxation of this rule in extreme conditions and not substitution of an unrelated rule.

favorable and less profitable patches, but overall was in good agreement with global G*. The most consistent trend away from global G* was seen during the dry season after day 240, as available forage declined and profitable cells were sparsely distributed (or located beyond the dry season foraging range). Although the estimate of G* is pessimistic (lower than the actual environmental mean), animals are unable to reach the profitable resources. Under such conditions, it is no advantage to have knowledge of better sites beyond local depressions in patchy resources as this inflates G*, and reduces the comparative profitability of local resources accessible during the dry season.

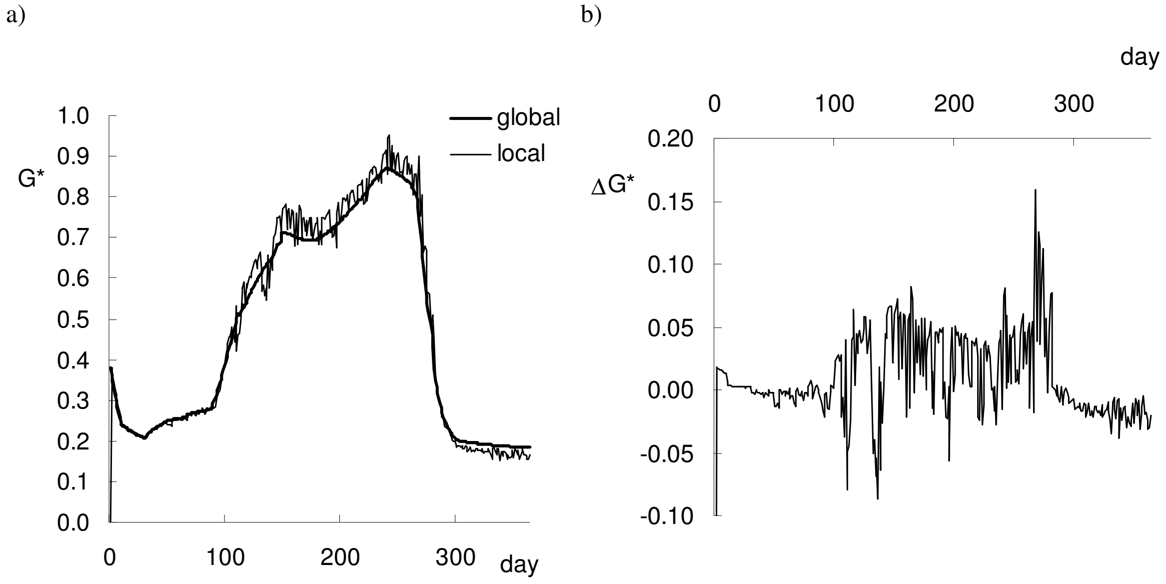

Fig. 3.5: Optimality in foraging strategies for two estimates of environmental mean resource levels. a) globally and locally derived measures of G* and b) the difference between global and local G*. The wet season started on day 30 of each year, and ran until the next dry season on day 240

Local G* would be expected to be an underestimate of global G* for established utilisation gradients. However, the starting conditions here are almost identical, with nearly homogeneous distributions of initial plant biomass the only potential source of variation. Cells encountered early in both simulations have similar resource levels.

Consequently, there is little difference between the estimates of local and global G*. Local G* responded to the wet season increase in resource heterogeneity, and showed signs of departure from global G* during the second dry season. To investigate the effect of the scale of assessment on optimal foraging behaviour, identical sets of simulations were made for local and global G* (Fig. 3.9 and Fig. 3.13).

3.13.9 Memory

There is some evidence that implicates learning and memory in reinforcement of visual cues, in goats (Illius *et al.* 1999) and other animals (cattle and sheep: Provenza 1995; sheep: Edwards *et al.* 1996, 1997; Arabian oryx: Tear *et al.* 1997). Derek Bailey and his colleagues have shown that foraging animals retain information gained from their search path and use it to facilitate future diet location (Bailey *et al.* 1989, Bailey 1995, Bailey & Sims 1998, Howery *et al.* 2000). Memory also provides additional information about expected profitability to supplement G*, thereby combining the global average with recent experience (Hewitson 2002). Memories of both positive and negative encounters are stored (Bailey *et al.* 1996, Hewitson 2002) – these are potential yields above and below what is expected. Negative encounters are remembered for longer than positive, as it is more costly to return to a feeding site that will incur an energetic loss. Using literature values for memory retention capacity in cattle (Bailey *et al.* 1996), memories were decayed with distinct half-life estimates (see Fig. 3.6) according to whether it was worthwhile feeding (the site offered E_{ij}^{R} above that expected) or not (the potential intake rate was below expectation)[3].

The model only has these positive and negative memory feedbacks, and lacks differential retention with respect to scale. For example, Fauchald (1999) showed how

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[3] A more sophisticated approach is to employ an Exponentially Weighted Moving Average (EWMA, Hunter 1986) model of memory retention in which devaluation of the information is dependent on the rate of change of the environment. This allows the forager to track environmental heterogeneity but involves as yet undocumented species-specific values for the influence of single resource encounters on the running average for remembered resource profitability.

memories related to high encounter rates at small scales are forgotten faster than long-term encounters at large scales.

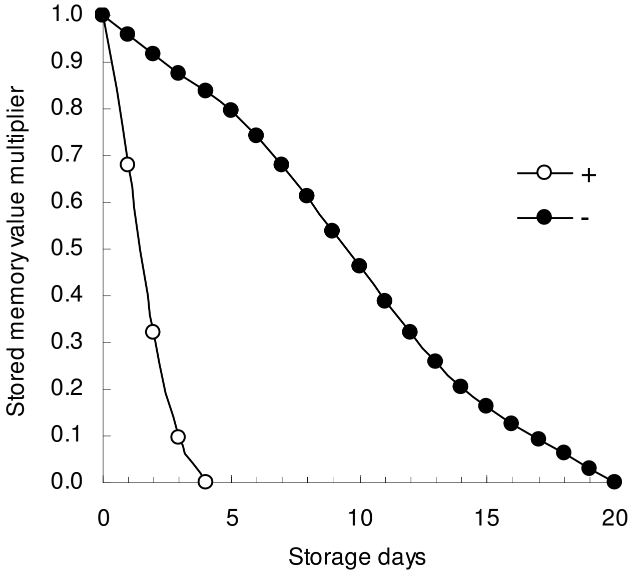
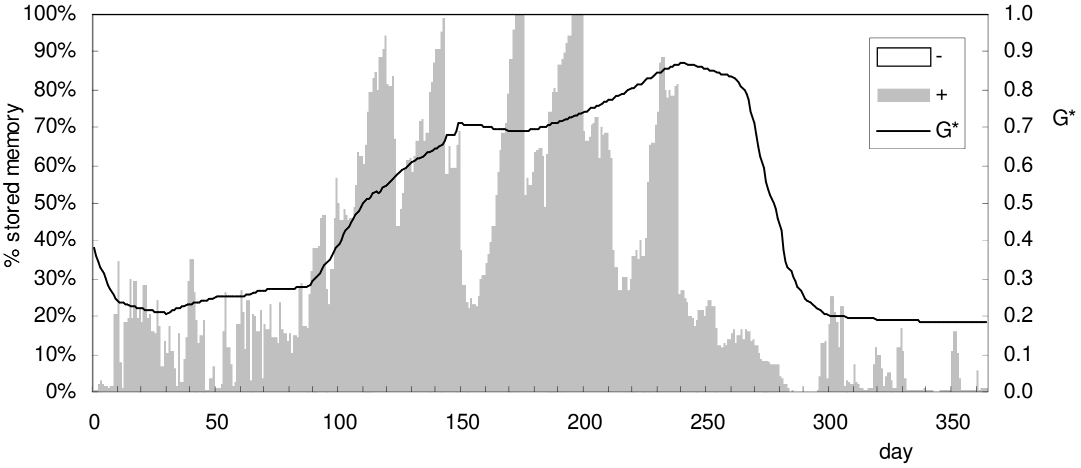


Fig. 3.6: Memory decay functions for stored positive and negative encounters based on literature half-life estimates of 2 days for positive memories and 10 days for negative memories.

Memory was integrated into the assessment of the above mentioned four grid segments as a summative influence underlying the decision, *which direction to travel next*. Thus, for a grid dominated by negative memories, animals are repelled from their latest locations towards less recently visited areas. This occurs mainly during the dry seasons (Fig. 3.7). When resources are more abundant, for most of the wet season, animals are attracted back to recently visited sites. It can be shown that while the number of positive encounters may be relatively high, the effective memory value may be low, depending on the season (*e.g.*, compare first ten days or the latter part of the wet season in Fig. 3.7a and Fig. 3.7b).

a)



b)

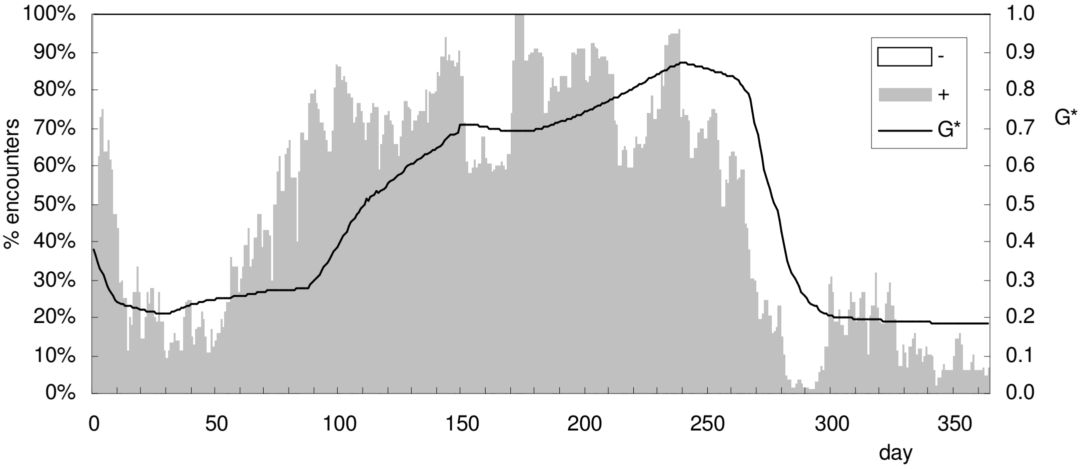


Fig. 3.7: Typical seasonal response in a) stored memory values expressed as a percentage for positive (shaded) and negative (clear) encounters in comparison with the environmental mean, G* (line), and b) the percentage of the number of those encounters giving rise to those memorized values. For a grid dominated by negative memories, animals are repelled from their latest locations towards less recently visited areas. This occurs mainly during the dry season. When resources are more abundant, for most of the wet season, animals are attracted back to recently visited sites.

Encounters were remembered for each cell (co-ordinates *ij*). Memory values (M_{ij}, J s^{-1}) from simulation of foraging on the current day were not used for assessment until the following day, and the means for each directional segment (see Section 3.13.7) were used to avoid bias from non-central herd positions.

3.13.10 Site selection

In this way the landscape was redefined in terms of energy intake profitability providing a common currency for the mechanisms of diet encounter, travel and memory. From any current location (x,y), HAL found the most profitable destination cell by maximization of an assessment of cell, directional and remembered profitability,

$$\text{Max}\left[e_{ij} + \frac{\sum_i \sum_j e_{dij}}{D_d} + \frac{\sum_i \sum_j M_{dij}}{M_d} \right] \qquad 3.7$$

where; D_d is the number of cells in direction d (1,…,4), and M_d is the number of cells remembered in direction d. i and j define the extent of search and are bounded by the extent of the grid ($0 \leq i \leq I$ and $0 \leq j \leq J$) and animal perception ($x-p \leq i \leq x+p$ and $y- p \leq j \leq y+p$). To avoid introducing edge effects, animal perception is not truncated by grid extent such that $p \leq (\text{Max}(x, I-x), \text{Max}(y, J-y))$. Note that the assessment includes the current animal location and therefore "no move" may prove most profitable. Also, because visual range may allow assessment of several cell-lengths from the current location, and grid-wide searches extend even further, some herd moves may involve "jumps" from the current location to the destination cell. This mechanism thereby adopts more direct and quicker movement between sparsely distributed forage resources (Etzenhouser *et al.* 1998). Travel costs are tallied correctly to include these longer movements.

Lastly, upon selection of a new cell destination, a linear relationship between the cell grass biomass (B_{ij}) and G* was used to convert e_{ij} into potential biomass intake (b_{ij}) for the herd (Equation 3.8).

$$b_{ij} = e_{ij} \sum_i \sum_j B_{ij} \Big/ \sum_i \sum_j E_{ij}^{R} \qquad 3.8$$

3.13.11 Constraints on intake

Once an estimate of potential intake for forage biomass had been obtained for the selected cell, tests of three constraint terms were carried out to test whether daily intake requirements had been satisfied or available foraging time used;

1. Digestive constraints. Daily herd potential intake was predicted from the gut capacity of animals to process forage of a given digestibility, weighted by herd composition. Forage digestibility was calculated as the weighted mean digestibility of plant parts in the diet mixture. Forage biomass was consumed until cumulative daily intake met herd potential intake, upon which foraging was terminated for the day.
2. Metabolic constraints. Daily herd potential metabolic energy intake was predicted as the running mean of the previous ten days of foraging. A running mean was used to minimize variation in the estimate. Forage biomass was consumed equivalent to the energy intake predicted by this upper limit.
3. Time constraints. The daily time available for foraging was net the time required to commute to the first cell in the daily foraging pathway, commute between cells, and return to water at the end of the day. During the wet season, there was no water-related time costs.

If the grid-wide search used as a last resort during assessment failed to reveal an accessible target cell for selection daily intake was terminated.

This conversion factor in Equation 3.8 required sufficient variation in E_{ij}^{R} to operate. A sensitivity analysis revealed a threshold value for the CV in E_{ij}^{R} equal to 1% and identified a solution for more homogeneous landscapes. This alternative "use biomass contingency rule for homogeneous landscapes" (*UBRule*) needed to be independent of energy intake rate to avoid seasonal effects, and simply allocated 50% of the forage biomass within a cell as potential intake, and available for consumption (Appendix 7).

3.13.12 Model 3 parameters and output

Where possible, model parameters were used to emulate fieldwork carried out using Nguni and Boer goats (*Capra hircus*) on False Thornveld (described by Acocks 1953) at the University of Fort Hare research farm, in the eastern Cape, South Africa[4]. Simulations used a sequence of daily rainfall data collected at Bulawayo aerodrome in Zimbabwe, Official Rain Station Name BULAWAYO-AIR, LAT -20.020 LONG 28.620 (ADDS 1996). For the 20 years between 1st September, 1972 and 31st August, 1991 the mean annual rainfall was 575 mm with CV = 39%, (compared to Fort Hare rainfall 617mm, CV = 22%)[5]. Taking the mean rainfall of the same day in each year gave a mean annual rainfall pattern that could be repeated for the duration of the simulation (>1 year), while minimizing the influence of the pattern of rainfall from any single year. The model was stocked with a constant herd of 1400 mature male goats, giving an animal density (stocking rate, SR) measured in livestock equivalents (LE, Illius *et al.* 1998) of 0.14 LE/ha. This SR was previously identified as the long-term ecological carrying capacity for the Bulawayo rainfall data set (Illius *et al.* 1996b).

The vegetation type grid was initialized with a stochastic distribution (CV 1%) of a mean 1410 kg ha^{-1} of a perennial grass. Grass parts were allocated from total biomass as follows: Dead Leaf 70.8%, Dead Stem 4.3%, Fallen Seed 0.0%, Green Leaf 21.3%, Green Stem 0.0%, Seed 0.0%, and Stores 3.6%. Digestibility values for the plant parts are shown in Table 3.8. The rainy summer coincided with the annual growth season for the perennial grass, which started on 30th September and ended on 28th April.

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[4] In fact, very little data was available. The model was parameterized with similarly sized goats to those studied in Fort Hare, and the vegetation comprised a perennial grass and an anonymous shrub not unlike *Acacia karoo*. This mix of plants reflected the dominant species identified at Fort Hare during the winter of 2000 (see Chapter 4). Other model parameters were extracted from literature about southern African rangeland (*e.g.*, tissue senescence, decomposition and invertebrate herbivory). The soil water model WATDYN used input based on semi-arid rangeland in Australia (*e.g.*, humidity, temperature, atmospheric pressure and wind speed).

[5] The South Africa Weather Bureau prices for rainfall data were prohibitive, whereas daily rainfall data was collected for free at source during travel in Zimbabwe and Botswana. From the data sets collected, Bulawayo was selected as having the nearest long-term mean annual rainfall *and* CV of annual rainfall. Data from Makaholi did have a mean that was closer (629 mm) but the CV was too high (45%).

	Green Leaf	Dead Leaf	Green Stem	Dead Stem	Fallen Seed
Herbaceous	0.7	0.5	0.6	0.35	-

Table 3.8. *In vitro* digestibility values for the edible plant components of herbaceous vegetation used to parameterize the plant module.

In addition to rainfall pattern and plant phenology, the rainy summer and the dry winter seasons differed by animal movements being only modified during the dry season[6] by relocation of the herd to the water point[7] at the end of each simulated day[8]. Commuting costs included those incurred whilst travelling to and from the water point. Total distance (D_{tot}) travelled daily was the sum of distances covered while foraging (D_{for}), commuting (D_{com}) and travelling from the water point (D_{wat}). D_{wat} comprised two parts, the distance travelled to the first selected cell (this is zero if the first cell visited is the same as the location of the water point) and the distance travelled while returning to the water point from the last selected cell. A fractal dimension was calculated to provide a scale-independent estimate of daily pathway tortuosity (*sensu* Turchin 1998) by relating actual distance travelled to the displacement from the commencement of foraging to the final cell visited (Turchin 1998, p158). The goats were given a visual range of 400 m and half-lives of 2 days for positive memories and 10 days for negative memories

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[6] It was assumed that animals become dependent on a water point for drinking water on the same date each year, heralding the start of the dry season. Similarly, they were released from the need to return to water daily on another date at the start of the rainy season. It would have been more realistic to have had a dynamic commencement of the dry season based on the depletion of surface water levels, and the start of the rainy season when the first rains arrived. Fixed seasons were used to facilitate the extraction of seasonal data required for analysis.

[7] Only one water point was considered. In a wildlife system this would be reasonable given the area simulated, especially in the current climate of *laissez faire* being set up in parks like Kruger (Pienaar *et al.* 1996), but in a typical 1000 ha livestock paddock it would be possible to have more than the single water point. Complexities of unified piosphere patterns and water point selection were avoided for the sake of simplicity.

[8] Animal water balance was not modelled. Instead, a daily drinking frequency was assumed sufficient to stop dehydration and the detrimental effects of water deficiency on food intake. This is possibly an overestimate of watering for the sake of simplicity and to conveniently match the simulation iteration interval. In reality, cattle need watering every three or four days (Nicholson, 1985) whilst sheep and goats need watering every one or two days (McDowell, 1972) but show no signs of distress up to five days without water (Nicholson, 1985), and Somali sheep and Galla goats need watering only once a week (Nicholson, 1985).

(Bailey *et al.* 1996). Foraging opportunity was constrained digestively and metabolically according to the potential for consumption of the available forage, and by 10 hours per day available time[9] (Illius & Gordon 1999). Total time spent daily was the sum of time spent foraging (T_{for}), commuting (T_{com}) and travelling to and from the water point (T_{wat}). Feeding and travel were assumed to be synchronized activities, so although times were calculated per individual animal, these were equal to the times for the herd. Animal number and herd composition were static and not managed in any further way.

A 1000 ha paddock was represented by a square spatial grid comprising 900 cells; therefore each cell was 1.11 ha. A single water point was centrally located in the grid. To test Hypothesis 1, simulations were repeated for a linear paddock akin to a runway. The 30 cell linear paddock did not have the geometry of the square grid for a water point placed centrally in its length. Runway area was scaled to give the same area per cell as the grid, and animal number was reduced accordingly (to 46 heads), ending up with the same SR.

The model was tailored to output data for each daily iteration that had been organized into distance bins. This involved all cells, and not only those included in the daily foraging path. Data collected was mean forage biomass, mean E_{ij}^{R} , and mean % Process 4. Foraging Process was one of the three mechanisms identified by Spalinger & Hobbs (1992) to describe the constraints that foraging animals experience while locating food items (Process 1), travelling between food items (Process 2) and handling food items (Process 3) (see Section 1.1.2). Following ingestion, a further constraint is imposed by the digestive capacity of the animal (Process 4) (see Section 4.2.1), and was included in the model as 'digestive constraints' (see Section 3.13.11, above). It was not possible to

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[9] Grazing time available per day was set static at 10 hours (see Section 3.11). However, observations of reindeer, sheep, wapiti, North American bison, African buffalo, topi and hartebeest all indicate that free-ranging animals are able to adapt the allocation of time for foraging to maintain daily intake; extending it in poor pastures and resting without ruminating during the dry season (Mysterud 1998). The optimal foraging algorithm only assumed maximization of daily intake rate based on evidence from the literature, and did not include maximization of total daily intake.

report the mean foraging Process as the average of these four processes for each distance bin. This would have been a meaningless measure of central tendency because it would have been derived from data that was both ordinal and without units. Instead, when analyzing discrete data, typically reported summary statistics are the median and mode. These measures were tested for the predicted foraging Process data, but discarded for the following reasons. The ‘median Process’ was not used because it would simply reflect the same range of values as the arithmetic mean, *e.g.*, “somewhere between Process 3 and Process 4”, or Process 3 and Process 2, and so on, but without the same sensitivity of the mean to extreme values. The ‘modal Process’ was not shown because this proved too insensitive in revealing any switching between the mechanisms for foraging constraint when it was apparent that there was a limited amount of variation. Dry season foraging was found mainly to be moderated by Process 4 digestive constraints (see Section 3.14.3, below), and the modal Process completely masked the involvement of the other mechanisms. The preferred statistic reported here used the daily predictions for potential intake within each grid cell. The model recorded the constraint mechanism operating for each cell on each day (Process 1, Process 2, Process 3 or Process 4), so it was possible to calculate the proportion of days for each cell on which potential intake was constrained by Process 4. This was re-expressed as a percentage of all days and averaged by distance bin. This value for “mean % Process 4” was included in the model output as a test for modified constraints on goat foraging with distance from water, and to provide an initial estimate of a mechanistic animal response during the generation of the piosphere pattern; something that previously had not been attempted. To test Hypothesis 2, a measure of utilisation, mean cumulative T_{for} was also output from the model by distance from water. Time spent has empirical support for use as an indicator of utilisation (*e.g.*, Lange & Willcocks 1978).

In an attempt to further understand animal foraging decisions that lead to the development and maintenance of a piosphere, a manipulation experiment was devised to test Hypothesis 3 and the role of travel costs in restraining animal populations in the vicinity of a waterhole. Therefore, the 20-year simulation was repeated for the grid with a range of values for a multiplier (c) that modified all instances of the costs of travelling the distances D_{for}, D_{com}, and D_{wat}. This included the estimates of travel costs made during the assessment of animal forage resources (see Equation 3.5). Simulations were repeated for 3 levels of *c* (0.1, 1.0 and 10.0).

3.14 Model 3 results and discussion

Only recent discovery of Adler & Hall's findings (*subm.*) required my rewriting this section to make direct comparisons with their work. Please note that, as in their model, there is also no *a priori* assumption about the distribution of animal spatial foraging.

Unless specified, results are reported for the simulation of the 900 cell, square "Basic Grid", using a Global estimate of G* and at travel cost multiplier level *c*=1. In a shorthand, this is represented by "[Basic Grid : Global G* : *c*=1]". In this simulation scenario, development of a recognizable piosphere pattern was rapid (Fig. 3.8). Within the first 10 days, herbivore impacts accumulated near the water point generating a gradient in grass biomass up to 500 m away. At this point the biomass level nearest water was halved from its starting value, although the extent of the sacrifice zone was minimal.

In the course of the next 20 days of simulation, the gradient shifted laterally to increasing distances from water by expansion of the sacrifice zone (out to ~150m). The strength and shape of the response were consistent over this period with little further decline in forage biomass within the sacrifice zone. There was a 10% decline in available forage beyond the extent of the piosphere because of grass leaf and stem senescence. A record of mean aboveground biomass would have shown a smaller tissue loss to maturation as it included non-forage biomass.

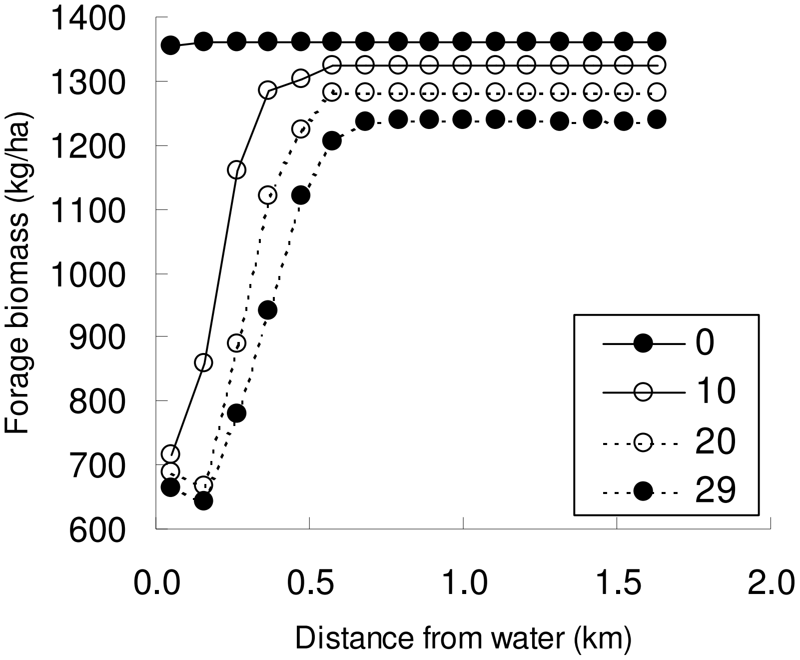


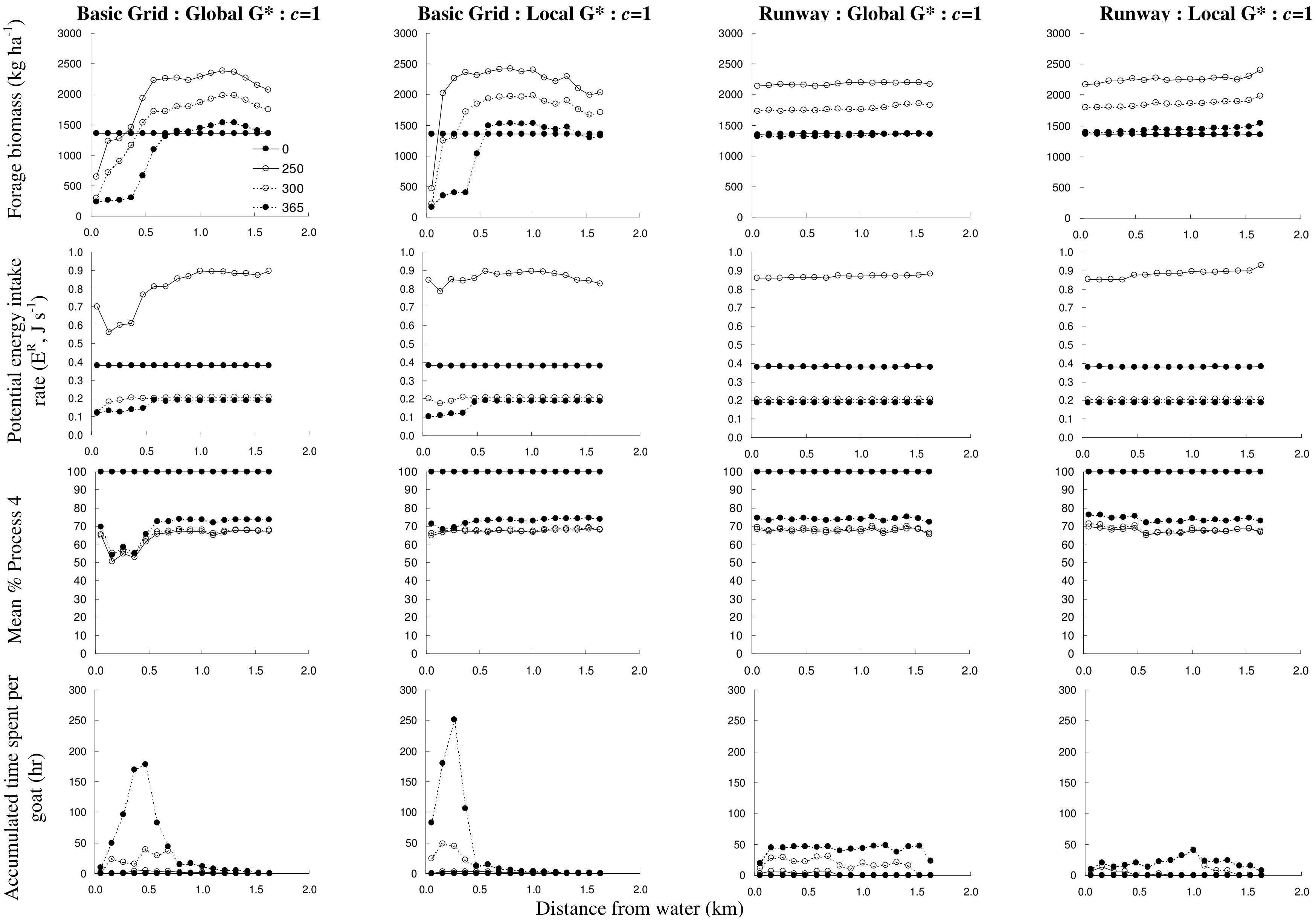
Fig. 3.8: Piosphere development in forage biomass for [Basic Grid : Global G* : *c*=1] simulation after 0, 10, 20 and 29 days of the first dry season.

On day 30 of each simulation, the wet season started, and the animals were not returned to water until the start of the next dry season on day 240. Wet season growth did not restore impacted biomass levels (see Fig. 3.9). Instead, re-growth increased with distance from water, from little or none nearest the water point, to a two-fold increase in biomass at furthest distances. The associated responses for the highest predicted values of E^R in the Global and Local G* simulations also showed seasonal variation (see Fig. 3.9). This is comparable with the annual output for G* first shown in Fig. 3.5. The G* starting value was about 0.4 J s^{-1}, which increased at the start of the growing season to 0.8 J s^{-1} and peaked at about 0.9 J s^{-1}, before decreasing to about 0.2 J s^{-1} during the second dry season. It can be seen in Fig. 3.9 that the highest values of E^R at each time step were similar across all simulations. Traces of foraging activity during the wet season beyond the extent of the piosphere were apparent in Basic Grid levels between day 29 and day 250, of, forage biomass (for both Global and Local G*, Fig. 3.9;

Fig. 3.10 and Fig. 3.11) and E^R (for Local G* only, Fig. 3.9). Senescence again reduced the biomass levels furthest from water maintaining these patterns in the Basic Grid for forage biomass from wet season foraging. In rough agreement with Lachica *et al.* (1999), predicted distances increased by 29.6% for the wet season (compared to their 32.8%)

Seasonal changes in biomass levels due to primary production are consistent with the literature, although examples of monitored re-growth within a piosphere are rare. Georgiadis (1987) found restorative grass growth proportional to distance from water at a field site receiving low rainfall in Kenya (342.3 mm *per annum*). At a wetter site (>720 mm *per annum*), also with higher soil nitrogen, the reverse was true, and primary production decreased with distance. Georgiadis concluded a strong interaction between soil moisture and fertility, which was inhibited by low rainfall and low infiltration. This is an illustration of how herbivores can promote resource heterogeneity by the concentration of nutrients, and by reducing infiltration from trampling, in addition to the direct effects of defoliation. However, in accordance with more generalized studies of semi-arid rangeland (*e.g.*, Dye & Spear 1982), the overriding determinant of variation in growth within the piosphere is rainfall (Georgiadis 1987, van Rooyen *et al.* 1990). The current model did lack the ability to modify soil properties from excretion and trampling. It also did not explicitly account for plant response to defoliation. However, the pattern for wet season re-growth was consistent with Georgiadis' dry sites.

Fig. 3.9 (*overleaf*): Model output of four variables against distance from water; mean forage biomass, mean potential energy intake rate (E^R), mean percentage Process 4 (see text for details) and accumulated dry season time spent per goat. Feeding was assumed synchronous, so the time spent per individual animal was equal to the time for the herd. Conditions were parameterized for four simulations; the Basic Grid using local and global estimates of G*, then repeated for the Runway. Each simulation was run at three levels of travel cost multiplier, *c*=0.01, 1.0 and 10.0. Each simulation started with 29 days of dry season followed by 210 days of wet season. The second dry season started on day 240. Results are shown for *c*=1 on days 0, 250, 300 and 365. 7


Basic Grid : Global G* : *c*=1
Basic Grid : Local G* : *c*=1
Runway : Global G* : *c*=1
Runway : Local G* : *c*=1
Forage biomass (kg ha^{-1})
Potential energy intake rate (E^R, J s^{-1})
Mean % Process 4
Accumulated time spent per goat (hr)
0
250
300
365
0
500
1000
1500
2000
2500
3000
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
10
20
30
40
50
60
70
80
90
100
50
100
150
200
250
300
0.0
0.5
1.0
1.5
2.0
Distance from water (km)

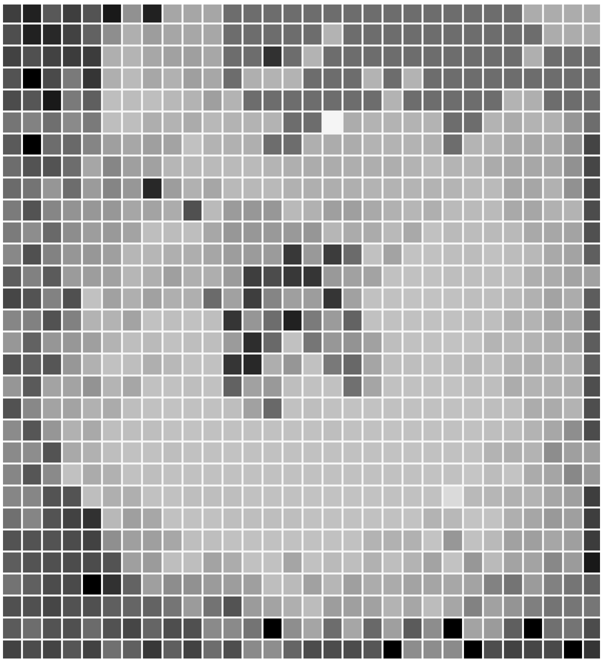


Fig. 3.10: Model output for the [Basic Grid : Global G* : *c*=1] simulation showing distribution of forage biomass on day 250. Increasing resource levels are shown with lighter shades. A white grid cell indicates the current herd position. Dry season foraging depleted central forage resources. Peripheral forage resources were mostly depleted during the wet season.

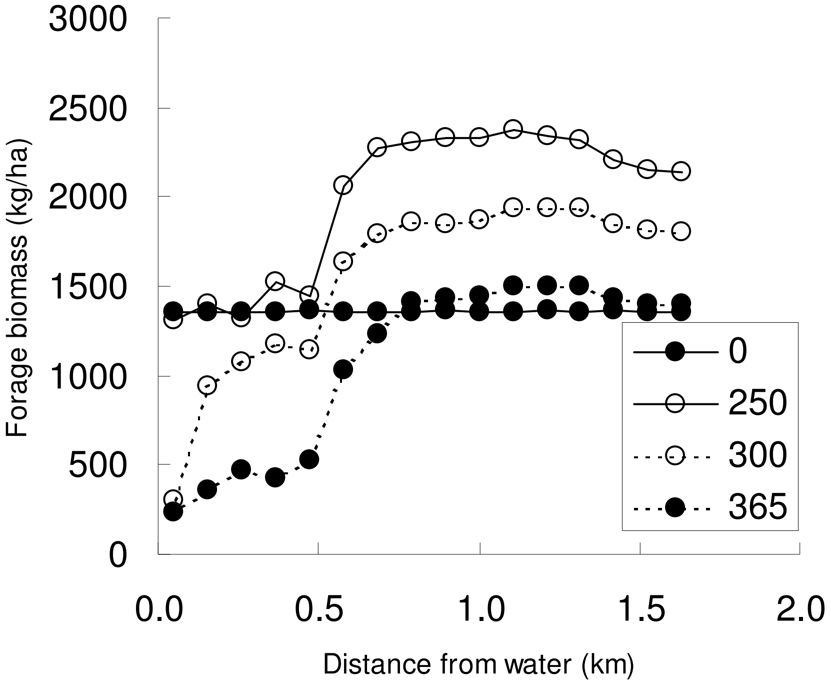


Fig. 3.11: Piosphere development in forage biomass for [Basic Grid : Global G* : *c*=1] simulation using unrestricted visual range. The piosphere response is shown for days 0, 250, 300 and 365 from the first year of simulation.

Differences from the estimates of environmental mean resource, local and global G*, influenced the initial extent of the piosphere response in grass biomass for the Basic Grid simulations (Fig. 3.9 and Fig. 3.13). Subsequent utilisation decreased this difference by the end of the simulations. Runway simulations using global and local G* exhibited even closer similarity.

The effect of visual range was tested by comparison of the results shown in Fig. 3.9 with simulation results using no restrictions on vision (Fig. 3.11). It can be seen that there was a marginal effect of removing the restriction on visual range. The development of the sacrifice zone initially favoured expansion of the zone in place of reduction of biomass levels (Fig. 3.11, day 250), but subsequent utilisation made the piosphere patterns analogous.

3.14.1 Test of Hypothesis 1: Geometry

Are piospheres the result of animal foraging decisions? (See hypothesis statement in Section 3.3). The comparison between a point water source in the Basic Grid and a Runway serves to show that piospheres can be explained as a function of available foraging area alone (Fig. 3.9). Where Basic Grid results showed development of the piosphere pattern, Runway simulation results showed no development of the gradient. There was a weak slope for the Runway using local G* generated by utilisation that was initially close to water, but by the end of the simulation, utilisation is comparable with the global G* Runway results where foraging activity was distributed uniformly so that all distances were utilized equally. Thus, the "neutral" model of a passive distribution of foraging impacts is applicable to piosphere pattern generation.

Consider the Runway to be constructed from a sequence of contiguous *blocks* and the grid to accommodate hypothetical areas within *annuli* defined by concentric circles of increasing radius. The distance between each block start and each concentric circle is the same. The water location is at a central position for each, at the centre of the grid, and in the cell at the middle distance along the length of the Runway. As mentioned previously (see Section 1.1.5 and Fig. 1.3), available foraging area within each *annulus* is given by $\pi x^2 - \pi(x-1)^2$, where x is a discrete distance interval from water. This simplifies to $\pi(2x-1)$. So, while block area is invariant with cumulative Runway area, annulus area increases linearly with cumulative available area. Consequently, the density of animals for the same herd moving away from water at a constant speed will decrease monotonically with distance for the grid proportional to $1/\pi(2x-1)$, but remain constant for the Runway. The corollary of these findings is that no utilisation gradients would be found for linear water systems (*e.g.*, rivers) where animals spend equal amounts of time at all distances from water, because spatial impacts were distributed evenly per unit area of Runway.

In reality, herbivore densities are not uniform, producing a clustering of their foraging activity. This was found for the goats in the preceding chapter (see Section 2.4.4 and Section 2.4.5), where browsing activity, which was shown related to the degree of impact, was distributed per unit area of landscape, but within distinct zones of that landscape. This can also be seen near rivers in cases of restricted access. Animals are known to habitually access rivers at certain watering points where the river bank may be shallow enough, or drainage lines from the surrounding landscape have eroded steep banks, thereby providing easier access to the water (Thrash & Derry 1999). In such cases, utilisation gradients will exist because these focal points have been introduced along the linear water source. The Runway experiment was hypothetical. If other herbivore impacts like trampling had been included in the model, a sacrifice zone may have been generated parallel to the line of the water, but the expectation would be for a more abrupt return close to the water source to surrounding forage levels than the gradual piosphere pattern. At the furthest point that animals are able to travel before returning to drink, the model would also be expected to predict a similarly abrupt rise to the unaffected forage resources beyond their daily foraging range, and not a utilisation gradient. This expectation is reasonable because the only published comparison between linear and point water sources by Cowley & Rodgers (1995) found the hypothetical gradient in stocking density of sheep in the Mulgalands of Australia with distance from water was less severe with linear water sources (bore drains) than with point water sources (troughs). They admitted the fact that they found any distance-related effect for linear watering systems was because both livestock and wildlife tended to concentrate at particular points along the bore drains.

Gradients in forage biomass were echoed in output for mean E^R in the Basic Grid simulations, although, the relative shapes and strengths differed. Most different was a near-water high value for E^R that discontinued the gradient under the Global G* scenario. In the Local G* results for the Basic Grid, the acute gradient in biomass was also masked by a near-water high value for E^R, implying that cells nearest the watering point had retained highly digestible forage components, not reflected by the reduction in biomass. 'Mean % Process 4' output closely followed E^R, although generated patterns were persistent, and unaffected by wet season re-growth. Initial conditions provided a sufficiency of forage biomass so that intake was determined entirely by digestive constraints (Process 4). Reductions in biomass limited forage to the point that instantaneous intake rate became limited by either bite density (Processes 1 and 2) or handling time (Process 3). During the wet season, bite sizes increased with plant growth (mean = 120.3 g), and bite rates decreased asymptotically (0.65 bites s^{-1}, *not shown* but see equivalent in Illius *et al.* 2002). But, during the dry season, bite size was comparatively low (109.1 g), and bite rate increased (0.78 bites s^{-1}) along with time spent grazing per day. But this was insufficient to maintain the mean daily wet season dry matter intake per head of 11.8 kg, which instead dropped to 8.6 kg on average during the dry season. Foraging Process (*sensu* Spalinger & Hobbs 1992) and intake rates are further studied in the next two chapters.

The flat responses from the Runway simulations are because animal foraging activity was distributed according to available foraging area, that is, foraging activity was equivalent per unit area. In the Basic Grid, where landscape geometry conspires to concentrate animal impacts towards water, spatiotemporal heterogeneity in utilisation alone produces a gradient. The success of this model, in parallel with the work of Adler & Hall (*subm.*), indicates that the appropriate scale for animal foraging strategy during the dry season is at the level of prey species aggregation and nearest-neighbour plants. Neither model includes assumptions about associations between individuals in plant communities. Instead directional movement is lead by aggregate levels of resources assessed at the scale of individuals within individual species.

Contradicting the "neutral" model, Adler & Hall's models (*subm.*) did develop a gradient response for their linear water system. For a simulation scenario employing global G*, knowledge of landscape-wide resource levels is not a limiting factor for animal intake. Nor is it a promoting factor. Instead, assumptions underlying site selection in their model must have given rise to the linear water system gradient. Most likely these were the assumptions involved in site assessment. Considering the TMin version of their model, animals were attracted to sites with intake rates in excess of a fraction of G* dictated by ET. Upon removal of a bite, G* would have decreased at a slower rate than biomass levels at the current position. The effect was to promote animal movement to a new destination within each day.

This process was repeated each time that foraging was restarted from the water point. Forage levels at distances visited on the previous day will have been above the current estimate of G* because of the utilisation of resources at further distances from water. This coupled with setting ET<1 maintained near-water utilisation whilst extending the range of utilisation (see Fig. 1.7b). Conversely, TMin run on the point water system showed a shift in a narrow utilisation peak (see Fig. 1.7a), again a direct result of the value of ET (0.2). This process underlies the generation of gradients in Adler & Hall's model (*subm.*), and explains the iterative nature of their gradient development, and the associated shift in the utilisation peaks.

The test of this interpretation is to reproduce Adler & Hall's results (*subm.*) for the effect of ET on gradient shape (see Fig. 1.8b). The current model was modified to include Adler & Hall's (*subm.*) parameter ET. Equations 3.5 and 3.8 were rewritten as Equations 3.9 and 3.10, respectively.

$$e_{ij} = E_{ij}^{R} - E_{ij}^{C} - E_{ij}^{F} - \left(ET \sum_{i} \sum_{j} E_{ij}^{R} \right) \Big/ IJ \qquad 3.9$$

$$b_{ij} = e_{ij} \sum_i \sum_j B_{ij} \Big/ ET \sum_i \sum_j E^R_{ij} \qquad 3.10$$

Two simulations were run, with ET=0.2 and ET=1, both for 300 days of dry season. The end results shown in Fig. 3.12 below are strikingly similar to Fig. 1.8b in terms of the shape of the response. In both graphs, a marked sacrifice zone developed for ET=0.2, from which there was a sharp increase in biomass to levels beyond the range of animal impacts. The ET=1 lines were flat except for an upturn furthest from water.

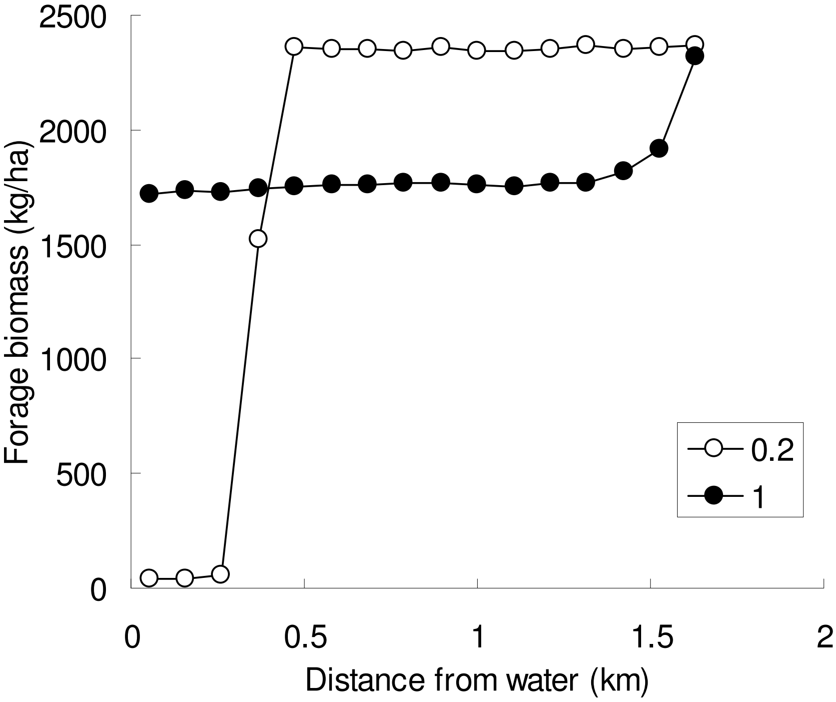


Fig. 3.12: Gradients in forage biomass for [Runway : Global G* : *c*=1] simulation after 300 days of dry season. The model was adapted to incorporate Adler & Hall's (*subm.*) 'start-eating' rule parameter ET. The simulations were run with ET=0.2 and ET=1.

The model was able to reproduce Adler & Hall's results (*subm.*) showing that the "neutral" model of piosphere generation as a condition of landscape geometry only holds for the assumptions about GUD's made for the Marginal Value Theorem (see Chapter 1, Section 1.2.11). No gradient resulted for ET=1. Manipulations of G* for ET<1 relaxed these assumptions and produced an artificial curve. However, we do not know fully how animals assess their resources and relate patch profitability to environmental supply. In a sense, the suppression of the gradient in the Runway, and hence support for the dependence of the piosphere pattern on landscape geometry were also artifacts, of ET=1.

3.14.2 Test of Hypothesis 2: Foraging activity

Is there a threshold distance at which animals optimally balance energy intake and expenditure? (See hypothesis statement in Section 3.3). Results here show a more consistently targeted, larger area for foraging activity than the results reported in Adler & Hall (*subm.*). Their peak in utilisation showed a shift to larger distances from water with no change in distance range. This implies a continual "chiseling" at the face of the cliff-like response reducing resources to the level of the sacrifice zone, as animal foraging was targeted at the boundary between the sacrifice zone and unutilized biomass. Animals would have bypassed profitable sites to recommence foraging at distances reached on the previous day, as echoed by the monotonic increase in daily distance travelled predicted by their model (*not shown*). This could be an optimal foraging strategy to minimize daily travel. However, it seems an oversimplification of the foraging options available to animals on a daily basis as they move away from water, and is most likely because Adler & Hall's model (*subm.*) does not account for constraints from travel costs and available foraging time. These factors in the decision process for forage selection act in parallel to reduce the attraction of remote sites and augment proximal resources. There is the possibility that the optimal solution may include some foraging at previously utilized distances.

Results from the current model showed foraging activity (T_{for}) accumulated across a broad range of distance from water. The distance at which the peak in this utilisation occurred was established early in the simulation, and did not shift (Fig. 3.9). This implies that whilst most utilisation took place at intermediate distances, animals did return to previously utilized distances to take advantage of profitable sites whilst travelling to the most abundant sites further away. In effect, animals followed a path comprised of "stepping stones" to make it possible to reach remote resources. The daily distances travelled ranged from 0.34 km to 3.80 km (mean = 1.24 km, standard deviation = 0.69 km), which is less than the furthest distances reported for goats in excess of 20 km, but this is probably exceptional. Instead, the quoted minimum distance for a herd of male goats (3.20 km, O'Brian 1984) compares favorably with the predicted distance, especially considering that the simulations were carried out for resource-rich landscapes, which would minimize the distances travelled. The predicted distance is also in close agreement with other reported distances for goat travel from water, assuming a 1-2 day watering frequency; 3.43 km (Western 1975), ~3 km (James *et al.* 1999), 3.4 km (Cumming & Cumming 2003). The constituent distances contributed to predicted total daily distance travelled as follows; D_{for} 35.3%, D_{com} 32.4% and D_{wat} 32.4%. The furthest distance travelled from water to the first utilized site at the start of the day was 0.89 km, and the furthest return distance at the end of foraging was 1.57 km. Total daily distance travelled did increase slightly from day 294, in order to maintain a daily dry season intake of about 0.7 kg per head, but importantly, this increase was not reflected in the upper range of utilisation.

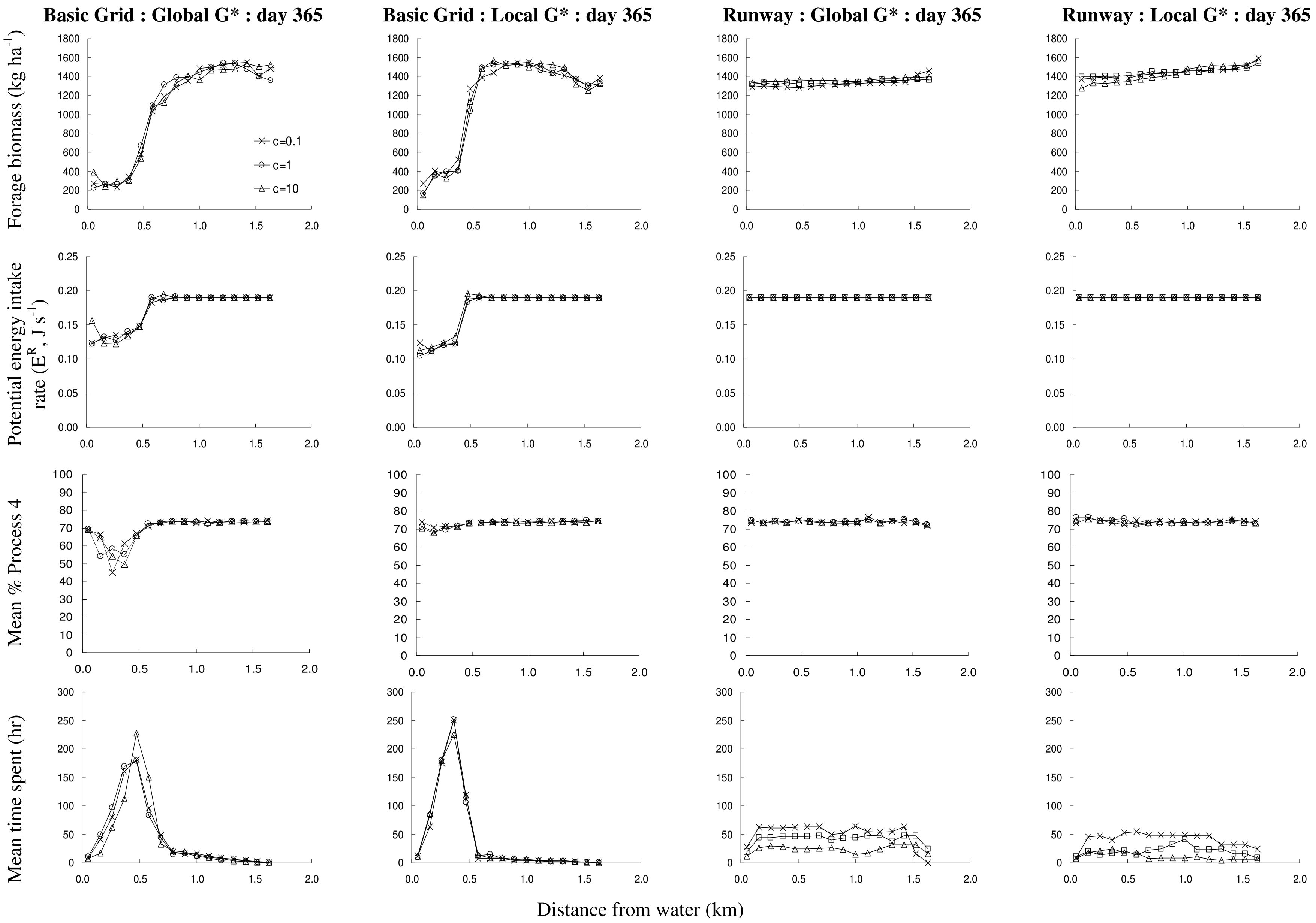
3.14.3 Test of Hypothesis 3: Travel costs

Do travel costs have some influence on foraging efficiency? (See hypothesis statement in Section 3.3). Crude manipulation of animal travel costs using the multiplier clearly showed a lack of variation in the responses from simulations using 3 levels, c=0.1, 1.0 and 10.0. Thus travel costs appeared to not directly influence piosphere development and piospheres seemed to be shaped independent of animal travel costs (Fig. 3.13). Nevertheless, travel costs were included in the model in the calculation of net potential energy intake rate and so helped to dictate available resource sites on a daily basis. So, there was sufficient energy gain in destination cells to provide a profit over the costs incurred travelling to the cell and feeding once arrived, although it is possible that an optimal strategy of only selecting few choice items ("creaming off the top") was prevalent. This would minimize foraging distances per cell and increase the amount of comparatively less energetically costly commuting ($E_{ij}^{C} \approx 0.7\, E_{ij}^{F}$). This is evident from a trend in the maximum distance travelled on any single day (D_{tot}) during the dry season at increasing levels of c

(correlation using $\log_{10}c = 0.99$), accompanied by a restriction in the range of daily distances. However, such a strategy is necessary to elicit profit only when travel costs are high enough to limit foraging distance. As $E_{ij}^{C} + E_{ij}^{F}$ can be as little as 0.01% of E_{ij}^{R}, only very large values of c would become inhibitory to all foraging and commuting activity. At smaller values, foraging activity was not limited, but the net energetic cost was enough to impact animal energy intake expressed in terms of their multiples of maintenance (*mm*). This is a measure of the energy required to maintain weight stasis subject to the animal's field metabolic rate (FMR, Nagy 1987). Thus, intake that is sufficient to maintain weight at, or above, the current weight corresponds to *mm*r1. However, the predicted goat multiples of maintenance fell below this, and was related to c by $mm = 0.868\ c - 0.058$ ($R^2 = 0.90$, se = 0.087, $F_{1,3} = 28.45$, P = 0.013), the consequences of which should have been a decline in animal density, but would not have been realized in the constant (static) herd of fixed size and composition (see Section 3.13.12).

Travel costs also helped to negate other sites from potential selection because their intake profitability was below G*. But, there was no accumulative effect on piosphere extent. Mean dry season time output from the Runway experiments approximately doubled for each ten-fold increase in the level of c. As only energy costs were modified by c, and not time costs, this was because potential foraging destinations were made unavailable by increasing the energy costs of travel and foraging. Consequently, available time could not be depleted by foraging activity at those locations and the daily foraging time was less for higher values of c. All other responses for all output variables remained consistent across the range of c, with only a slightly reduced range of utilisation occurring for the [Basic Grid : Global G* : c=10] simulation, but at a slightly further peak distance.

Fig. 3.13 (*overleaf*): Model output of four variables against distance from water; mean forage biomass, mean potential energy intake rate (E^R), mean percentage Process 4 (see text for details) and mean dry season time spent. Conditions were parameterized for four simulations; the Basic Grid using local and global estimates of G*, then repeated for the Runway. Each simulation was run at three levels of travel cost multiplier. Each simulation started with 29 days of dry season followed by 210 days of wet season. The second dry season started on day 240. Results are shown for c=0.01, 1.0 and 10.0 on day 365.


Basic Grid : Global G* : day 365
Basic Grid : Local G* : day 365
Runway : Global G* : day 365
Runway : Local G* : day 365
Forage biomass (kg ha^{-1})
Potential energy intake rate (E^R, J s^{-1})
Mean % Process 4
Mean time spent (hr)
c=0.1
c=1
c=10
0
200
400
600
800
1000
1200
1400
1600
1800
0.00
0.05
0.10
0.15
0.20
0.25
0
10
20
30
40
50
60
70
80
90
100
0
50
100
150
200
250
300
0.0
0.5
1.0
1.5
2.0
Distance from water (km)

This suggests that under conditions set by the Marginal Value Theorem, constraints on foraging activity other than travel costs determined piosphere extent. This immediately raises two questions,

1. If daily foraging range is moderated by travel costs, then why is piosphere extent independent of travel costs?
2. What is more influential than travel costs in dictating utilisation patterns and determining piosphere extent?

Daily foraging ranges do not necessarily compare to animal home range (see Section 3.9). The actual distance from water travelled would be expected to be a function of foraging path tortuosity. That is, the more direct (less tortuous) a foraging path of given length, the further the terminus will be from water. In addition, there needs to be adequate defoliation for the impacts to register in the piosphere response. However, on reaching the furthest distances from water energetically achievable during the foraging day, animals may be nearing their intake requirements. Departure from 1 for tortuosity signals curvature in the path. This deviation was found to decrease for foraging paths terminating furthest from water (*deviation* = -0.0001 *distance* + 0.122, $R^2 = 0.65$, $F_{1,14} = 26.17$, $P < 0.001$). The effect is that there is less consumption with distance from water (*dry matter intake / head / cell* = -0.0001 *distance* + 0.267, $R^2 = 0.70$, $F_{1,14} = 32.25$, $P < 0.001$), but the effect on the piosphere response is negligible. Chapter 5 takes a further look at the use of foraging path tortuosity as part of an optimal strategy in response to resource density.

Digestive constraints (Process 4) are considered fundamental to the optimization of browser diets (*e.g.*, roe deer, Illius *et al.* 2002). The model predicted that daily foraging was terminated by digestive constraints on 85% of the days in the dry season. Digestive constraints operate on a daily time-scale and were calculated in the model as daily herd potential intake, based on capacity of the gut to process forage of a given digestibility. This was not affected by travel costs and so would not be expected to respond to the value of *c* (see ‘mean % Process 4’ plotted in Fig. 3.13). However, it does highlight the role of diet digestibility in determining dry season foraging patterns. It also suggests a parallel with Adler & Hall's (*subm.*) EMax-Q model for which they used an animal functional response derived from the assumption that digestible energy gain, a function of forage quantity and quality, peaks at intermediate forage biomass. Although the current model produced comparable results, the mechanisms used were arguably less deterministic.

3.15 Conclusions

The reasons for piosphere generation needed testing. Animal water metabolism would be expected to determine watering frequency, which in turn would be expected to determine the opportunity for foraging between drinking events. Piosphere generation would be expected to be faster with increased use of a watering point. Perkins (1991) had already identified the likely cause of piospheres as the decrease in available foraging area on nearing water. Lange's (1969) initial work had attempted a measure of herbivore intensity (tracks) and Georgiadis (1987) (and others, including Perkins 1991) provided further animal-based evidence (*e.g.*, dung). However, it doesn't follow from this that spatial impacts are being distributed according to available foraging area mainly because these are only indicators of animal location and not forage utilisation. Stronger evidence came from measurements of affected vegetation and soil properties (*e.g.*, Andrew & Lange 1986a, Andrew & Lange 1986b), but the link with animal foraging effort was not made. It is an important consideration for foraging science whether animals are actively determining the use of their environment. The alternative is that passive (external) processes dominate.

My findings show a mixture of influences across a range of spatial and temporal scales. Animals select what to eat (active matching), but their dry season defoliation impacts accumulate over time to mirror the space available (passive matching).

- In dry conditions, water requirements are higher in exotic breeds than indigenous breeds, and lowest in wildlife.
- Within species, water requirements vary according to reproductive state.
- Allometric relations for water intake and turnover predict that smaller animals should have higher water requirements per unit body mass than large animals. This is true within species but is not reflected in all data.
- Indigenous goats can have several days between each drinking event (which effectively extends daily foraging range), but a daily watering frequency is implied for domestic breeds.
- Goats have been observed in excess of 10 km from water during the dry season, but about 3 km is a more reasonable estimate for daily travel while foraging.
- Allometric scaling of velocity confirmed the upper range for observed travel of about 20 km for goats (Model 1).
- Introducing terms for energy balance did not greatly affect this estimate (Model 2).
- Introducing constraints on animal intake reduced the estimate of goat foraging range (Model 3).
- Total foraging range does not determine piosphere extent.
- Piospheres are the result of landscape geometry as a function of water point location.
- Within this geometric constraint on available foraging area, further constraints on animal daily intake are required to give rise to spatial foraging behaviour that distributes herbivore impacts along a utilisation gradient
- Direct comparison of simulations using equivalent implementations of GUDs and the Marginal Value Theorem indicate that these constraints are travel costs and limits on available foraging time and digestive capacity, and that they act daily.

- Daily foraging was mainly terminated by animal digestive constraints during the dry season suggesting a greater control over the piosphere response than animal travel costs.
- Modifications to the critical density for resource exploitation underlying the Marginal Value Theorem have a strong effect on the simulated piosphere response. However, the scope of reference used to derive this threshold value was less influential.

CHAPTER 4 - CONSEQUENCES OF A UTILISATION GRADIENT ON INDIVIDUAL INTAKE

Abstract

- Recent models of functional response imply that defoliation has limited impact on browser intake rate, suggesting that utilisation gradients may have few consequences for browser intake.
- The consequences of a utilisation gradient were investigated for individual intake in small mammalian browsers.
- On a stretch of land with an already existing gradient of tree density, the utilisation gradient was generated by exposure of contiguous experimental blocks to a decreasing series of herbivore pressure.
- Following this treatment, utilisation gradients were found in both remaining bite size and bite density.
- Animal response to the utilisation gradient was recorded as bite rates within each experimental block, and was found to increase with decreasing utilisation.
- Animal functional response to the utilisation gradient showed a switch from handling-limited intake to encounter-limited intake as a consequence of higher utilisation.
- Intake rate in browsing animals was found to decline as a consequence of the utilisation gradient.

4.1 Objectives

1. To investigate the response of animal intake rate to a gradient in resource utilisation.
2. To investigate the constraints on animal intake rate under conditions of a utilisation gradient.

4.2 Introduction

IBHOKWE ISELA AMANZI	*Goats drink water*
IBHOKWE INYA UMNGA	*Goats eat acacia*

Xhosa translation by Lethando Dziba

The presence of a focal point for animal activity in a landscape concentrates and organises spatial impacts as a function of animal density (Andrew 1988, Palmer *et al.* 2003). The concentration of herbivore densities around watering points gives rise to the *piosphere*, a gradient of utilisation pressure that is greatest near the water and decreases as a function of distance from it (see Thrash & Derry 1999 for review). Most pronounced in arid and semi-arid zones where animals are most dependent on drinking water sites, these piosphere patterns have been reported in herbaceous species composition, range condition, grass production, biomass, understory cover, standing crop and basal cover. In areas populated by elephants, tree density and cover have also been found directly proportional to distance from water (Thrash & Derry 1999). Water dependence is assumed to be detrimental to animals because it restricts their foraging range during the dry season to areas depleted of resources by the high utilisation pressure (Redfern *et al.* 2003). Whilst seasonal animal distributions have been modelled as a function of distance from water (*e.g.*, Senft *et al.* 1983, Arnold & Maller 1985, Wade *et al.* 1998), to date little is known about the consequences of the piosphere for animal foraging behaviour on a daily basis. However, since forage availability appears to increase with distance from water (*e.g.*, Mphinyane 2001), it may be hypothesised that the piosphere poses animals with a conflict between their water and nutritional requirements. Simply put, distance travelled away from water in search of food has to be matched by return travel when animals next need to drink. An optimal foraging solution predicts that there should exist a distance from water at which animals would be expected to maximise their net energy gain as a result of the trade-off between energy gain from food intake and energy expended on travel between food and water.

Factors limiting food intake rate are critical for the immediate energy balance of an animal. For browsing animals, the problems involved each day with obtaining sufficient food are largely associated with the spatial and temporal distribution of forage resources (extrinsic constraints), and the capacity for food digestion (intrinsic constraints). An example of the former is the organisation of browse resources into patches (branch, tree: Åström *et al.* 1990, etc.), where the degree of spatial heterogeneity or patchiness is defined by a consumer's response to its environment (Wiens 1976). Animal behavioural response to the spatial heterogeneity of the piosphere pattern has not been assessed, but the self-organisation of impacts that generates the piosphere is likely to result in a continuum of patch profitability which animals must exploit optimally in order to maximise their energy gain.

Foraging animals are expected to respond to the spatial heterogeneity of their food resources (Pyke 1984) but little progress has been made towards the quantification of that response. An important obstacle to overcome involves evaluation of the environment in terms that are directly relevant to the animal (Wiens 1976). Although under certain conditions patchy foraging behaviour can result from continuous food distributions (Arditi & Dacorogna 1988), the logical expectation is that the animal feeding response to the piosphere mirrors the gradient in their forage resource. The resultant intake rate in response to the variation in food abundance is the animal functional response (Hobbs *et al.* 2003), and is central to our understanding of plant-herbivore equilibria and the predictive power of current models of foraging behaviour. A corresponding gradual functional response would imply a corresponding gradual variation in the effect from intake rate constraints. The aim of this work was to test this assumption.

4.2.1 The herbivore functional response

Spalinger & Hobbs (1992) provided a means with which to relate the functional response of foraging herbivores to the logistical problems that they encounter whilst searching for food. The rate an animal can consume food is dependent on the initial locating of food items, the travel between those food items, and the speed of cropping, chewing and swallowing of food once arrived. These activities are grouped into three processes, the boundary conditions for animals moving between the processes being a function of the spatial distribution of their food. Spalinger & Hobbs (1992) treated the initial search for food (their Process 1) and the movement between locations where identified food items may be consumed (Process 2) as both being dependent on the animal's maximum foraging velocity. Thus, Processes 1 and 2 describe whole animal movement between patches of feeding sites (stations) and are, therefore, operating at a spatial scale determined by the gait (stride length) of the animal. The Process 2 equation includes a term for the density of (D, bites m^{-2}), relating the animal's rate of biting (B_2, bites s^{-1}) to the density of bites available and the maximum foraging velocity of that animal between those bites ($V_{\max}$, m s^{-1}),

$$B_2 = \frac{V_{\max}\sqrt{D}}{1 + \bar{h}V_{\max}\sqrt{D}} \qquad 4.1$$

where, $\bar{h}$ (s bite^{-1}) is the handling time required to crop a new bite and, therefore, deducted from time available for processing previous bites. Inclusion of this term allows for situations in which handling is carried out whilst searching for future bites, and this distinguishes it from previous models of herbivore functional response (Farnsworth & Illius 1998).

Maximum velocity has since been identified as a source for overestimation of the animal encounter rate with food items. A better parameter is an animal's average foraging velocity ($\bar{V}$, m s^{-1}) because of the components of acceleration from the previous food item and the deceleration towards their next (Shipley *et al.* 1996). It should be noted that there is no explicit spatial scale associated with this formula. Rather, the scale at which bite density is measured will define the operational scale for animal velocity.

Lastly in the Spalinger & Hobbs formulation is Process 3, a process dependent on the animal's rate of cropping and handling plant material. Thus, Process 3 describes an animal's bite rate (B_3, bites s^{-1}) when it is constrained by the need for processing (chewing and swallowing) previously cropped bites,

$$B_3 = \frac{R_{\max}}{S + R_{\max}\bar{h}} \qquad 4.2$$

where, $R_{\max}$ (mg s^{-1}) is the theoretical maximum processing rate of the herbivore. In each case, an animal's instantaneous or short-term intake rate is simply the product of its bite rate and the size of the bites consumed (S, mg).

The Spalinger & Hobbs processing model has been validated across a range of animal species feeding on a range of browse plants (Shipley & Spalinger 1992), for which there is minimal effort involved in parameterisation. Parameter values are easily estimated from field measurements, or derived via allometric relations with body size (*e.g.*, Illius & FitzGibbon 1994, Shipley *et al.* 1994). Additionally, the model's attraction is furthered by its reduction of the potential suite of resource factors that give rise to complex animal foraging behaviour (such as consumed plant biomass) to only two essential forage properties; bite size and bite density (Gordon 2003). However, subsequent development of this model of functional response has revealed an additional mechanism of intake constraint. This Process 4 involves the digestive capacity of the animal rather than its harvesting potential (Shipley *et al.* 1999). Consequently, Process 4 operates across hours or whole days of foraging, a much longer temporal scale than that of the instantaneous intake rate predicted by the mechanistic model (Fortin *et al.* 2002).

4.2.2 The browser functional response

The familiar Holling Type II functional response of browsing animals shows a saturating curve that increases steeply but is uniform (flat-topped) above low resource density (Gordon 2003). This was reported by Owen-Smith (2002) who used a Michaelis-Menten model of Kudu nutrient intake (Owen-Smith & Novellie 1982) which budgeted foraging time between search (travel between patches) and handling (ingestion within patches). Intake rate was made dependent on the bite sizes and biting rates within patches, which varied with plant species and plant parts selected. However, for browse species, bite size was assumed to be virtually constant, with the result that patch depletion reduced *D* but *S* was unchanged, and intake rate did not begin to decrease with forage abundance until resources were almost entirely depleted (below ~20 g m^{-2}). Parallels may be made with the Spalinger & Hobbs' (1992) form of the functional response. The asymptotic portion of the functional response curve was a function of the animal search rate, and, therefore, equates to Process 1 and Process 2, whereas within patch intake was assumed to be constrained by processing and so is an alternative to Process 3. Illius (*in prep.*) recently corroborated these findings by application of the Spalinger & Hobbs model under conditions of variable bite density and constant bite size. The predicted functional response rose steeply at low resources, firstly operating under Process 1 constraints, and then Process 2 constraints. Above a threshold resource density the predicted intake rate reached its asymptotic maximum value determined by Process 3 constraints. The predicted intake rate did not vary from this maximum value for resources above this threshold (~5 g m^{-2}).

Both models predicted that animal intake rate would only decline at very low resources under conditions of variable *D* and constant *S*. The corollary is that above very low resources, animal intake rate within browse patches is constrained by Process 3. Some evidence of this was supplied by Gross *et al.* (1993) who validated the Spalinger & Hobbs model tested against intake rate data from a range of animals including a few browsers. They found instantaneous intake rate to be predominantly handling-limited operating via the determinants of bite size (*e.g.*, leaf size and geometry, spinescence). Stronger empirical proof has been provided by Illius *et al.* (2002) who used an optimisation technique (see Section 4.3.6) to identify which form of the Spalinger & Hobbs (1992) model best described the rate of biting in roe deer (*Capreolus capreolus*) hand-fed branches from a range of tree species. They observed that animals selected bites in order of size, the largest first, from which it follows that a lower intake rate should result from this reduction in bite size available to subsequent bites. Instead, they found little evidence of intake rate decline due to an accompanying increase in bite rate that was sufficient to maintain the short-term intake rate. They concluded Process 3 was the operational mechanism by which an animal's feeding rate is constrained whilst in position at a feeding site, within a patch.

Hobbs *et al.* (2003) tested the Spalinger & Hobbs model across two orders of magnitude of bite size and also bite density. They predicted a threshold in the distance between bites at which animal intake rate would switch from being regulated by handling time to constraints due to encounter rate. $S/R_{\max}$ gives the time taken to chew and swallow a bite of given mass, so the boundary condition was set by the capacity of the animal to travel between bites at the known velocity whilst handling bites at this rate. Arrival at the next bite before handling is complete is described by Process 3, and finishing handling with time to spare conforms to Process 2. The critical distance between bites (d*, m) was given by,

$$d^* = \frac{V_{\max} S}{R_{\max}} \tag{4.3}$$

Hobbs *et al.* (2003) combined Process 2 (equation 4.1) and Process 3 (equation 4.2) to construct a composite model, the applicability of each equation being defined by the boundary condition stated in equation 4.3. They tested the model against real animal data (recorded in Gross *et al.* 1993) and found that applying the threshold bite distance lead to an improved model performance over the equivalent predictions that assumed intake limitation by only one of the mechanisms.

A restricted foraging range due to water requirements would seem to be a disadvantage because of the resource depletion associated with water points. But, if the predictions for exclusivity of handling-limited constraints are correct then our expectations for the consequences of piospheres on dry season foraging would need re-evaluation, because it would follow that utilisation gradients have little influence on a browser's intake rate. Even though many woody plant species growing in semi-arid regions exhibit a morphology that is not conducive to herbivory by large mammals the browser's functional response would not be expected to reflect the variation in extrinsic conditions present across the utilisation gradient. In addition to spinescence, leaves may be distributed unevenly (*e.g.*, *Maytenus heterophylla*) or sparingly (*e.g.*, *Acacia karoo*), but it would have to be concluded that energy intake rate in browsers is largely unrelated to these and other traditionally considered determinants of patch profitability (*e.g.*, plant biomass). Alternatively, there is the equally untested possibility of the composite model of browser functional response that combines alternative mechanisms of intake rate constraint.

4.2.3 Specific research questions

This study seeks to evaluate the consequences that piospheres have for energy gain in browsing animals by identifying the appropriate constraints on food intake rate presented by a utilisation gradient in semi-arid rangeland. Does animal intake rate increase with resource abundance and distance from water? It is hypothesised that this is the case because animals are expected to respond to the local extrinsic conditions within patches across a continuum of resource abundance generated as a function of herbivore density.

4.3 Methods

4.3.1 Paddock structure

Trials were carried out in June during the dry season of 2000 in a tailor-made “Runway” paddock, 5 km long and 50 m wide, in part of the Honeydale Section, on the research farm belonging to the University of Fort Hare, in the Eastern Cape, South Africa (32°47’S, 26°51’E). The vegetation type has been described as "False Thornveld of Eastern Cape" (Acocks 1953), a mixed savanna dominated by the invasive woody "Sweet Thorn" (*Acacia karoo* Hayne). The variety in the study area grows no more than 2 m high. The long-term (1970-2000) mean annual rainfall is 617 mm (22% CV) of which two-thirds typically fall between October and April. 659 mm fell between July 1999 and June 2000, and 519 mm fell between October 1999 and April 2000, the wet season preceding the experiment.

The paddock was split into five blocks. Each block measured 1 km in length and was further divided into twenty plots of 50 m x 50 m marked by posts in the perimeter fence. One end of the Runway contained a watering point and was designated the "water". The *plot distance* was the distance from this water to the mid-point in each plot, and the *block distance* was the distance to the mid-point in each block. The paddock was also sited to incorporate a naturally occurring gradient in tree density (*see below*).

4.3.2 Paddock treatment

A utilisation gradient was established by sequential treatment of the paddock blocks with a decreasing number of browsing days at further distance from water. A herd of approximately 200 Nguni and Boer goats (*Capra hircus*) was used to levy 2000, 1800, 1200, 400 and 0 animal browsing days on Blocks 1,2,3,4 and 5, respectively, in order to generate a utilisation gradient in controlled circumstances that would be comparable with naturally existing gradients. Some insight into the defoliation intensities required to generate such a gradient was provided by the long-term study of goat feeding behaviour at the University of Fort Hare.

4.3.3 Vegetation survey

Assessments of defoliation impacts resulting from the treatment phase of the experiment, in addition to assessments of the plant morphology relevant to the animal-based measurement, were carried out using the Point Quarter Method (Cottan & Curtis 1956). For each survey, approximately half of the plots within each block were randomly selected for survey. Working from a central transect running the length of the paddock, the four nearest individual *Acacia karoo* to a random distance from the beginning of the plot were selected for measurement. For assessment of the utilisation gradient, the numbers of leaf clusters within 30 cm of the branch tip were recorded for the lowest browsed and unbrowsed branches. Mean percentage defoliation for the plot was calculated from the average number of remaining leaf clusters on browsed branches related to the leaf clusters on the unbrowsed branches. Trees were located in the same way for the assessment of bite density and bite size. For these assessments four branches were identified on each tree according to magnetic North, South, East and West, but at a random height not in excess of 2 m, the maximum observed browsing height for a goat (Steele 1996). The type of measurements carried out on these branches was particular to the assessment being carried out. Average leaf cluster density for each plot was measured by recording the distance, within 30 cm, from the tip of the branch to the point where each leaf cluster stem joined the branch. Average bite sizes for each plot were measured by collection of the intact leaf cluster nearest the tip of the branch for recording of dry weight. Leaf clusters were stored in brown paper bags for drying in an oven overnight (60 ^{o}C) prior to weighing. Complications from growth of leaf and shoot material were avoided by scheduling the experiment during the dry season, and observations confirmed that the bites remaining on the branch were remains of old leaf clusters and not new tissue. Tree density (a surrogate for the density of feeding sites) was calculated from the average distance between the canopy edges of the four individuals within each plot selected for assessment of the utilisation gradient.

4.3.4 Bite rate

A Dictaphone (AIWA TP-M720) was used to tape record the frequency of observed bites made by 39 goats randomly sampled according to 5 kg intervals across a range of body sizes (35-75 kg, mean = 48.4 kg, S.D. = 8.48 kg). These goats were sampled from the larger herd of 200 animals that had been used to treat the paddock (see Section 4.3.2, above). Each day, the smaller flock was collected from an overnight kraal (an enclosure with drinking water), and herded to each of a randomly selected sequence of plots within the Runway paddock. Feeding was minimal between plots, so feeding activity was rapid on arrival at the next plot designated for observations. Herding was discontinued upon reaching the plot, but the animals tended to move systematically through the plot. Observations commenced immediately on arrival at the plot. An observer announced the identification of the goat by a coded number and the distance from water as indicated by plot marker number. Plant species was also recorded although this was almost exclusively *Acacia karoo*, and bite rate estimates only used data collected for this species. Individual leaf cluster bites were signalled with the word “bite”. Shoot bites and bites delayed by the processing of previous bites (visible chewing) and steps between feeding sites were separately identified on the recording. After a period of familiarisation the least disruptive way to get close to the animals was by sitting at a point forward of the herd's progress and awaiting their arrival. This allowed close range observations to be made and enabled visual confirmation that other than shoots, single leaf clusters were indeed the target of cropping activity. The information on the tape recordings was captured into a computer using custom written software in which keystrokes could be coded for each activity (Appendix 8). The pressing of keys generated a sequence of activities each stamped with a time signature, although all that was needed for analysis was patch residence (total sequence duration) and the number of bites, and bite intervals were not used. Bite rates were calculated as the number of bites divided by the period of patch residence for each sequence. Operator performance was assessed by comparison of captured timings from known, artificially constructed sequences. To minimise this error during data capture only sequences of 5 or more bites were used for analysis. 470 bite rate observations were made for the randomly sampled goats (mean = 52.1 kg, S.D. = 9.22 kg).

4.3.5 Foraging velocity

The number of steps taken by a walking goat was counted for timed travel between feeding sites by a randomly selected animal of known body size across a range of randomly sampled plots. The distance travelled was measured after the goat had moved away. The routes of more tortuous paths were plotted using a sequence of numbered tennis balls that could either be laid on the ground or held in place on a tree with a thorn. The mean travelling velocity was calculated for a range of distances within randomly selected plots (n=34) within each block. In total, 126 observations of goat movement were made.

Results were compared with those of Shipley *et al.* (1996). A curvilinear regression (using the FITNONLINEAR function in GENSTAT 5.3.2, GENSTAT 5 Committee 1993) of time against distance fitted their model (equation 4.4) for the mean foraging velocity of an animal ($\overline{V}$, m s^{-1}) travelling distance d (m), with constant acceleration a_0 (m s^{-2}) to a maximum velocity between feeding sites (*inter-site* $V_{\max}$, m s^{-1}),

$$\overline{V} = \frac{V_{\max} d}{d + \frac{V_{\max}^{2}}{a_0}} \qquad 4.4$$

4.3.6 Analysis

Residual Maximum Likelihood (REML) estimates of block means were obtained to ensure that repeated measurement of individual trees or animals could be compared against the correct error term; an improvement on Generalised Linear Regression by inclusion of both random and fixed effects in REML. Block midpoint distance from water was fitted as the fixed effect to explain variation in tree density, bite size and bite density. Tree identity was fitted as the random term. Variables were transformed where necessary to meet assumptions of normality and homoscedasticity.

The significance of fixed-effect Wald statistics were assessed using the method of Elston (1998) and tested at conservative degrees of freedom as discussed in Appendix 2. Variation from significant effects was partitioned between blocks using the standard error of differences between pairs reported by the REML procedure.

The resolution of the vegetation-based data was initially investigated by looking for further explanatory power by including *plot distance* in the linear regression model. Model-2 regression is appropriate when two variables are measured with error (*i.e.*, for data with bivariate normal distributions), or when there may be no causal structure between the two variables. However, the treatments here gave rise to a causal structure between defoliation and bite size, and defoliation and bite density. Even so, slopes are not computed by Least Squares Regression because Reduced Major Axis slopes presume either that error in one variable is similar to that in the other, or that one variable is not to be predicted from the other, neither of which is true in this case. (Ricker 1973, Sokal & Rohlf 1995).

Animal-based measurements of bite rate and patch residence were analysed in the same way, but with goat identity fitted as the random term. Short-term intake rate was calculated by multiplying each sequence bite rate by the appropriate estimate for block mean bite size. The optimisation technique of Illius *et al.* (2002) was then used to investigate the goats' functional response by ascertaining which form of the Spalinger & Hobbs (1992) model best described the animal rate of biting, and thus if intake was limited by encounter rate or handling time. This technique used linear forms of Equations 4.1 and 4.2, which had been rearranged to give the time taken per bite T_b (s bite^{-1}) for each Process:

Process 2: $$T_{b2} = \bar{h} + \frac{1}{V_{\max}} \frac{1}{\sqrt{D}} \qquad 4.5$$

Process 3: $$T_{b3} = \bar{h} + \frac{1}{R_{\max}} S \qquad 4.6$$

Equations 4.5 and 4.6 were simultaneously fitted to the recorded time taken per bite (s bite^{-1}) using an optimisation procedure (FITNONLINEAR, GENSTAT 5 Committee 1993) to predict the appropriate parameter estimates for $\bar{h}$, $V_{\max}$ and $R_{\max}$ that maximised bite rate, and defined the Process that applied to each plot. Block mean and modal values for Process were summarised from these predictions. The bite rate data was obtained from measurements made within a feeding site with no relocation of the animal, therefore, this is an estimate of *intra-site* $V_{\max}$ which represents the velocity of head movements made in reaching individual bites. Furthermore, equation 4.5 uses the square root of the two-dimensional bite density included in the original formulation of the Process 2 equation (equation 4.1) by Spalinger & Hobbs (1992). Therefore, the actual value of the linear measure of bite density recorded during the vegetation survey (see Section 4.3.3, above) was used, and not the square root, as it was already in the correct units of bites m^{-1}. All analyses were carried out GENSTAT 5.3.2 (GENSTAT 5 Committee 1993).

4.4 Results

4.4.1 Paddock character

Including *plot distance* did not improve the model fit for any variable (*see below*), therefore, only block means are presented (Table 4.1). The paddock was first characterised in terms of the gradients in resources that it contained. Tree density differed significantly between blocks ($F_{4,3} = 17.65$, $P < 0.001$), giving a naturally occurring gradient revealed by mean inter-canopy distance (Fig. 4.1). Blocks 4 and 5 were the most similar with an average 3.94 m between tree canopies. *Plot distance* did not a significantly improve the regression fit ($F_{1,270} = 0.01$, $P = 0.94$).

Exposing the paddock to differential herbivore pressure generated a utilisation gradient, comprising about 89, 87, 82, 55 and 3% defoliation of the *Acacia karoo* in each block (Fig. 4.2). There appeared to be a lower limit in plant biomass for browsing activity given by an upper asymptote at about 89% defoliation. The utilisation rate was retarded by 3.21% defoliation with every 100 browsing days accumulated. This decrease in utilisation with distance from water would have been partly due to the gradient in tree density as well being caused by less goat browsing activity; the estimated goat browsing days per individual tree assuming even distribution of trees at the measured canopy distances in Blocks 1, 2, 3, 4 and 5 were, 52.0, 19.5, 5.1, 0.2 and 0.0 days, respectively.

Remaining bite size differed significantly between blocks (Fig. 4.4a), presenting three pooled mean sizes for the gradient: 86.1 mg DM (Blocks 1 and 2), 103.3 mg DM (Blocks 2 and 3) and 160.6 mg DM (Blocks 4 and 5). *Plot distance* did not significantly improve the regression fit ($F_{1,145} = 0.71$, $P = 0.40$). There was a 1 mg DM reduction in mean bite size following removal of the number of bites equivalent to 1% defoliation (*bite size* = 182.74 - 0.96 *defoliation*, $R^2 = 0.79$, $F_{1,3} = 15.9$, $P < 0.05$), resulting in a two-fold range in bite size (Fig. 4.3).

Source of variation	Variable	N	*Block* Means with same suffix letters are <u>not</u> significantly different at P ≤ 0.05. Standard errors in brackets.					*Sig. of block effect*
			1	2	3	4	5	
NATURAL	*Tree distance* (m) [1]	276	36.07 (2.611)	23.27 (3.692)	14.64 (3.481)	4.65^{a} (3.481)	3.23^{a} (5.222)	$F_{4,3}$ 17.65 ***
TREATMENT	*Browsing days*	-	2000	1800	1200	400	0	-
	Defoliation (%)	412	88.94^{a} (2.438)	87.04^{ab} (3.147)	82.11^{b} (3.257)	54.47 (3.317)	2.89 (4.781)	$F_{4,2}$ 79.18 ***
	Bite size (mg DM)	412	81.94^{a} (13.910)	90.18^{ab} (17.040)	116.41^{b} (11.890)	149.93^{c} (11.580)	171.25^{c} (13.200)	$F_{4,4}$ 7.78 ***
	Bite distance (m)	412	0.066^{a} (0.005)	0.063^{ab} (0.004)	0.053^{b} (0.005)	0.046 (0.005)	0.025 (0.005)	$F_{4,3}$ 12.80 ***
	Bite density (bites m^{-1})	412	18.85^{ab} (1.768)	19.24^{ac} (1.65)	21.90^{bc} (1.768)	26.30 (1.768)	42.60 (1.736)	$F_{4,2}$ 32.45 ***
RESPONSE	*Foraging mode*	-	G	G	B	B	B	-
	Process	-	-	-	2.10 (0.100)	2.06 (0.056)	2.88 (0.125)	-
	Modal Process	-	-	-	2	2	3	-
	Short-term bite rate (bites s^{-1})	470	0.678^{+}	0.684^{+}	0.635 (0.029)	0.790^{a} (0.020)	0.808^{a} (0.028)	$F_{4,3}$ 14.60 ***
	Short-term intake rate (g s^{-1}) [2]	470	0.056^{+}	0.062^{+}	0.074 (0.004)	0.118 (0.003)	0.139 (0.004)	$F_{4,2}$ 72.00 ***
	Patch residence (s) [3]	470	-	-	17.25^{a} (1.301)	16.48^{a} (0.890)	12.51 (1.290)	$F_{4,10}$ 4.25 *
	Inter-site distance (m)	126			7.96^{ab} (1.408)	5.67^{a} (0.819)	8.78^{b} (1.245)	$F_{4,29}$ 3.25 *
	Inter-site $\overline{V}$ (m s^{-1}) [4]	126	-	-	0.579^{ab} (0.0396)	0.597^{ac} (0.0216)	0.597^{bc} (0.0366)	n.s.
	Inter-site a_o (m s^{-2}) †	-	-	-	2.065 (0.0867)	0.688 (0.1603)	0.392 (0.1285)	-
	Inter-site V_{max} (m s^{-1}) †	-	-	-	0.605 (0.0250)	0.783 (0.0232)	0.805 (0.0366)	-
	Inter-site travel time (s) ‡ [5]	-	-	-	25.29	7.79	5.41	-
	Long-term intake rate (g s^{-1}) ¥	-	-	-	0.030	0.080	0.097	-

† Estimated using Shipley *et al.* (1996) model, equation 4.4

‡ Using block means ${}^{[1]}\!/_{[4]}$

¥ Using block means ${}^{[2]\times[3]}\!/_{[3]+[5]}$

$^{+}$Values derived from equation 4.1

Table 4.1: Results for block means in resource distribution and animal response estimated by Residual Maximum Likelihood (REML) analyses unless stated otherwise.

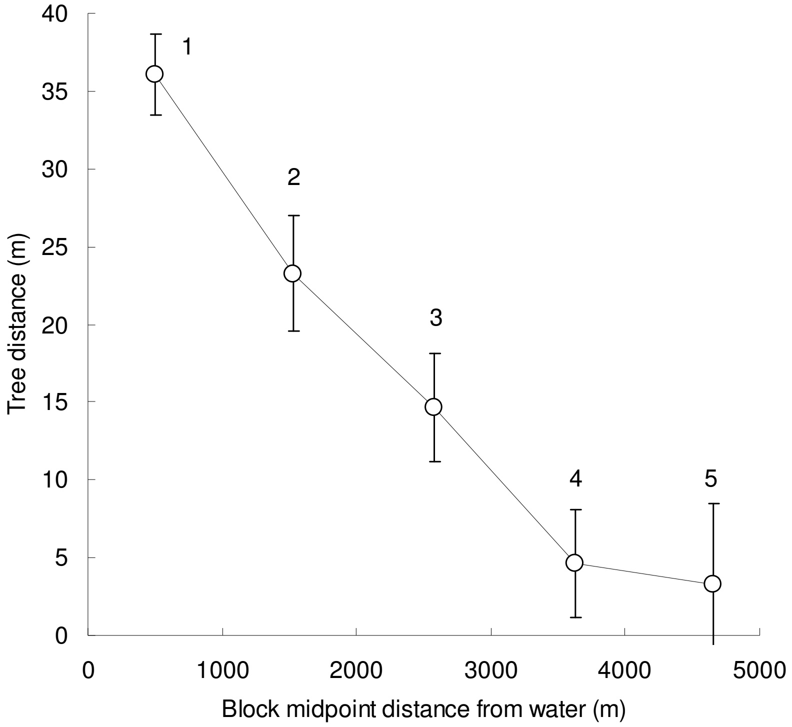


Fig. 4.1: The paddock already had a naturally occurring gradient in tree density (given here as inter-canopy distance). Block numbers are given and the standard errors of block means are shown.

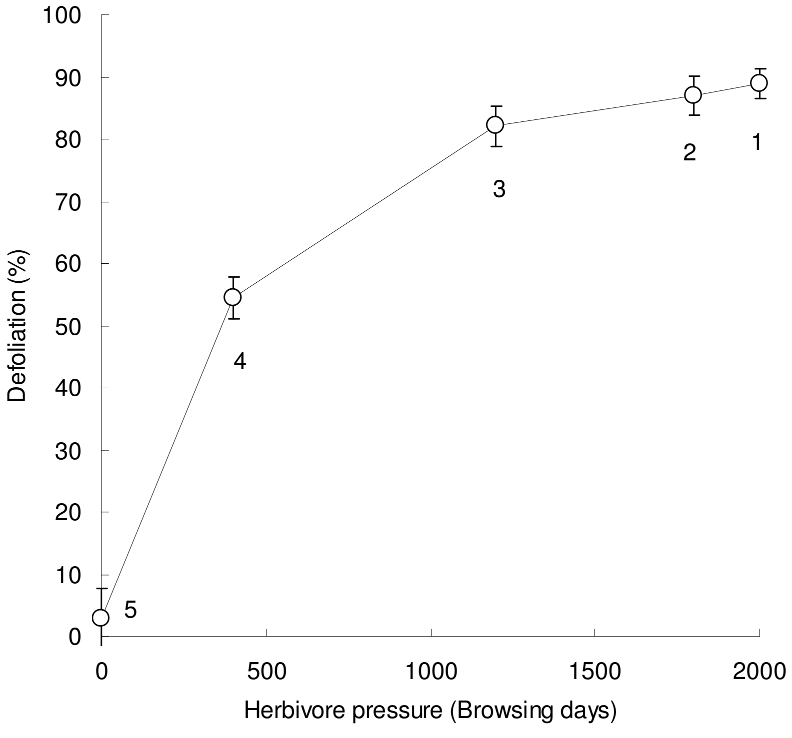


Fig. 4.2: Exposing the 5 treatment blocks to decreasing goat-browsing activity generated a utilisation gradient. Block numbers are given and the standard errors of block means are shown.

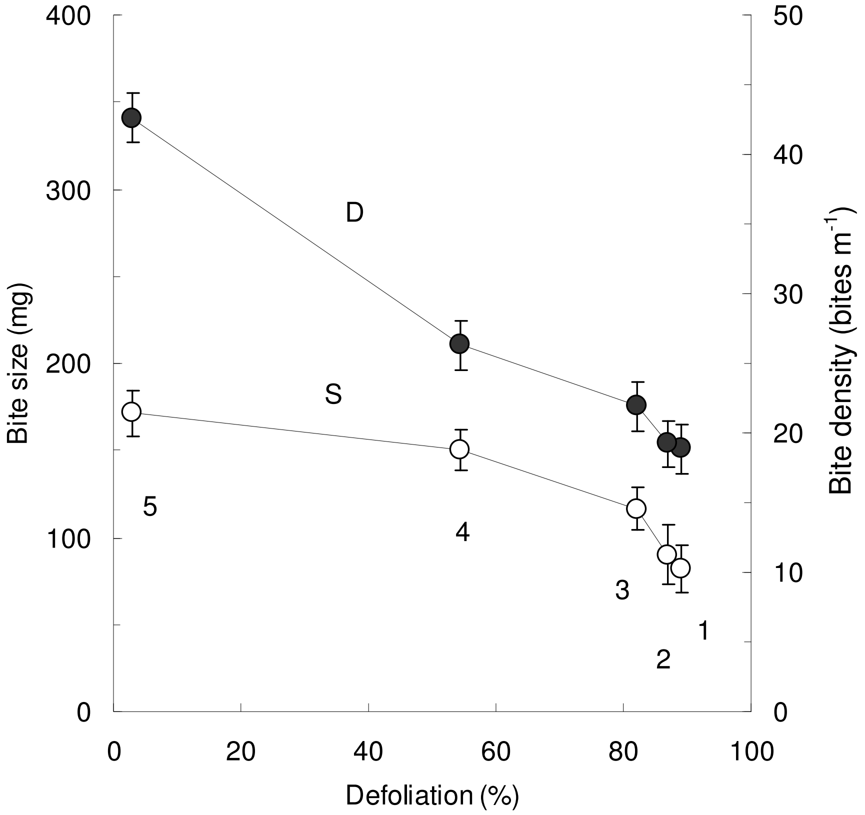


Fig. 4.3: Treatment effects of utilisation pressure on bite size (S mg DM, open circles) and bite density (D bites m^{-1}, closed circles). Block numbers and standard errors are marked.

The distance (m) between individual bites decreased exponentially with *block distance* from water, and increased linearly with defoliation (*bite distance* = 0.0003 *defoliation* + 0.022, $R^2 = 0.96$, $F_{1,3} = 88.2$, $P < 0.01$, Fig. 4.3). Expressed as bite density (bites m^{-1}), this showed an exponential increase with distance from water (Fig. 4.4b), giving a lower mean for Blocks 1, 2 and 3 (20.0 bites m^{-1}), and two significantly different means (26.3 and 42.6 bites m^{-1}) at further distances from water. *Plot distance* did not significantly improve the regression fit ($F_{1,134} = 0.03$, $P = 0.86$).

4.4.2 Foraging velocity

Mean foraging velocities, calculated from the time taken to travel a given distance, ranged from 0.22 m s^{-1} to 0.95 m s^{-1}, with mean 0.60 m s^{-1} (S.D. = 0.190). Applying the model of Shipley *et al.* (1996), it was possible to obtain paddock-wide parameter estimates for *inter-site* $V_{\max} = 0.75$ m s^{-1} and acceleration $a_0 = 0.70$ m s^{-2} (S.E. = 0.15, $R^2 = 0.58$) and block-specific estimates for these parameters (Table 4.1).

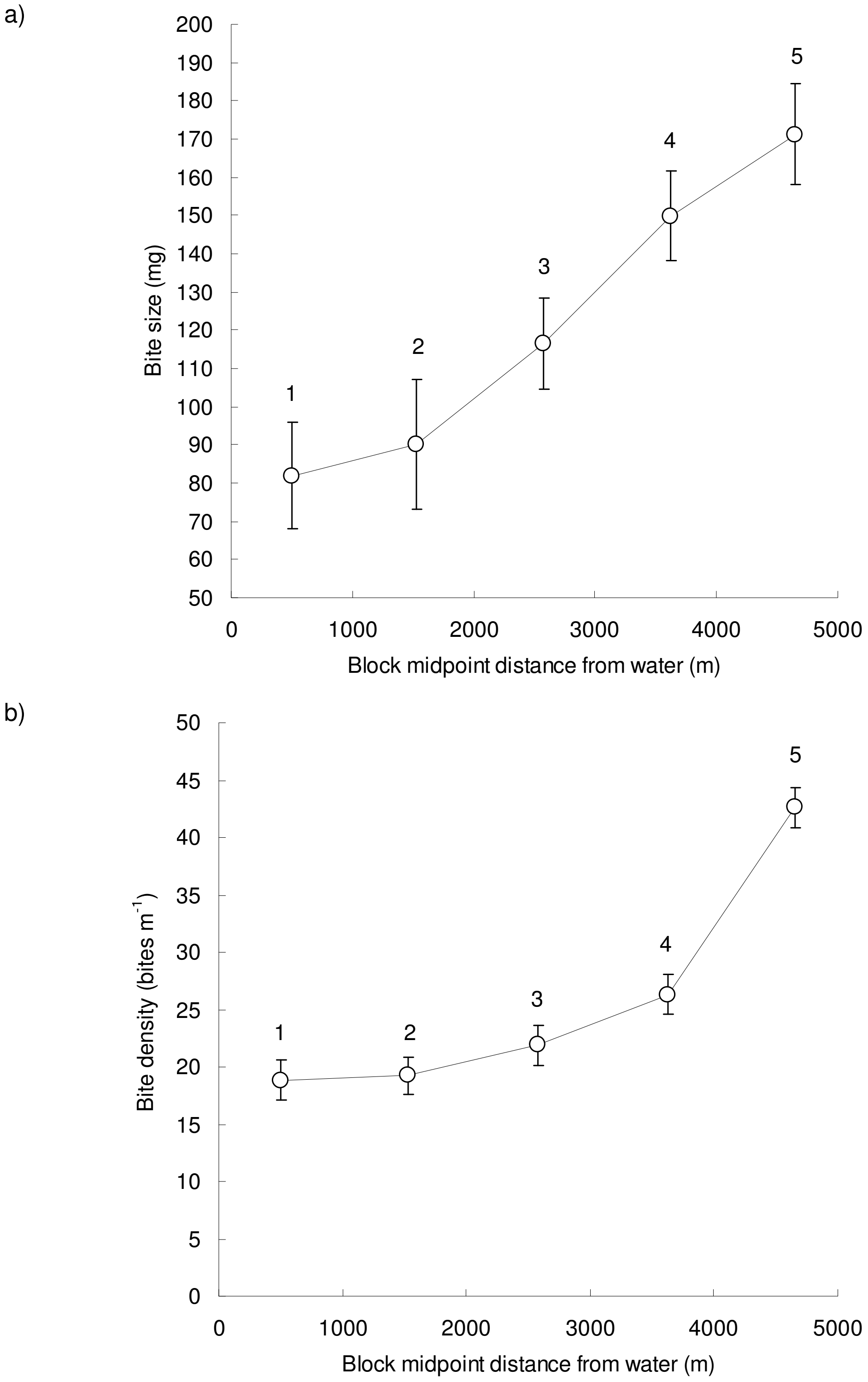


Fig. 4.4: The utilisation gradient in a) bite size (mg DM) and b) bite density (bites m^{-1}). Block numbers are given and the standard errors of block means are shown.

The data from these experiments (Fig. 4.5) shows a four-fold increase in mean velocity across a 27 m range in distances sampled. The fitted model of Shipley *et al.* (1996) reaches an upper asymptote at about 0.7 m s^{-1}.

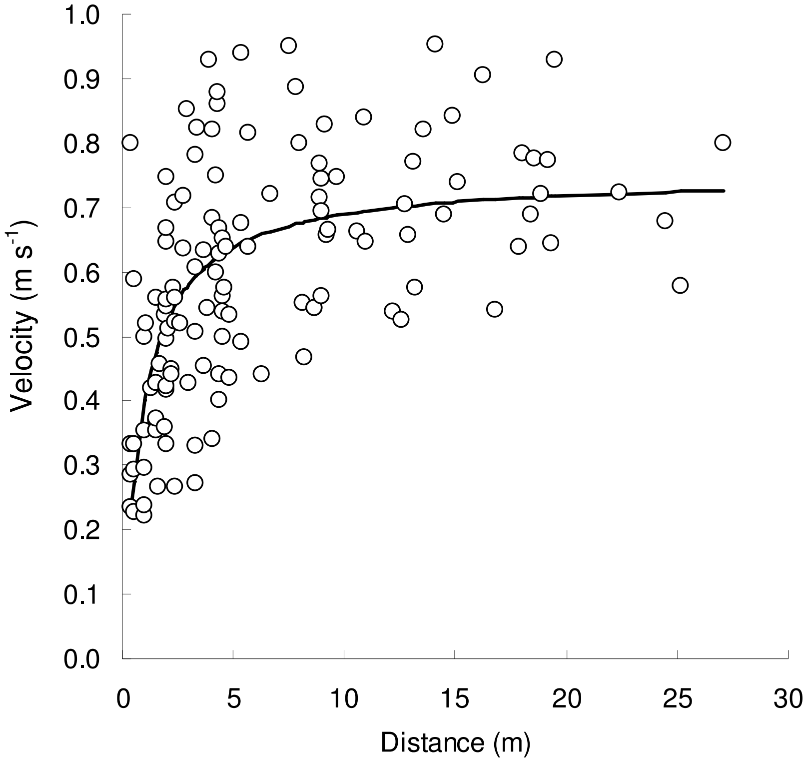


Fig. 4.5: Goat foraging velocity in relation to distance between feeding sites. The curve shows the fitted Shipley *et al.* (1996) model.

The data here was more scattered than measurements reported for goats by Shipley *et al.* (1996). This is because the contrived runway environment that they presented to their animals featured evenly arranged plants. The clustering in their data ($R^2 = 0.70$) reflects these arrangements, whereas the heterogeneous distribution of plants in the Runway paddock at Fort Hare gave rise to a more comprehensive range of interplant distances.

While $\overline{V}$ was constant throughout the paddock, a_0 increased with tree distance, increasing the *inter-site* V_{max} achieved with distance from water. This meant that in addition to the shorter distances between canopies in blocks furthest from water, the goats spent less time travelling those distances through denser resource areas, than equivalent distances in less dense areas. Although data was limited (N=3), animals appeared to adjust their maximum foraging velocity (*Inter-site* $V_{\max}$) with respect to tree distance (Pearson product moment correlation coefficient of means for Blocks 3, 4 and 5, Table 4.1, r = -0.99). The decrease in total time spent travelling between sites also reflects the increased opportunity in foraging time with distance from water.

4.4.3 Animal feeding response to the utilisation gradient

Goat feeding behaviour exhibited the switching in foraging mode from browsing (B) to grazing (G) that had been previously observed after sufficiently high utilisation of resources in Boer goats foraging on similar rangeland (Raats *et al.* 1996). Thus, the goats were observed exclusively grazing in Blocks 1 and 2, and exclusively browsing in Blocks 3, 4 and 5. Bite rates were recorded in a total of 48 plots (36 distinct plots giving 60% coverage of all available plots in Blocks 3, 4 and 5) during four consecutive days. When browsing, the goats were seen to remove only individual leaf clusters and shoot tips when taking a bite. The error associated with data capture of bite sequences (mean sequence error = ±0.21 s, minimum = 0.06 s, maximum = 0.72 s, S.D. = 0.166 s) was found to be within the range of standard errors for estimates of patch residence. However, there was a large skew in this error for short bite sequences. Consequently, sequences of 4 or less bites were excluded from the analysis, equivalent to 0.84 standard deviations below the mean sequence length of 12.24 bites. Mean patch residence differed only in Block 5 where the goats spent 26% less time at individual feeding sites than in Blocks 3 and 4 nearer water (means = 12.5 s and 16.9 s).

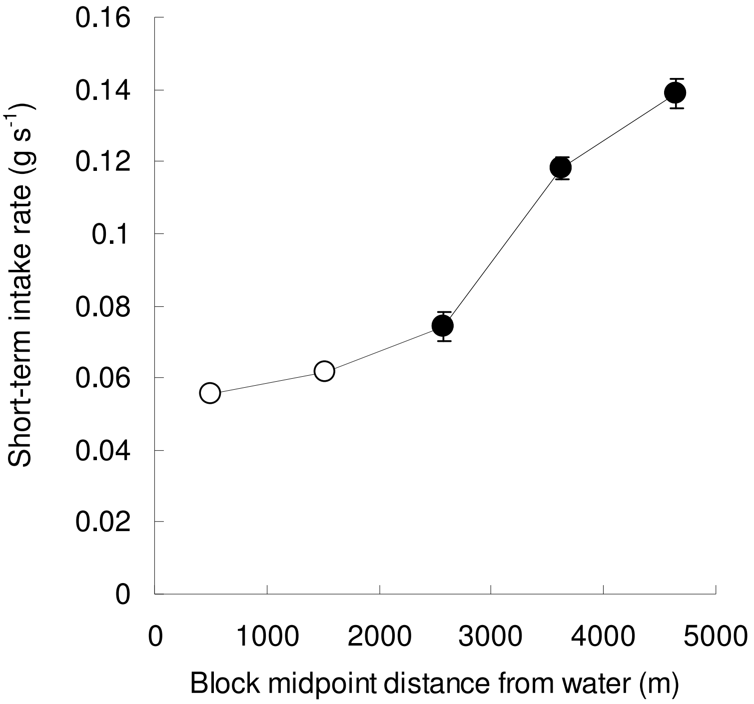
4.4.4 Intake rate

Animals were unable to match their higher rate of biting achieved furthest from water at the location closest to water. This produced two rates of animal response equal to 0.64 bites s^{-1} (Block 3) and 0.80 bites s^{-1} (Blocks 4 and 5). Although Blocks 4 and 5 showed no significant difference in bite sizes and bite rates, estimates of short-term intake rate did vary across the extent of the utilisation gradient (Fig. 4.6a) for which animal measurements were made ($F_{4,2} = 72.0$, $P<0.001$). The three estimated intakes rates for the goats were 0.07 g s^{-1} (Block 3), 0.12 g s^{-1} (Block 4) and 0.14 g s^{-1} (Block 5).

Using the optimisation technique of Illius *et al.* (2002) parameter estimates were obtained by regression of the calculated bite rate data simultaneously using equations 4.5 and 4.6 ($R^2 = 0.11$, $F_{3,32} = 374.44$, $P < 0.001$) which gave *intra-site* $V_{\max} =$ 0.090 m s^{-1} (S.E. = 0.037), $\bar{h} = 0.885$ s $bite^{-1}$ (S.E. = 0.214) and $R_{\max} = 460$ mg s^{-1} (S.E. = 237.0). This procedure reported whether Process 2 or 3 better described the limiting mechanism operating in each experimental plot. It was estimated that the goats' intake rate was limited by handling cropped bites in only 9 of the 36 plots. This is contrary to previous expectations for an animal in position at a feeding site, where it was assumed intake rate would be solely moderated by bite size, and not by the distribution of bites within that feeding site. From these findings it was possible to ascertain both the mean block Process and the modal Process value for each experimental block. The block means were closest for Block 3 (mean Process = 2.10) and Block 4 (mean Process = 2.06), both lower than the value for Block 5 (mean Process = 2.88). This grouping is reflected by the modal values such that Process 2 was most prevalent (r 90%) in Blocks 3 and 4, and Process 3 was most common in Block 5 (88%).

It was assumed that the same limitation on intake would apply in Blocks 1 and 2, where there were even lower bite densities and smaller bite sizes than those present in Block 3. Therefore, the parameter estimates obtained for $V_{\max}$ and $\bar{h}$ were substituted into equation 4.1 along with the block mean estimates for bite density. The resulting predictions of short-term bite rate for Blocks 1 and 2 do not rank in order with the estimated block means obtained by measurement. The estimated mean for Block 3 (0.635 bites s^{-1}) is lower than both of the calculated bite rates for Blocks 1 and 2. However, the mean bite sizes remaining after treatment in each block are distributed such that a gradient in short-term intake rate was produced when bite rate predictions were multiplied by the corresponding bite size estimates (Fig. 4.6b).

a)



b)

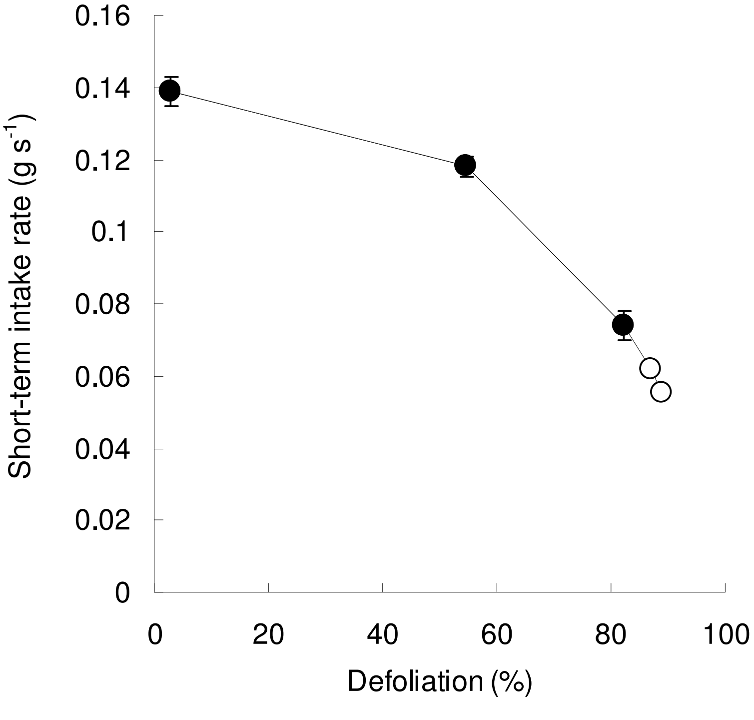


Fig. 4.6: Observed (filled circles) and predicted (open circles) short-term intake rates for goats a) with distance from water, and b) in response to the defoliation treatment. Standard errors are marked. Predicted values assume that intake is solely encounter-limited (Process 2), and were calculated using equation 4.1 and the parameter estimates from the optimisation technique of Illius *et al.* (2002), with *intra-site* V_{max} = 0.090 m s^{-1} and $\bar{h}$ = 0.885 s $bite^{-1}$.

4.4.5 Functional response

Bite density (bites m^{-1}) estimates for each block were combined with the corresponding bite size (mg) estimates and re-expressed in terms of edible plant biomass (g m^{-2}). This calculation assumed the possibility of translating the recorded unidimensional measure of bite density into two dimensions (bites m^{-2}). The translation was felt justified because tree canopy morphology was considered sufficiently dense and convoluted for there to be a consistent enough distribution of bites between branches. Lowest branches were often within half a metre of the ground, and sometimes as low as 0.1 m, which meant that most of the above ground tree consisted of the dense canopy. Archibald & Bond (2003) measured *Acacia karroo* [*sic*] in an arid shrubland and found a comparable mean height of first branching at 0.47 m, and more basal stems in that habitat than in the same species in the four other habitats that they studied. The result was that the trees at that site exhibited a "densely ramified growth form" which produced canopies that were "cage-like". Although drier (150 mm mean annual rainfall), the arid shrubland was located within 700 km at a similar altitude (800 m above mean sea level) to the Fort Hare study site (500-600 m above mean sea level), and the descriptions and photographs included in their paper bear close similarity to the trees in the Runway paddock. Even though tree morphology seemed to support this translation of bite density, ideally, bite density within a tree canopy should be expressed in three dimensions, but two dimensions were preferred to facilitate direct comparison with previous estimates of forage density (see below).

The plot of short-term intake rate against edible plant biomass is the goat functional response and clearly shows the Holling Type II asymptotic relationship between forage abundance and animal intake rate (Fig. 4.7), where intake rate rises with edible plant biomass towards an asymptote. In this classic relationship, the hypothetical maximum intake rate is determined by the reciprocal of the handling time per bite ($1/\bar{h}$), and the rate at which intake rate increases with increasing forage abundance towards that maximum value depends on the animal's searching efficiency.

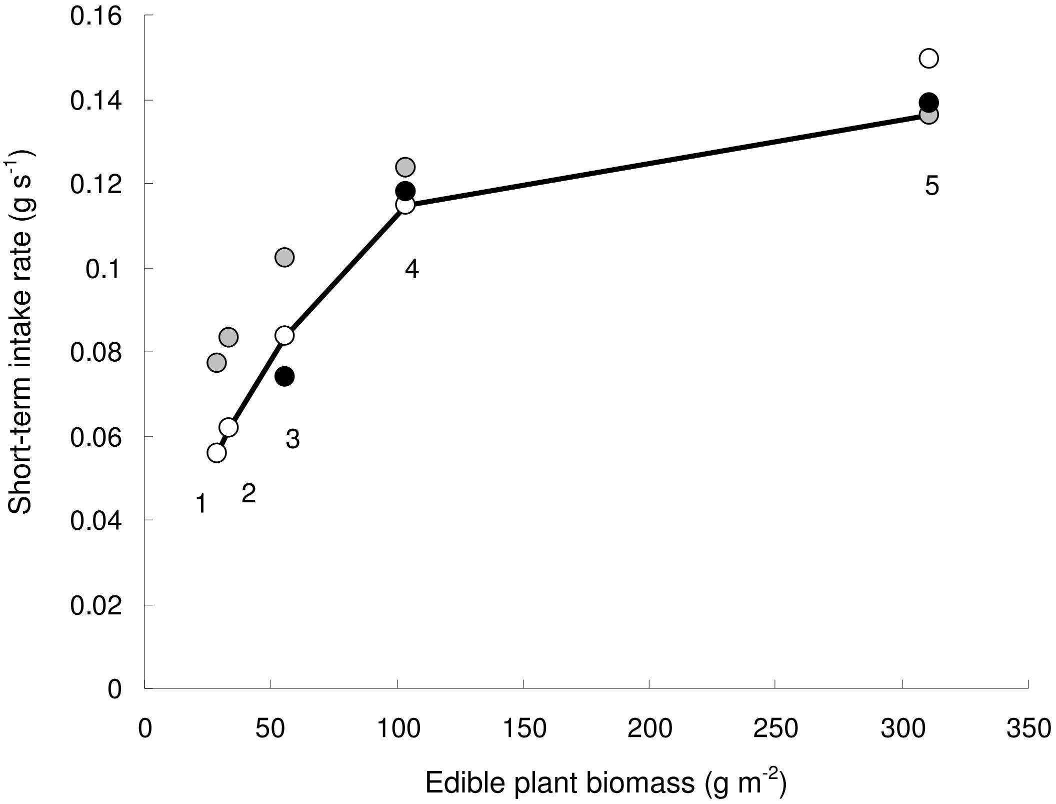


Fig. 4.7: Functional response of animals across the utilisation gradient. Values derived from the experimental results (black circles) are in good agreement with the predicted functional response of Spalinger & Hobbs (1992). Process 2 (white circles) used equation 4.1 and Process 3 (grey circles) used equation 4.2, and the parameter estimates from the optimisation technique of Illius *et al.* (2002), with *intra-site* $V_{\max} = 0.090$ m s^{-1}, $R_{\max} = 460$ mg s^{-1} and $\bar{h} = 0.885$ s $bite^{-1}$. The line shows the minimum predicted using these equations, and therefore the limiting conditions for animal intake rate. Block numbers are marked.

In terms of Spalinger & Hobbs processes, handling rate-limited intake would be under the conditions applicable to Process 3, whereas Process 1 and Process 2 define intake constraints from searching and movement. Process 2 was found to be the predominant constraining mechanism for animal intake in Blocks 3 and 4, and Process 3 in Block 5. Process 2 was assumed to be exclusive in Blocks 1 and 2.

The functional response curve did not stabilise within the range of available forage density, and intake continued to increase at resources ten-times more than the saturation thresholds predicted by Owen-Smith (~20 g m^{-2}, Owen-Smith 2002) and Illius (~5 g m^{-2}, Illius *in prep.*). The corresponding threshold in resource density at which the switch from Process 3 to Process 2 occurred in the Runway paddock was crudely estimated to be in the range 150 to 250 g m^{-2} (Fig. 4.7).

4.5 Discussion

A utilisation gradient was generated in savanna dominated by *Acacia karoo*, across a series of experimental blocks, by varying exposure to goat browsing. Similar, naturally occurring gradients have been quantified in terms of the impact of herbivory on vegetation variables along transects emanating from a focus, such as a watering point. But this study is the first to attempt quantification of animal response to the piosphere in terms of the consequences of the gradient for animal foraging behaviour. Using the model of Spalinger & Hobbs (1992) that derives the animal functional response to variation in the distribution and size of bites that can be cropped from their forage resource, the results show that intake rate varied in response to the gradient as a function of distance from water.

Long-term intake rate includes the travel time between feeding sites. The goats spent less time travelling shorter distances between feeding sites. This was not because of the increasing tree density with distance from water as animal velocities were estimated for similar inter-site distances. Rather, they produced a faster *inter-site* $V_{\max}$, the maximum travelling speed of the animals, through denser areas. This was in response to the accompanying decrease in the acceleration component *Inter-site* a_o of the average velocity *Inter-site* $\overline{V}$. But browsing animals have been observed to follow tortuous foraging paths through dense habitats but travel more directly and quicker between sparsely spaced bushes (Etzenhouser *et al.* 1998). This seems to disagree with the findings here until it can be seen that the time to reach the maximum velocity ($V_{\max}/a_o$, s) increased markedly with distance from water (Block 3: 0.3 s, Block 4: 1.1 s, Block 5: 2.1 s). Assuming that acceleration and deceleration are equal (Shipley *et al.* 1996), the time left for travelling between feeding sites at the maximum velocity (*Inter-site travel time* - $2V_{\max}/a_o$, s) through dense areas is small (Block 3: 15.0 s, Block 4: 4.3 s, Block 5: 1.1 s). Although *inter-site* $V_{\max}$ is lower in sparse areas, there are more prolonged distances travelled at this speed. Short distances (~1 m) travelled at *inter-site* $V_{\max}$ in the densest areas may minimise travel and maximise long-term intake rate, because in areas of abundant resources, there is a reduced cost to missed opportunities by a rapidly travelling animal

The determinants of short-term intake rate were revealed by application of an optimisation technique that identified the appropriate constraint under the set of foraging conditions within each experimental block. The procedure resulted in paddock-wide estimates for $V_{\max}$, $R_{\max}$ and $\bar{h}$. The estimate for *intra-site* $V_{\max}$ reflects the scale at which measurements were made, namely for the static animal at a feeding site, within the browse patch. Therefore, *intra-site* $V_{\max}$ refers to animal head movements. Unfortunately there are no known literature values against which to compare this estimate, except that it is roughly ten-times less than estimates for whole animal movement (*inter-site* $V_{\max}$). Caution while moving the head might be expected when accurately selecting individual bites, especially from a spinescent plant, but it is not possible to further assess the speed of goat head movements. The value for $R_{\max}$ estimated by the optimisation procedure is higher than 176 mg DM s^{-1} which is the predicted value for the animal mean body size (M) using scaling relationships ($0.70M^{0.70}$, Shipley *et al.* 1994). The effect of such a reduction in $R_{\max}$ for the conditions in the piosphere would be that *d** would occur for combinations of smaller bite size and lower bite density. However, the inflated estimate for $R_{\max}$ in this study is not dissimilar from 391 mg DM s^{-1}, the processing rate found by Shipley & Spalinger (1992) for white-tailed deer of about the same body size as these goats (47 kg), browsing red maple (*Acer rubrum*). The corresponding estimate of $\bar{h}$ for these deer was 1.8 s, more than twice the estimate here, which however, is in good agreement with handling times (about 1 s) previously found for goats feeding on other small-leafed woody species (Illius *et al.* 2002). The longer handling time for red maple may be because of this tree's large leaves which are problematic for smaller browsers (Shipley & Spalinger 1992). $V_{\max} \times \bar{h}$ is the average distance an animal moves its head to prehend each bite. This is about 0.08 m, further than the block mean distances between bites, which suggests that animals do not simply move their heads laterally between neighbouring bites, and supports the conclusion that they are more selective than simply cropping adjacent bites. Moreover, while cropping a bite, browsers may make a sharp backward motion to sever thick stems (Laca *et al.* 1994) which repositions the head away from the branch.

4.5.1 A note on spinescence

This study has taken the first step in redefining utilisation gradients such as the piosphere directly in terms of the animal response to the extrinsic conditions presented by the gradient. Within a patch, the animal must negotiate the physical barriers posed by woody plant architecture. In *Acacia karoo* the overlap of branches creates a complex 3-dimensional space bordered by thorns into which the animal must insert its head in order to access the preferred leaves and shoots. Leaves are clustered on 2 to 7 pairs of pinnae, each bearing 8 to 20 pairs of oblong leaflets, each 4 to 7 by 1 to 3 mm in length (Coates Palgrave 1996). Between each leaf cluster the spinescent stipules are paired and each is 7 cm or longer. It has been proposed that thorns provide plants with physical defence against browsing (*e.g.*, Cooper & Owen-Smith 1986). This would seem particularly likely in acacias as thorn growth can be induced by defoliation (Dangerfield *et al.* 1996, Karban *et al.* 1999), although this does not occur in all species (Gadd *et al.* 2001). Archibald & Bond (2003) recorded the longest spine lengths (up to 7 cm) in arid karoo shrubland for *Acacia karoo* from five habitat types; where tree morphology in arid karoo shrubland was similar to that observed in the arid shrubland during this study.

It is possible that the entire incidence of intake rate constraint by Process 2 found for the utilisation gradient was simply a result of thorns separating neighbouring bites on the same branch. The increased spacing of the remaining bites by successive removal of the largest intermediate bites explains the switch in intake rate constraint, but it is likely that plant architecture also interacted with the intensity of defoliation. Gowda (1996) showed that intake rate in goats was negatively correlated with the density of thorns on shoots of *Acacia tortilis*, describing goat biting in two ways; pruning (removal of both twigs and leaves) and picking (only leaves removed). Gowda (1996) found that increased thorn density negatively affected the proportion of shoot that could be pruned, but picked bite sizes were unaffected, which suggests that thorns force animals to pick in order to maximise bite size. In the absence of thorns, the optimal cropping strategy is probably to move the head systematically sideways between successive bites keeping the mouth close to the branch. This is less selective than the forward-back picking motion, but would give the fastest cropping technique even for large bites not entirely obscured by stipulate thorns. Protrusion of leaf clusters beyond the extent of the thorns would present only a fraction of the total bite implying a reduction in handling time and a trade-off between bite size and the rate of cropping.

The presence of thorns between bites can be expected to impede lateral head movements so the removal of each bite must be followed by a retreat from the branch. Thus, the retardation of encounter rate due to the depletion of the density and size of bites on the branch would be exacerbated by the presence of thorns, because thorns better shield smaller bites. Several studies have reported reduced food intake rate because of spinescence through an effective decrease in bite size (*see* Illius *et al.* 2002). Why this does not result in encounter-limited intake regardless of bite size implies that there is a minimal bite size at which impedance by thorns comes into effect, above which handling time constraints outweigh the delays caused by thorn-avoiding head movements. Illius *et al.* (2002) found that the effect of spinescence on the animal functional response varied according to the thorn characteristics of each plant species, but because handling-limited intake was assumed, this was only tested in the parameters associated with Process 3 (equation 4.6). This omitted *intra-site* $V_{\max}$, the parameter for Process 2 (equation 4.5) which could have reflected the effects of thorns on encounter rate through the interaction of bite depletion and spinescence.

4.5.2 Thresholds in patch browsing

Where forage was sufficiently abundant at distances furthest from water, intake rate was constrained by the time taken for chewing and swallowing bites, and therefore best described by Process 3. Nearer water, the effects of this handling time might have been lessened by the smaller bite sizes because the goats had already preferentially removed the larger bites. But, bite density was also reduced by previous browsing activity such that the rate of encounter with bites, described by

Process 2, became the predominant factor influencing intake rate. It should be noted that because bite density was measured within patches, it was assumed that there was no influence of the already present gradient in tree density on animal intake rate. Long-term bite rates that incorporate feeding at two or more sites could have been affected, as the reduction in tree density nearer water would have implicated Process 2 (or even Process 1). However, bite density was measured on the branch, and not as the distance between feeding sites, therefore any detection of Process 2 also applies to this *intra-site* spatial scale.

The results presented here confirm that energy gain in browsers is limited by handling constraints when animals are in position within a resource patch. However, in contradiction of recently reported findings, intake rate within a patch was also constrained by encounter rate. This means that Process 3 cannot be assumed to operate exclusively for patch browsing. This conclusion is in disagreement with Illius *et al.* (2002) and Owen-Smith (2002) because these other studies did not allow for the simultaneous depletion of both bite size and bite density. The amount of defoliation within each block generated relatively the same degree of impact on both bite parameters leading to a two-fold range in both bite density and bite size (Fig. 4.3). This accompanying decrease in bite density was sufficient to suppress animal bite rate under the Process 3 model because it could not account for the delay in cropping due to the additional time for head movements. Thus, the animals were unable to accommodate the decrease in bite size with an increase in their rate of cropping under Process 3, as observed by Illius *et al.* (2002). Consequently, intake rate constraint is better described by Process 2 when the conditions within a patch cause the distance between bites to exceed *d**. But this critical distance also depends on the animal's ability to handle bites of a given size, such that it is the combination of bite parameters which causes the switch in the intake rate-limiting mechanism (Fig. 4.8).

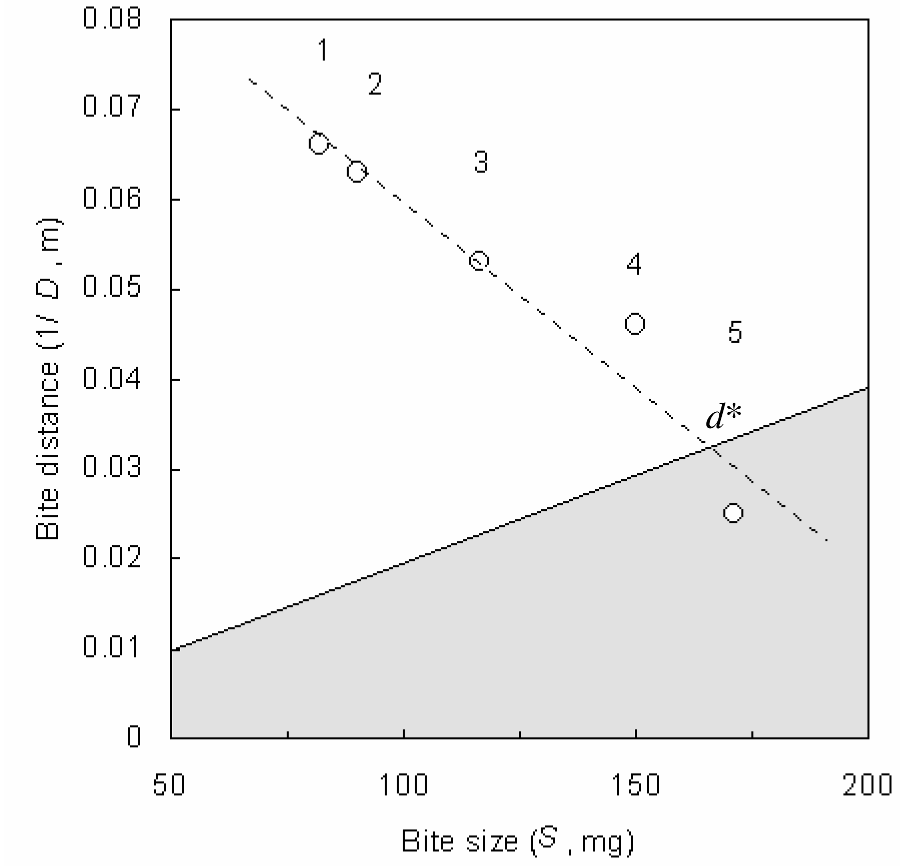


Fig. 4.8: The simultaneous modification of bite density (given here as bite distance = 1/*D* m bite^{-1}) and bite size (mg DM) as a consequence of defoliation. Browsers remove largest bites first giving the negative relationship between bite density and bite size (open circles). The solid line is the bite distance threshold *d** (equation 4.3) calculated using $V_{\max}$=0.09 m s^{-1} and $R_{\max}$=460 mg s^{-1}, which defines the conditions where intake rate switches from being handling-limited (shaded) to encounter-limited (unshaded). The dotted line is the regression $1/D$=0.1009-0.0004S (R^2=0.93, $F_{1,3}$=38.48, P<0.01), and shows the trajectory of the piosphere through this parameter space. The intercept of the two lines gives the parameter combination causing the mechanism switch in the piosphere. Block numbers are marked.

These findings are in agreement with Hobbs *et al.* (2003) and confirm their prediction that shorter distances between bites become more critical for the mechanism switch with diminishing bite sizes. The switch occurred in the piosphere for approximately $S < 170$ mg and $1/D > 0.03$ m. Using these values, and making the same assumptions about translating bite density from one to two dimensions, it was possible to improve on the above estimate for the critical density of available forage that elicited the switch in foraging Process (see Section 4.4.5). The critical density was calculated to be approximately 189 g m^{-2}, which is within the previously estimated range of 150 to 250 g m^{-2}..

The patch residence times recorded here conform to the prediction of the Marginal Value Theorem that animals should remain at feeding sites for longer when food patches are depleted. Encounter rate-limited intake was found for these depleted patches, but this analysis involved aggregating results across patches and extrapolation of parameter values to provide estimates where measurements had not been possible. Therefore, the predicted functional response applies across the length of the piosphere, at no particular temporal scale. It should not be inferred that patch depression would necessarily result because of a decrease in intake rate in response to collateral food depletion during a single feeding bout. Indeed, patch residence times were too brief for enough defoliation to occur in this experiment (*cf.* Fig. 4.2), but future experiments should investigate the proposed lack of patch depression for browsers (Illius *et al.* 2002) given the reports of encounter rate-limited intake from this study.

4.6 Conclusions

- This study is a mechanistic interpretation of the consequences that the spatially heterogeneous food resource present in the piosphere pattern has for animal intake.
- When browse is abundant, intake rate in browsing animals is limited by the time required to chew and swallow food.
- In depleted patches where food is less abundant encounter rate is a more important determinant of animal intake rate.
- It can be seen from the methods used here that utilisation gradients have direct consequences for animal energy gain, contrary to the predictions of recent models of functional response.
- This is because resources are depleted in abundance and distribution as animal density is concentrated which causes browser intake rate to decrease as they approach water.

CHAPTER 5 - EMERGENCE OF SPATIAL PATTERN AND ITS CONSEQUENCES FOR DRY SEASON SURVIVAL

Abstract

- Spatially explicit models are providing new ways in which to test concepts in ecological theory such as the hierarchical approach to ecosystem dynamics.
- This hierarchy is ordered in terms of spatial scale, and the scale issues that are associated with modern theory dictate our ability to accurately measure and analyse the dynamics of these systems.
- Ecosystem dynamics are the composite result of the dynamics of each level in the hierarchy, with emergent properties arising from the dynamic interaction within and between hierarchy levels of increasing spatial scale.
- Two types of emergence in an African semi-arid grazing system are investigated here; the generation of a grazing gradient by the focus of animal impacts around a water point, and the consequences of this gradient for animal foraging efficiency.
- Differential time lags were found to operate in the maintenance of the gradient, and the density dependent moderation of the animal population.
- Animals were unable to match the distribution of their resources because of their daily drinking requirements, with the effect that animal forage intake was compromised by the low density of dry season forage in the vicinity of the water point.
- In contrast, forage density was found not to be the primary limiting factor for animal intake rates during the rainy season when animals are less dependent on water points.
- It is concluded that animal populations are at equilibrium with their dry season resources.
- This chapter shows how the dynamics of the modelled ecosystem, including its emergent properties, were a result of the dynamic interaction within and between patches of the system scale hierarchy.

5.1 Objectives

1. To identify the emergent properties of spatial pattern generation.
2. To investigate the consequences of the utilisation gradient for the maximisation of daily forage intake rate and optimal foraging.
3. To investigate the degree of association between animal population dynamics and dry season resources.

5.2 Introduction

Space is the place — SUN RA

5.2.1 2001: A spatial odyssey

This is the typical story of a contemporary ecological model in the early third millennium. Typical because development of the model has involved eventual consideration of the spatial distribution of its components (*see* "Methods", Section 5.3). Over the last decade there has been an average 24% annual increase in the number of papers listing “model” and “spatial” as keywords in the ecological literature (ISI 2002). The question arises as to what the attraction is for the extra dimensions. Space is the bit of an ecosystem in which we are not interested. It is unoccupied, void. However, it is also the arena in which the players in the system act out their biological roles. In this unoccupied space, the interaction between components takes place, where the location of their properties coincide (Derry 1998). It is the distance between component properties within an ecosystem, and the range of their effect that defines the potential for interaction between species members, and between species members and their habitats. The prospect of modelling such species-habitat relationships arrived with the development of spatially explicit population models (Turner *et al.* 1995).

5.2.2 Emergent properties

Justification for spatio-temporal modelling of ecological space is often found in the discovery of emergent properties (*e.g.*, Pacala & Deutschman 1996, Parrish & Turchin 1997), which would otherwise not be apparent from unidimensional (temporal) simulation (Steinberg & Kareiva 1997). Thus it is increasingly easy to find papers linking emergence with ecological modelling, not least in recent volumes of the ecological modelling literature (even by title *e.g.*, Ball & Gimblett 1992, Olson & Sequiera 1995, Krebs & Bossell 1997). The value of spatial modelling, therefore, largely rests on a tenet that it is possible to recognise emergence when it occurs. However, this may prove difficult. The elucidatory work of Bergandi (Bergandi & Blandin 1998, Bergandi 2000a, 2000b) highlighted a history of mistakes when identifying emergence made in the name of ecosystem, landscape and community ecology. It seems that a common misunderstanding fails to acknowledge that emergent properties of the whole are not collective properties of the aggregated parts (*i.e.*, statistics), but that they exhibit qualities distinct to those of their constituent elements (Bergandi & Blandin 1998). Goldstein (1999) objected to the “flurry of recent [conservation literature] papers devoted to quantifying imagined properties of communities” and suggestions that "perceived or imagined emergent properties of communities should be at the root of conservation planning", especially when the work attempts a process-orientated, functional approach to landscape management. It is worth noting that this may indicate more a misunderstanding of ecosystem processes by Goldstein than by the authors that he targets (Walker 1999). Either way, it remains that confusion exists about the nature of emergence.

5.2.3 The nature of emergence

The discovery of complex patterns arising from elementary constituents occurred comparatively early for sociology (Parsons 1937) and embryology (Turing 1952). In ecology, however, although ecological space has been a concern for some time (*e.g.*, Gause 1934 cited in Tilman & Kareiva 1997), it is only the recent advances in computing that have allowed simulations of integrated spatial systems. These studies have elicited pattern formation at individual (*e.g.*, Krebs & Bossell 1997), patch (*e.g.*, Parrish & Edelstein-Keshet 2000), population (*e.g.*, Olson & Sequiera 1995) and landscape levels (*e.g.*, Wade *et al.* 1998). This organization of structure and function into a spatially ordered hierarchy of scale has necessitated revision of established concepts and primarily led to our current comprehension of ecological systems (Schneider 1998). Contemporary dicta based on the scale hierarchy even advocate holistic analysis in the place of reductionism (Li 2000). Neither ecological holism (Odum 1953), nor the hierarchical approach are recent introductions (in abstraction, *e.g.*, Scholes 1990, and simulation, *e.g.*, Auger 1990), but the modern synthesis has allowed the application of scale relationships to integrate across those hierarchies (Wiegand *et al.* 1999).

Scale hierarchies in landscape utilisation provide us with a model of an animal’s perception of its environment (Senft *et al.* 1987). Habitat selection, and, therefore, animal distribution, is deemed to be scale dependent (Morris 1992), with selection at the habitat scale being a decision made prior to subsequent foraging decisions at smaller scales (Orians & Wittenberger 1991, Bailey *et al.* 1996, Adler *et al.* 2001). Additionally, there is some evidence that the strength of selection increases for smaller scales (Schaefer & Messier 1995). Indeed, there is experimental evidence for how animal diet selection can be influenced by the fine scale distribution of their food resources (Edwards *et al.* 1994, Turner 1999), and how this selectivity is affected by the scale of patchiness in their resource (Wallis De Vries *et al.* 1999). Alternatively, when their diet is constant, an animal's functional response (Holling Types I, II or III, Holling 1959) is spatially scale sensitive (Morgan *et al.* 1997). However, it should be noted that alternative evidence implies random or nearest-neighbour search strategies with little or no active habitat selection (Turner *et al.* 1993, Gross *et al.* 1995, Forcadi *et al.* 1996 and Chapter 2 in this thesis).

Species of different size perceive the environment differently, defining the scale of patchiness in their environment (Wiens 1976). Whilst the scale of patchiness resulting from spatial impacts is determined by animal density (Rietkerk *et al.* 2000), the size of resource patches selected by an animal is related to its body mass (Wilmshurst *et al.* 2000). Comprehension of these ecological scale differences and the fundamental allometric laws that relate them now enables predictions of herbivore diversity to be made directly from estimates of patch use (Ritchie & Olff 1999). The latest development along these lines (Haskell *et al.* 2002) relates resource distribution to resource density and enables a new model of home range-body size scaling. Central to this contemporary view of ecosystem dynamic structure is a paradigm of hierarchical patch dynamics that integrates patch dynamics with hierarchy theory (Wu & Loucks 1995). Scale and landscape heterogeneity are now explicitly linked by a system of nested hierarchies, where each level is a mosaic of patches of a given spatial scale (Nikora *et al.* 1999), with ecosystem dynamics being the composite result of the dynamics of those hierarchy levels. Emergence results from this complexity, as the dynamic interaction of patches and patch mosaics within and between hierarchy levels of increasing spatial scale (see Fig. 5.1).

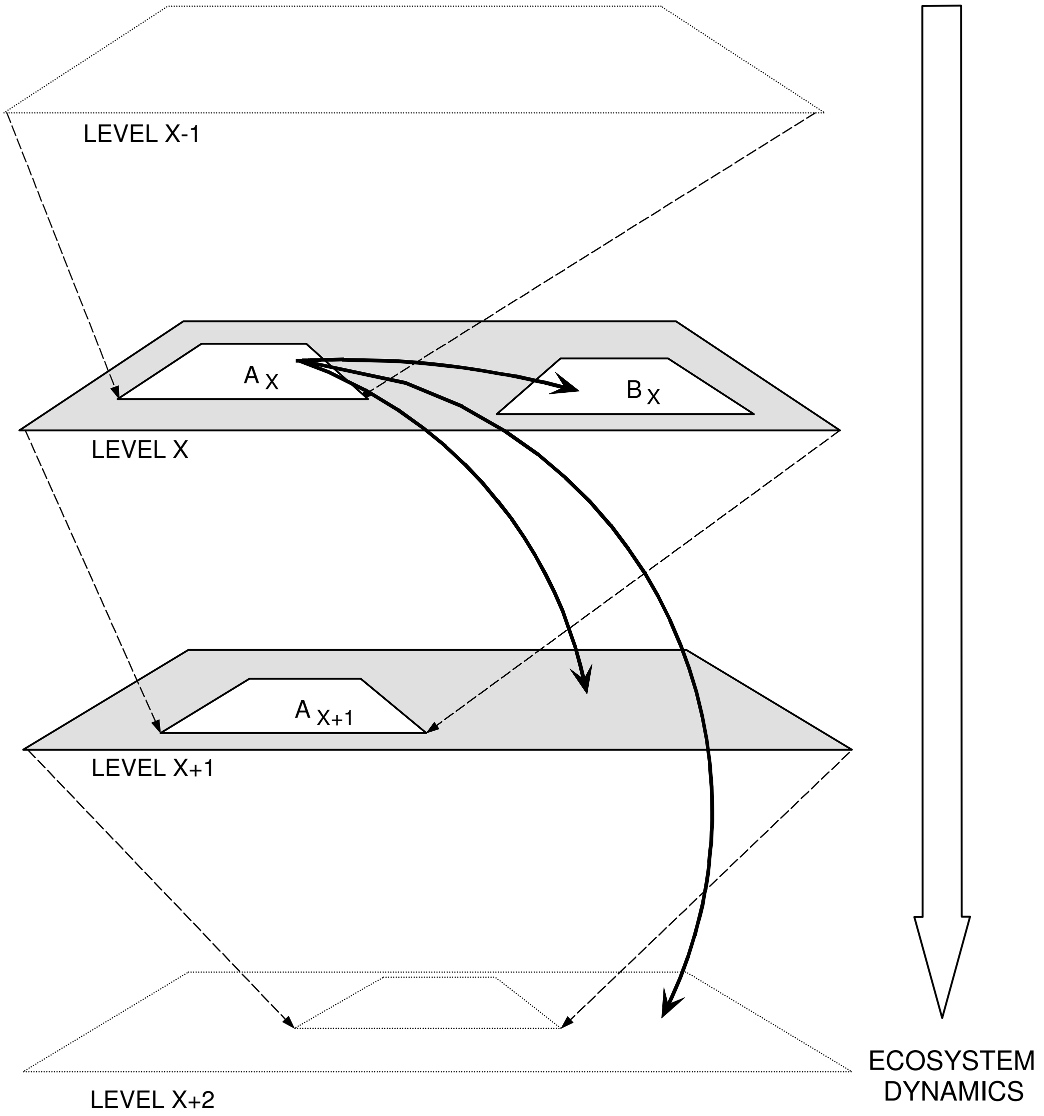


Fig. 5.1: Emergence results from the interaction of patch dynamics (A, B, …) within and between nested hierarchical levels of increasing spatial scale (…, X-1, X, X+1, X+2, …) in landscape organisation (solid arrows). Ecosystem dynamics are the composite result of the dynamics of those hierarchy levels.

There is a continuing need to develop spatial ecology, to explain the determinants of species interactions in a spatial context (Kareiva 1994), and our ability to test current spatial ecology theory with simulation experiments should not be neglected (Dunning *et al.* 1995). However, spatial modelling needs to consider scale differences between field data and model parameters (Wiegand *et al.* 2000, Huenneke *et al.* 2001). Therefore, to have confidence in our inferences, there is a clear need for consideration of spatial scale issues in experiment design (Dutilleul 1998a) and data analysis (Dutilleul 1998b). Restrictive sampling scales have been shown to produce biased results in several models of animal movement, otherwise avoided by correcting for heterogeneous sampling and by distance weighting (Porter & Dooley 1993). Consideration of temporal scale has also been proved important when making inferences from behavioural measurements. For example, failure to account for both short-term and long-term energy intake rates has led to contradictory conclusions being formed about optimal foraging in bovids (Fortin *et al.* 2002). Also, successful detection of autocorrelation effects is dependent upon the time interval for sampling animal movements (Swihart & Slade 1985, Rooney *et al.* 1998, Turchin 1998). Therefore, improved statistical methodology, that accounts for autocorrelation in spatial data, is critical for better examination of ecosystem processes (Koenig 1999), clarification of their component effects and the accurate identification of emergent properties.

5.2.4 Defining emergence

An emergent property may be defined in one of three ways:

i. A property of an integrated system arising at a level of organization higher than that of the components of that system, and that may be explained by the occurrence of those components.

ii. A property of an integrated system arising at a level of organization higher than that of the components of that system, that we fail to predict, infer or extrapolate from study of the components of that system, but subsequently may be explained by the occurrence of those components.

iii. A property of an integrated system arising at a level of organization higher than that of the components of that system, that we fail to predict, infer or extrapolate from study of the components of that system, and remains unexplainable by the occurrence of those components.

These definitions are in close agreement with Shalizi (2001). The first definition is probably the most commonly used in the literature, epitomised by the saying “the whole is greater than the sum of the parts”. For example, “a cake has emergent properties of texture and flavour that are not apparent from a survey of the ingredients” (Pidwirny 2001). In their simplest form, these are “second-order effects … that result from local interactions and produce patterns associated with the covariance structure among ecological units” (Wiegand *et al.* 1998). Definition *ii.* may be considered a restrictive form of definition *iii.*, in which the confinement of the emergence by higher levels is explicit (Müller *et al.* 2000). This is when our comprehension of an organisational level depends upon the simultaneous study of other levels (higher and lower) of organization (Donato Bergandi *personal communication*). For the purposes of this thesis only the first two definitions will be considered because solutions to the third type are either trivial or supernatural.

These emergent properties give rise to two distinct types of emergence as identified by Olson & Sequeira (1995),

1. *Syntactic emergence*. The emergence of structure and form, (*e.g.*, spider web-building, Krink & Vollrath 1998, and the double helix, Watson & Crick 1953).

2. *Semantic emergence*. The emergence of “meaning” in biological structures, (*e.g.*, optimal self-replicating genetic code, Freeland 2002). The perception and storage of sensory cues (*e.g.*, of the presence of prey), is also derived from semantic emergence.

It should be noted that further to the vagaries surrounding definitions of emergence, ecological modelling techniques might also cause confusion when investigating emergent properties. Spontaneous pattern formation has been demonstrated in reaction-diffusion models and neural networks of homogeneous systems containing one mobile species (Ermentrout & Lewis 1997). The “Life” program (Gardner 1971) is an example of pattern formation in a cellular automaton, wherein simple rules propagate self-organization in such cellular automata (Wolfram 1984), a process which is scale dependent (Wolfram 1983). Forms of this emergence equate to emergent property definitions *i.* and *ii.*, "some global properties of cellular automata can be described by entropies and Lyaponov exponents." (Packard & Wolfram 1985), and definition *iii.* where "behaviour is formally undecidable" (Packard & Wolfram 1985). Subsequently, it has been shown that self-organization is not purely a simulation artefact by testing models using stochastic parameters (Bascompte & Solé 1998).

In summary, spatial ecological models can be used to test current ecological theory that includes emergence in ecological systems. However, miscomprehension of the definitions for emergence in addition to complexities of scale in spatial models and their parameters may confound accurate identification of emergent properties. This chapter sets out to illustrate how it is possible to capture valid emergent properties of a landscape ecosystem model and in doing so highlights a method for extending non-spatial formulations into fully integrated spatial systems models. Two examples of emergence are presented to illustrate combinations of emergent property and emergence type (see Table 5.1).

		Property definition	
		i	**ii**
Type definition	*Syntactic*	Example 1	-
	Semantic	-	Example 2

Table 5.1: Examples of emergence considered in this chapter.

5.2.5 Tests of Emergence

The ecosystem can be considered as a continuum of gradients, where most ecological gradients are emergent properties resulting from processes leading to ecosystem self-organization (Müller 1998). Rainfall infiltration and the spatial redistribution of runoff water are the predominant factors determining patterns in semi-arid vegetation (HilleRisLambers *et al.* 2001), but grazing impacts do contribute to the generation, and the subsequent maintenance of that spatial heterogeneity (van de Koppel & Prins 1998, Abrams 2000). To wit, patterns in herbivore density may arise directly from individual differences in movement through a heterogeneous environment (Turchin 1991), differential selection of resources in a heterogeneous environment (Shigesada *et al.* 1986), or simply from random [diffusive] animal dispersal in a homogeneous environment (Lewis 1994). However, in [heterogeneous] semi-arid rangeland there is the added factor of animal movement between places used for feeding and places used for drinking. The spatial impact associated with the congregation of animals at a watering point, and the dissipation of this grazing pressure upon movement away from the focus, gives rise to a defoliation gradient termed the piosphere pattern (reviewed by Thrash & Derry 1999).

In addition to consumption of leaf and stem material from herbaceous plants and shrubs, coincidental depletion of the seed bank may contribute to long-term reductions in surface cover (Hunt 2001b). Trampling, defecation and urination in particular contribute to generation of the sacrifice zone (an area of near-zero cover), with trampling having a greater impact on surface cover than that caused by grazing in the immediate vicinity of watering points (Senzota & Mtahko 1990). Trampling also exposes topsoil by destroying canopy structure and disturbing litter, which reduces infiltration (Kelly & Walker 1976), and the exposed topsoil dust can either be eroded by wind action or fixed by rainwater to form a soil crust (Georgiadis 1987), further reducing infiltration and increasing run-off (Thrash 1997). Once initiated, plant-soil relations may trigger a positive feedback between reduced plant density and reduced soil nutrient availability that may result an irreversible decline in primary production (Dean *et al.* 1995, Rietkerk & van de Koppel 1997). Alternatively, trampling of lichen crusts reduces nitrogen fixation inhibiting plant productivity with toxic concentrations of nitrogen in dung and urine (Andrew & Lange 1986a).

It is possible for our analytical methodology to artificially import system organization, leading to misidentification of emergent properties (Donato Bergandi, *personal communication*). Syntactic emergence is the emergence of structure; the diversity of responses in the environment attest that piospheres are naturally occurring structures, and are unitary entities that feature in the spatial organization of the landscape (*e.g.*, Cridland & Stafford Smith 1993, Owen-Smith 1996). But does their generation involve the integration of simple rules akin to a cellular automaton, without any prescribed organisation?

In the absence of a water point, resource distributions are clumped, with no discernible patch structure (see Chapter 2). Considering patches as areas of resource profitability, it is possible to redefine the landscape functionally in terms of energy gain (net profitability). At this level of abstraction, the spatial plant-herbivore system comprises the basic elements of the foraging pathway that redefine utilised resource patches in terms of state and nearest-neighbour association. The *state* of a patch is given by its patch profitability. Its *association* with neighbouring patches is their patch profitabilities net the travel costs incurred in reaching them (note that utilised patches can be considered pathway "neighbours" if closer patches are bypassed when travelling between feeding sites).

Utilisation patterns result from modifications to patch state, while which patches are modified is determined by a daily foraging pathway constructed from the most closely associated patches. Such patterns are recognised in a level of organisation at a larger spatial scale than the single patch and result from the integration of simple rules at lower levels. It can be seen that piospheres are examples of a syntactic emergent property and satisfy our first type definition for emergence.

While the consequences of grazing gradients on animal foraging provide feedback mechanisms that influence the spatial redistribution of seeds, nutrients and water in the landscape, the major effect is on forage availability. Ideal Free theory (Fretwell & Lucas 1970) predicts that herbivore densities should reflect resource distribution in a heterogeneous environment, assuming that animals have perfect (“ideal”) knowledge of resource profitability and are “free” to move between resource sites. Causes of deviation from the Ideal Free Distribution (IFD) arise from limitations in resource perception (not “ideal”; Abrahams 1986, Gray & Kennedy 1994, Fritz & De Garine-Wichatitsky 1996, Spencer *et al.* 1996, Carter & Abrahams 1997, Farnsworth & Beecham 1999, Ranta *et al.* 1999, Ranta *et al.* 2000) and resource utilisation (Ollason

& Yearsley 2001, Ruxton *et al.* 2001). Alternatively, unbalanced inter-patch emigration and disproportionate survival costs incurred during travel also cause deviation from the IFD (not “free”; Palmqvist *et al.* 2000). IFD theory predicts perfect matching of animal distribution to the distribution of their resource, *i.e.*, IFD is the distribution at which animal populations are in equilibrium with their resource (Tyler & Hargrove 1997). Overmatching is the utilisation of available resources at a rate above the ideal. More commonplace in the real world, however, is undermatching, the failure to meet the IFD (Ranta *et al.* 1999) because of real world constraints on resource accessibility and animal perception. It is worth noting that as the IFD applies to all resource locations within an environment, undermatching involves negative deviation from IFD predictions at highly profitable resource sites balanced by an equal amount of positive deviation from low profitability sites.

For the free-ranging, water dependent animal, the distance that can be travelled between drinking events defines the limit for foraging search effort. Thus introducing focal points such as drinking water location within a resource landscape restricts free-ranging travel. The gradient in foragers’ profitability emanating from those foci introduce departures from the IFD because foraging strategies become compromised as the distance between two locations (*e.g.*, water and a feeding site) increases (Stephens & Stevens 2001). It is reasonable to expect that the consequences of grazing gradients on animal foraging behaviour and on the ability of animals to maximize their intake rate according to an optimal foraging strategy (Stephens & Krebs 1986) are examples of semantic emergent properties. They are harder to predict than the syntactic emergent properties described above, and therefore satisfy our second definition for emergence.

5.2.6 Specific research questions

Is the foraging of free-ranging animals limited during the dry season by the need to drink water? Drinking involves a daily return to the water point before the next opportunity to seek profitable forage resources. The extra costs incurred travelling to and from water, plus the imposition of a static starting point for the daily foraging path at the "bottom" of the grazing gradient, is expected to present a conflict for the animals. The conflict is between the need to eat and the need to drink. In an ideal world it may be possible to predict a critical distance at which animals are able to maximise their rate of energy gain above travel costs. Basic geometry can be used to calculate the available foraging area at a given distance from water, from which the grazing gradient would simply be a density effect, and travel costs a linear function of available foraging area. However, reality is more likely compounded by spatial and temporal heterogeneity of resources, grazing history and autocorrelation in foraging behaviour. Therefore, it may be sufficient to simply identify that travel costs restrict animal foraging range during the dry season, leading to the development and maintenance of the piosphere pattern (see Chapter 3).

The next hypothesis deals with the consequences of a restricted dry season foraging range. Field observations and modelling exercises have shown that the maximisation of daily energy gain is the rationale for optimal foraging strategies (Fryxell *et al.* 2001) and the primary determinant of animal movement patterns (Wilmshurst *et al.* 1999). By definition, foraging decisions made within the scope of the established piosphere will need to account for previous defoliation impacts. For the selective forager it is likely that a renewing resource outside the growth season will not offer a consistent energy intake rate. So, what are the consequences of a restricted dry season range for maximisation of daily forage intake rate and optimal foraging?

In an animal that must meet daily intake requirements for maintenance of body weight, days of not doing so have a direct implication for survival and fecundity in the individual, and for the numerical response of the herd. The potential for dry season resources to influence population dynamics, therefore, cannot be ignored. As the grazing gradient is a result of the concentration of grazing pressure, it is likely that animal density will influence the development and maintenance of the piosphere. In addition, because animals are then constrained to the dry season foraging range, the existence of a feedback mechanism might be expected to relate population size to the forage resources available within the extent of the piosphere. Does such a mechanism exist?

The final hypothesis collates the preceding hypotheses within a framework of contemporary ecological theory and seeks to test that theory by application of a spatial semi-arid grazing systems model. Initial development of a piosphere pattern during the dry season would be expected from the integration of system components. The organisation of spatial impacts along a gradient of grazing pressure is a predictable consequence of introducing a focus for animal impacts. Less obvious are the consequences that this grazing gradient subsequently confers on the animal population. Will an outcome emerge for the animal population and, in hindsight, is it possible to identify processes operating in patches at smaller scales as causal agents?

This work is novel on three counts. Previous spatial models of grazing systems have not been used to identify forms of emergence (*e.g.*, Starfield *et al.* 1982, Senft *et al.* 1983, NMSU 1988, Stafford Smith & Foran 1990, Coughenour 1993), although recently, pattern formation has been studied extensively, thereby reflecting the increasing interest in forager responses to spatial resource distribution (*e.g.*, Turner *et al*. 1994, Jeltsch *et al.* 1996, Dolman & Sutherland 1997, Jeltsch *et al.* 1997, Pickup & Bastin 1997, Beecham & Farnsworth 1998, Grünbaum 1998, Wade *et al.* 1998, Schwinning & Parsons 1999, Abrams 2000, Weber *et al.* 2000, Hutchings & Gordon 2001), and the added effect of spatial scale (*e.g.*, Turner *et al*. 1993, Lewis 1994, Wu & Levin 1994, Ritchie 1998, Weber *et al.* 1998, Farnsworth & Beecham 1999, Ranta *et al.* 2000). Secondly, while piospheres have been included in simulation models as a factor influencing pastoral economics (Duraiappah & Perkins 1999), and the impact of grazing on the survival of plant life within piospheres has also been modelled (Cridland & Stafford Smith 1993, Hunt 2001a), piosphere development has featured in only two other models. The first (Jeltsch *et al.* 1997) differed notably from the current model as it imposed a predefined utilisation gradient rather than explicitly modelling animal movement and feeding behaviour, whereas the second model (Adler & Hall *subm.*) involved untenable modification to Marginal Value Theory (see Chapter 1, Section 1.2.11). Finally, whilst there have been a number of surveys published that illustrate the impact of drinking water location on rangeland vegetation, the consequence of drinking water requirement on the foraging efficiency of free-ranging animals has not been addressed.

5.3 Methods

The "contemporary ecological model" used was 'Model 3' as described in Chapter 3, Section 3.13.

5.3.1 Model Parameters

Parameterisation was similar to that used for the application in Chapter 3 (see Section 3.13.12). Again, Bulawayo rainfall data was used, in its unmodified 20-year entirety. But this time the model was initialised with a dynamic herd of 245 mature female goats and 5 mature males, giving an initial animal density of 0.017 LE/ha. Sexed age classes for neonates, juveniles and mature adults were modelled, with sexual maturity in animals from 2 years old. A full description of this age structure can be found in Derry (1998). Population dynamics were mediated via state-dependent mortality and reproduction (see Illius & Gordon 1999 for detail). Animal number was not managed in any further way.

Only the 1000 ha "Basic Grid" was used. Vegetation types were initialised with independent stochastic distributions (CV 1%), with a mean 1410 kg/ha of a perennial grass and 1466 kg/ha of a woody shrub. Grass parts were allocated from total biomass as follows: Dead Leaf 70.8%, Dead Stem 4.3%, Fallen Seed 0.0%, Green Leaf 21.3%, Green Stem 0.0%, Seed 0.0%, and Stores 3.6%. Shrub components were initialised with the following proportions; Dead Leaf 13.6%, Dead Stem (Wood) 6.8%, Fallen Seed 68.2% (as an initial supplementary food supply), Green Leaf 9.1%, Green Stem 0.0%, Seed 0.0%, and Stores 2.3%. Edible grass and shrub component digestibilities are given below in Table 5.2. The shrub growth season ran between 10th September and 28th April.

	Green Leaf	Dead Leaf	Green Stem	Dead Stem	Fallen Seed
Herbaceous	0.7	0.5	0.6	0.35	-
Woody	0.5	0.35	Variable[1]	-	0.56

[1] taken with leaves and weighted according to leaf/stem mixture

Table 5.2. In vitro digestibility values for the edible plant components of herbaceous and woody vegetation types used to parameterize the plant module.

Comparative simulations were run for scenarios with and without a centrally located water point. When present, the water point was the location for the herd at the start of each day during the dry season.

5.3.2 Model Output and Analysis

Differences arising from the seasonal climate and plant phenology were controlled for by comparing results from simulations in the absence of a water point with results from simulations with a centrally placed water point. A further control of climatic variability was achieved using replication by randomisation of the sequence of years within the 20-year rainfall sequence[1]. The effect is to vary the frequency and severity of drought events whilst maintaining the mean and CV of annual rainfall over the 20 years. The effects of dry season drinking water requirements on annual animal performance (count, reproduction, mortality and intake) in replicated simulations were tested with single-factor and two-factor design F-Tests (ANOVA), with sequence included as a block structure (df = 38). Trends were revealed using simple and multiple linear regression and non-linear curve fitting. All calculations were carried out in Microsoft® Excel 97 and GENSTAT 5.3.2 (GENSTAT 5 Committee 1996).

5.3.3 Emergence Test 1

Model output was collected for mean E_{ij}^{R} across a range of distances from water, across seasons, at the end of each simulated month. Jeltsch *et al.* (1997) noted that piosphere dimensions responded to precipitation via forage production, therefore, midsummer output, at peak re-growth, was used to monitor permanency in the piosphere effect. To include the effects of climate-induced variation in vegetation on

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[1] This method was previously devised to investigate optimal stocking strategies using a non-spatial version of the model (Illius *et al.* 1998). 20 replicates were adequate for convergence of the standard error to within 5% of the mean, and used for all simulations. The spatial model is a larger program and executes some of the sub-models within each grid cell. Consequently it is much slower in completing a simulation, meaning that compromises were made in the experimental designs to enable completion of the study. It was necessary to replicate the water point treatment from which stocking rates were predicted and comments made about animal population dynamics. This is because annual climate variation and drought frequency largely determine population survival. Subsequent experiments that looked at piosphere development and seasonal differences in foraging behaviour did not require replication, although given the opportunity, this may have given more robust results.

piosphere development, the 20-year rainfall sequence was used. To make comparisons between years, each data set comprising predictions for E_{ij}^{R} paired with given distances from the water source was normalized with respect to its maximum E_{ij}^{R}.

The logistic model recommended by Graetz & Ludwig (1978) was then fitted to each set of data using Marquardt-Levenberg non-linear regression in SigmaPlot (SPSS Inc. 1997) and included the adjustment term y_0 introduced by Thrash (1998b) for non-zero lower asymptotes (see equation 5.1), equivalent to $K/(1+e^{a})$ (see Fig. 1.6).

$$y = y_0 + \frac{K}{1 + e^{a-bx}} \qquad 5.1$$

Maple (Waterloo Maple Inc. 1998) was then used to differentiate the logistic formula to obtain an expression that allowed calculation of the midpoint distance from water (x') at which mean potential intake reached half of its maximum value (y') by maximization of the first derivative (see equation 5.2).

$$y' = \max\left[\frac{dy}{dx}\right] = \frac{Kbe^{(a-bx')}}{\left[1 + e^{(a-bx')}\right]^{2}} \qquad 5.2$$

Equation 5.2 was solved for x', to monitor long-term piosphere development by comparison with the animal population response, using a two-sample t-test for means (df = 18) and linear regression.

5.3.4 Emergence Test 2

IFD theory has been most successfully used to predict the spatial distributions of animals in heterogeneous environments at the scale of the maximum daily animal foraging range (Tyler & Hargrove 1997). Departures from the IFD in the same data used for "Emergence Test 1" (Section 5.3.3) were compared against seasonal differences in model response. Generalized Linear Models (GLMs) were constructed for the rate of resource utilisation (actual net energy intake rate) plotted against the mean rate of resource delivery (equal to G*). Slopes and intercepts were compared across seasons and simulations and to regression parameters predicted by IFD Theory using a method developed for comparing slopes other than equal to zero (Zar 1996). The effect of season on mean resource delivery and utilisation was investigated using ANOVA (total df = 7298, dry season df = 3098, wet season df = 4298). A mechanistic interpretation of the consequences of piosphere establishment on animal foraging efficiency and their functional response was developed using a two-sample t-test for means and multiple regression.

5.4 Results and Discussion

Summary tables for comparable results are provided below (see Section 5.4.4).

Results from simulations using the replicated rainfall sequence showed that long-term animal stocking rate was lower in the presence of a water point (means = 0.028 LE/ha sd = 0.008 and 0.020 LE/ha sd = 0.007, $F_{1,38} = 12.22$, $P < 0.01$). Stocking rate was reduced as a result of both a higher herd mortality rate (means = 53.62% and 65.12%, $F_{1,38} = 56.78$, $P < 0.001$) and a smaller herd mass (means = 7814.1kg and 5508.9kg, $F_{1,38} = 12.32$, $P < 0.01$), and not as a result of a reduction in fecundity (pooled mean = 1.22 births/female/year, $F_{1,38} = 0.23$, $P = 0.637$). Mortality in the model was state dependent and, therefore, dependent on mass, which was directly determined by the total amount of herbaceous forage consumed ($mass = 142.0\,forage + 14656.0$ kg/ha, $R^2 = 0.91$, se = 11339.0, $F_{1,38} = 518.64$, $P < 0.001$). Thus, in the simulation without a water point, 34% more grass was consumed than in the simulation with ($F_{1,98} = 5.91$, $P = 0.017$), and 49% more shrub ($F_{1,98} = 16.95$, $P < 0.001$). However, this was not sufficient to significantly affect the proportions of these components, with the overall diet being consistently dominated by woody shrub (pooled means = 73.6%, $F_{1,38} = 0.07$, $P = 0.787$).

For any given area, increasing the animal density will reduce the resources available to the individual. Hence, the distance travelled whilst foraging per animal within each cell scaled negatively with stocking rate ($D_{for} = 0.076\ SR^{-0.471}$ km/cell, $R^2 = 0.88$, se = 0.018, $F_{1,38} = 356.48$, $P < 0.001$). So, to meet the collective nutritional requirements of larger herds, more cells were visited daily, thereby increasing daily commuting distance per LE ($D_{com} = 14.288SR - 0.034$ km, $R^2 = 0.76$, se = 1.076, $F_{1,38} = 150.70$, $P < 0.001$). However, introducing a water point constrained D_{com} (means = 3.02 km and 1.67 km, $F_{1,38} = 131.48$, $P < 0.001$) which constituted 99.7% of the daily pathway distance ($F_{1,38} = 17503.10$, $P < 0.001$). D_{wat} did not significantly contribute to D_{com} in the water point simulation (mean = 0.91 km, $F_{1,38} = 0.03$, $P = 0.854$), and T_{wat} did not significantly contribute to T_{com} (mean = 0.37 hours, $F_{1,38} = 0.18$, $P = 0.675$). However, in the same simulation, D_{for} was extended (means = 1.37 km and 1.85 km, $F_{1,38} = 62.88$, $P < 0.001$) as was T_{for} (means = 8.38 hours and 8.60 hours, $F_{1,38} = 20.42$, $P < 0.001$). T_{for} contributed 71.2% of the total time spent daily ($F_{1,38} = 121.93$, $P < 0.001$) with no significant contribution from T_{wat}.

Daily dry matter intake per kilogram of animal (W^{-1}) was less during the dry season in the simulation with a water point than in the simulation without (means = 0.0070 kg/ha/W^{-1} and 0.0067 kg/ha/W^{-1}, $F_{1,38} = 4.77$, $P = 0.034$). It is thus implied that the herd was unable to maintain levels of intake during the dry season because they were unable to expand their foraging range by visiting more cells than those visited in the simulation without a water point (means = 9.2 cells and 6.9 cells, $F_{1,38} = 23.89$, $P < 0.001$) nor by increasing their pathway to include more profitable areas (pooled means = 921.1 km/year, $F_{1,38} = 0.76$, $P = 0.390$). This is also indicated by the spatial distribution of dry season foraging time focussed about the water point (see Fig. 5.2), suggesting that areas were regrazed more often, reducing forage biomass and, therefore, intake.

The tortuosity (*sensu* Turchin 1998) of the daily pathway was best described by a second order relationship with D_{com} ($tortuosity = 1.080 + 0.047D_{com} - 0.003D_{com}^2$, $R^2 = 0.96$, se = 0.016, $F_{2,47} = 251.95$, $P < 0.001$) which reaches a maximum of 1.29 at 8.98 km. Pathway tortuosity was also positively related to the coefficient of variation for E_{ij}^R ($tortuosity = 1.399CV - 0.145$, $R^2 = 0.60$, se = 0.131, $F_{1,38} = 70.83$,

$P < 0.001$), showing that animal movements were sensitive to the spatial distribution of their resources and revealing a foraging strategy that gave rise to tortuous foraging pathways when patch density was high. Pathway tortuosity was higher during the wet season (means = 1.212 and 1.185, $F_{1,98} = 5.78$, $P = 0.018$).

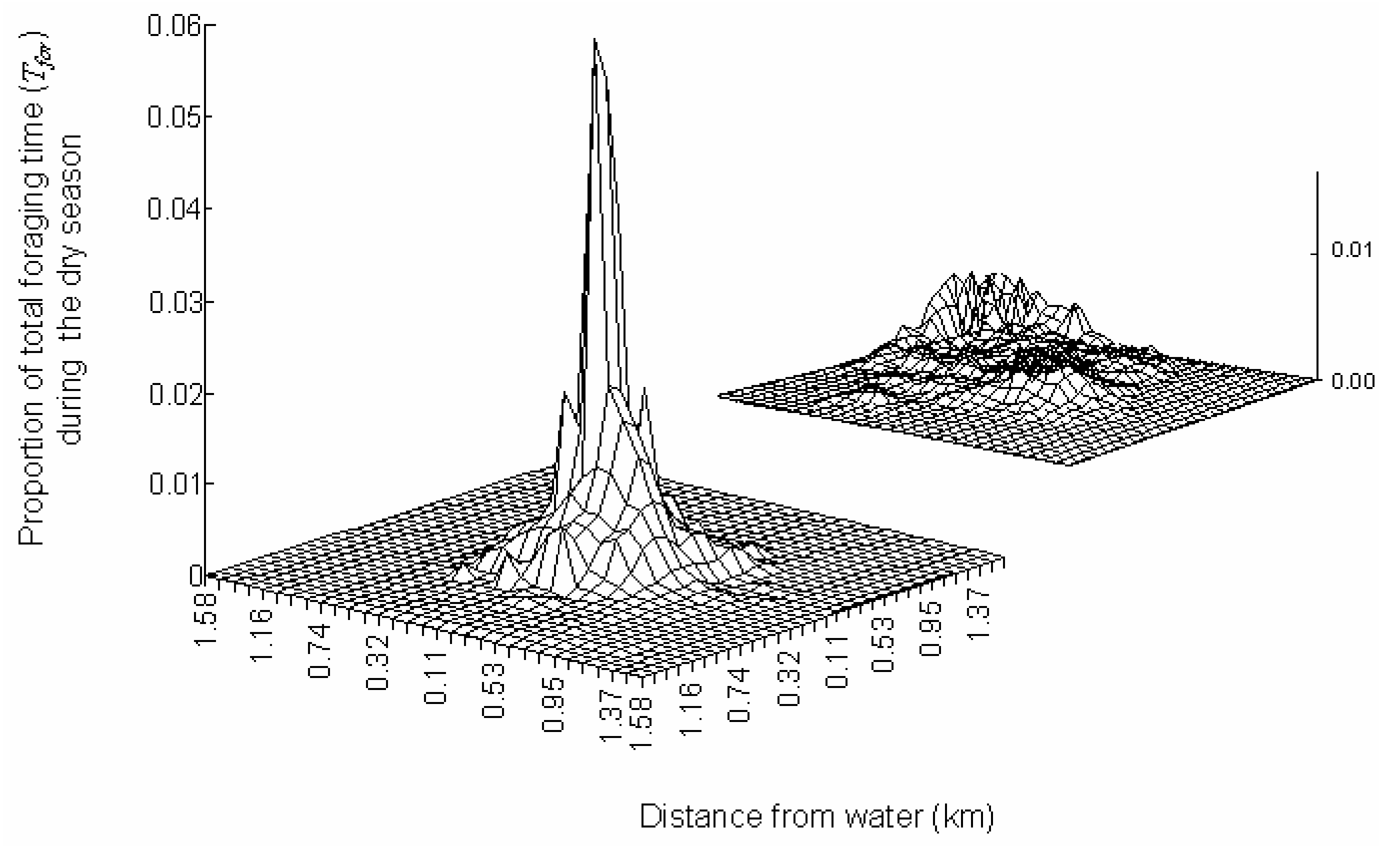


Fig. 5.2: Dry season foraging time was distributed local to the water point indicating a restriction in foraging range, compared to the less focussed wet season foraging (inset).

5.4.1 Example 1 - Syntactic emergence

Plotting E_{ij}^{R} against distance from the water point over the first 5 years of simulation using the 20-year rainfall sequence shows that the piosphere developed by reduction of forage nearest to the water point and by outward expansion of the sacrifice zone (see Fig. 5.3). After 4 years the sacrifice zone had a radius of 0.12 km, estimated using the 95% Confidence Interval of the fitted curve. This is a typical size for sacrifice zones measured in the field (see Thrash & Derry 1999). Jeltsch *et al.* (1997)

explicitly modelled bush encroachment in areas of decreased herbaceous cover by cattle local to a watering hole. They found that a piosphere pattern of similar dimensions (sacrifice zone ca.150 m) appeared in the herbaceous layer within a 4-year simulation for a constant *SR* roughly 3-times the initial animal density used here, and for a location annually receiving 385 mm of rain. Jeltsch *et al.*'s use of cattle limited the role of woody species in their piosphere response. The selectivity of larger animals favours low-quality forage, whereas the feeding ecology and smaller body size of goats used here allowed for a mixed diet of more balanced herbaceous and woody proportions (Illius & Gordon 1987, Illius & Gordon 1993).

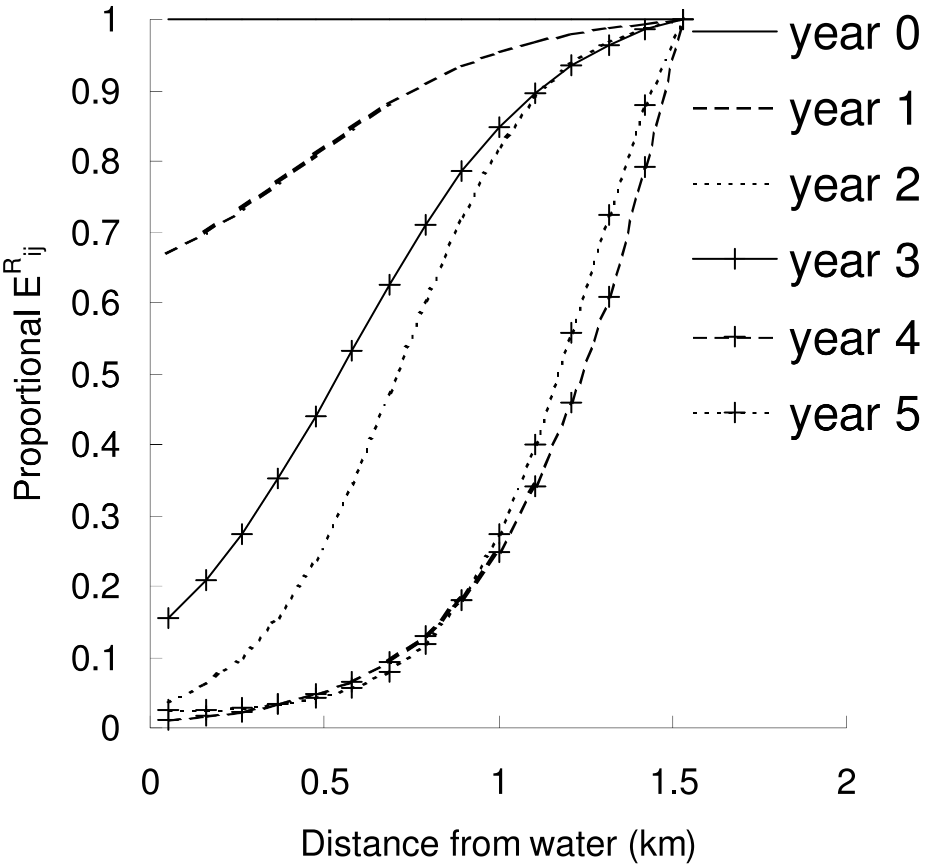


Fig. 5.3: Development of the piosphere pattern in potential energy intake rate (E^R_{ij}, KJ/s) over the course of the first 5 years of simulation, recorded at midsummer peak vegetation biomass.

As might be expected, the extent of the piosphere indicated by the calculated spatial value *x*' was positively correlated (Pearson Product Moment Correlation coefficient, ρ) with animal density, $\rho_{SR,x'} = 0.37$, though regression analysis revealed this relationship was strongest after a 2-year lag between SR and x' ($x' = 8.859SR + 0.725$ km, $R^2 = 0.39$, se = 0.547, $F_{1,16} = 7.82$, $P = 0.013$). The larger lag interval of 3 years also produced a significant relationship between SR and x', but the 2-year lag model was accepted on the basis of having the smaller Akaike's Information Criterion (AIC = 0.50 and 0.56, Akaike 1973). The 2-year lag equates to the duration of conception (a maximum of 6 months between the onset of the dry season and the start of the gestation period that leads up to the median birth date), gestation (5 months) and maturation of new recruits (12 months).

In contrast, the net annual rate of increase for the population was inversely related to piosphere dimension x' in year t ($N_{t+1}/N_t = 1.521 - 0.359x'$, $R^2 = 0.40$, se = 0.304, $F_{1,17} = 11.10$, $P = 0.004$). In the model, animal reproduction was state dependent, requiring 50% of the estimated fat mass of a mature female for an animal to become pregnant. Daily dry matter intake per kilogram weight was related to x' only during the dry season ($DMI = 0.022 - 0.003x'$ kg/ha, $R^2 = 0.22$, se = 0.003, $F_{1,18} = 5.15$, $P = 0.036$). The *per capita* recruitment rate was higher in the wet season (means = 0.65 births/female/year and 1.22 births/female/year, $t_{18} = 7.59$, $P < 0.001$) and the average birth date weighted by the daily number of births was 15th March (median = 9th April). As gestation took 146 days, it may be concluded that the reduction in birth rate stemmed from the decrease in daily dry matter intake that occurred during the dry season.

As a result, trophism manipulated the piosphere as a function of future animal number following growth of the current population, while at a different temporal scale, growth of the animal population itself was constrained by the extent of the grazing gradient. Reduced dry matter intake in the dry season in the water point simulation had no additional affect on survival as the annual state-dependent mortality rate remained unchanged (pooled means = 20.30% herd/year, $t_{18} = 0.69$, $P = 0.495$). However the herd mortality rate was higher during the dry season than the wet season (means = 9.44% and 15.31%, $t_{18} = 3.37$, $P = 0.002$).

Schwinning & Parsons (1999) suggested that a seasonal climate gives rise to a grazing system that is often in a transient state, following an equilibrium that shifts with season. However, the findings presented here provide supporting evidence that environmental stochasticity and density dependence operate outside the breeding season through a common effect on resource supply that regulates animal populations via mortality and state-dependent reproduction (Sæther 1997). Tropical ungulates exhibit less density-dependent calf mortality than ungulates in temperate regions, but density-dependent adult mortality has been observed in African buffalo and wildebeest (Sinclair *et al.* 1985 cited in Sæther 1997). The availability of dry season forage determines the rate of utilisation of body fat reserves generated during the wet season and the subsequent rates of survival and reproduction. By definition, animal populations are in equilibrium with their resources accessible within the extent of the piosphere (see also Illius & O'Connor 1999, 2000 and Section 5.5.2).

Further evidence that supports the coupling of animal population dynamics to their dry season resources comes from the prediction that defoliation intensities during the wet season will be more if a dry season foraging range sustains the animal population than if a dry season range is absent (Illius & O'Connor 2000). This was indeed the case; the rate of utilisation (actual net energy intake rate) was higher for the wet season from the replicated water point simulation (means = 0.725 J/s and 0.851 J/s, $F_{1,38} = 10.78$, $P = 0.001$). Equilibrium-related plant and animal responses may not be immediate; levels of consumption by the current generation may reduce the supply of food available to subsequent generations (Caughley 1979), as indicated by the predicted differential time lags in piosphere development, *SR* and animal number. An example of time lags in demographic response in a similar sized animal was observed in the interaction between white-tailed deer and their food supply where *per capita* recruitment rate showed a 3-year lag to changes in population density (Fryxell *et al.* 1991).

5.4.2 Example 2 - Semantic emergence

Deviations from the IFD were investigated in GLMs of actual energy utilisation rate plotted against G* (see Table 5.3).

	Seasons	Regression model	df	F	Std.Error	R^2	Deviation from IFD		$\bar{x}$	$\bar{y}$
							t-stat	P		
No Water point	ALL YEAR	y=1.003x-0.0070	7299	187875.9	0.044	0.96	0.0008	0.999	0.467	0.461
	DRY	y=1.023x-0.0138	3099	26461.2	0.038	0.90	0.0130	0.990	0.304	0.297
	WET	y=0.996x-0.0021	4199	78099.3	0.047	0.95	0.3260	0.745	0.587	0.583
Water point	ALL YEAR	y=0.939x+0.0007	7299	95193.0	0.058	0.93	0.0124	0.010	0.444	0.418
	DRY	y=0.897x-0.0002	3099	7807.6	0.058	0.72	0.0321	0.026	0.295	0.265
	WET	y=0.950x+0.0369	4199	55330.4	0.059	0.93	0.0131	0.011	0.555	0.563

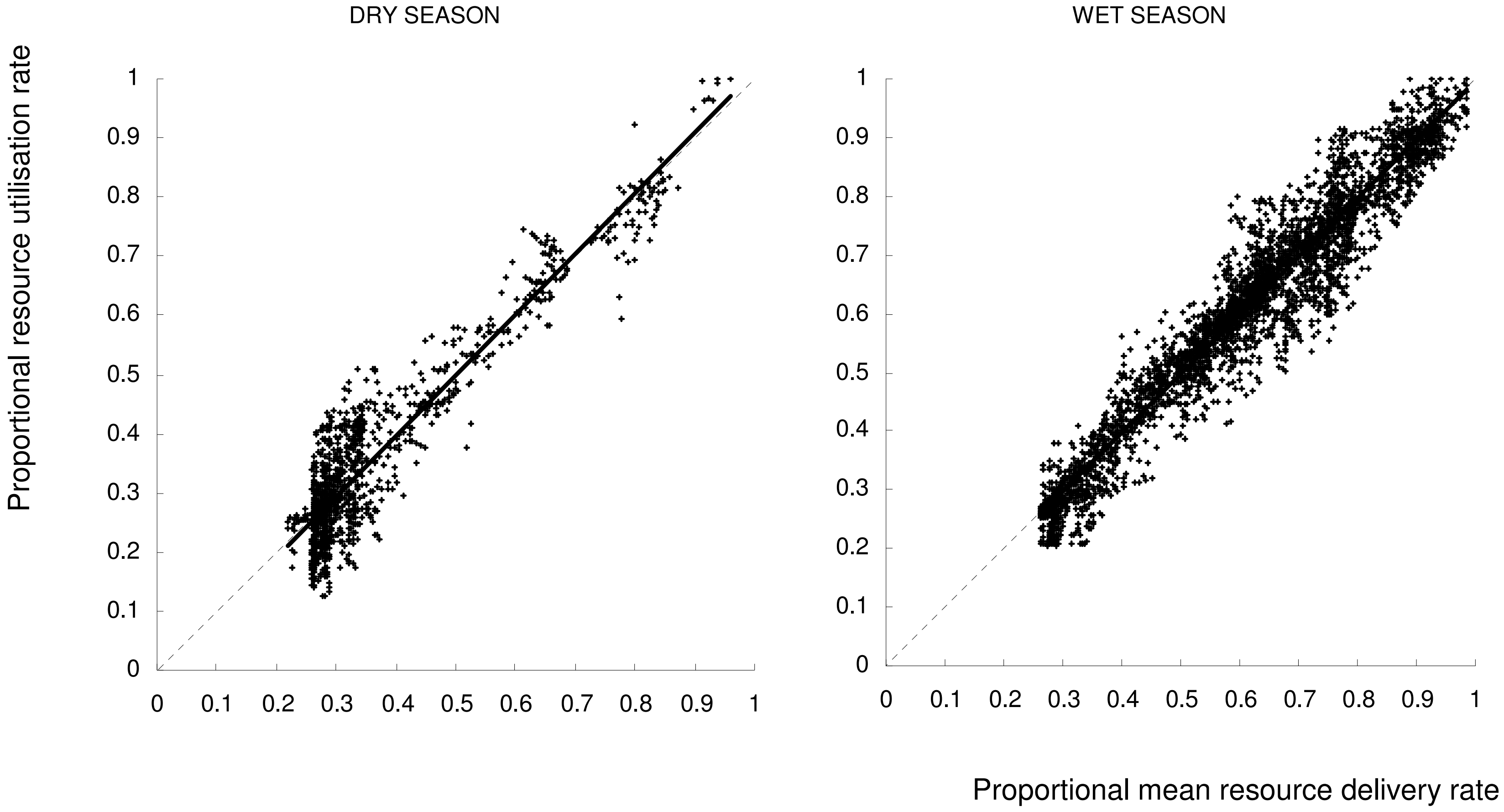
Table 5.3: Linear regressions of actual energy utilisation rate (*y*) against G* (*x*), deviation of the regression from IFD predictions and means ($\bar{x}$ and $\bar{y}$), for all data and seasonal data sets from simulations with a water point absent and present. The reported standard error (Std Error) is the standard deviation from predicted values, equal to the square root of the error MS, from which it is possible to calculate the regression MS (error MS x F), or the approximate 95% confidence intervals for predicted values ($t_{0.05,df}$ x ± Std Error).

Analysis of data from the simulation without the seasonal modification of herd position to the water point produced linear regression parameters equivalent to those of the IFD, however, dry season values were lower than the wet season for both mean G* ($F_{1,7298} = 4937.12$, $P < 0.001$) and mean energy utilisation rate ($F_{1,7298} = 4695.22$, $P < 0.001$). The simulation with the water point produced linear regression parameters that differed from IFD predictions. Dry season values were also lower than in the wet season for G* ($F_{1,7298} = 3583.70$, $P < 0.001$) and mean energy utilisation rate ($F_{1,7298} = 4816.49$, $P < 0.001$). There was a difference between seasons for the regressions from the water point simulation ($t_{3099} = 0.017$, $P = 0.013$). It is apparent from the GLMs that introducing a water point caused undermatching of the IFD by compromising energy intake during the dry season (see Fig. 5.4).

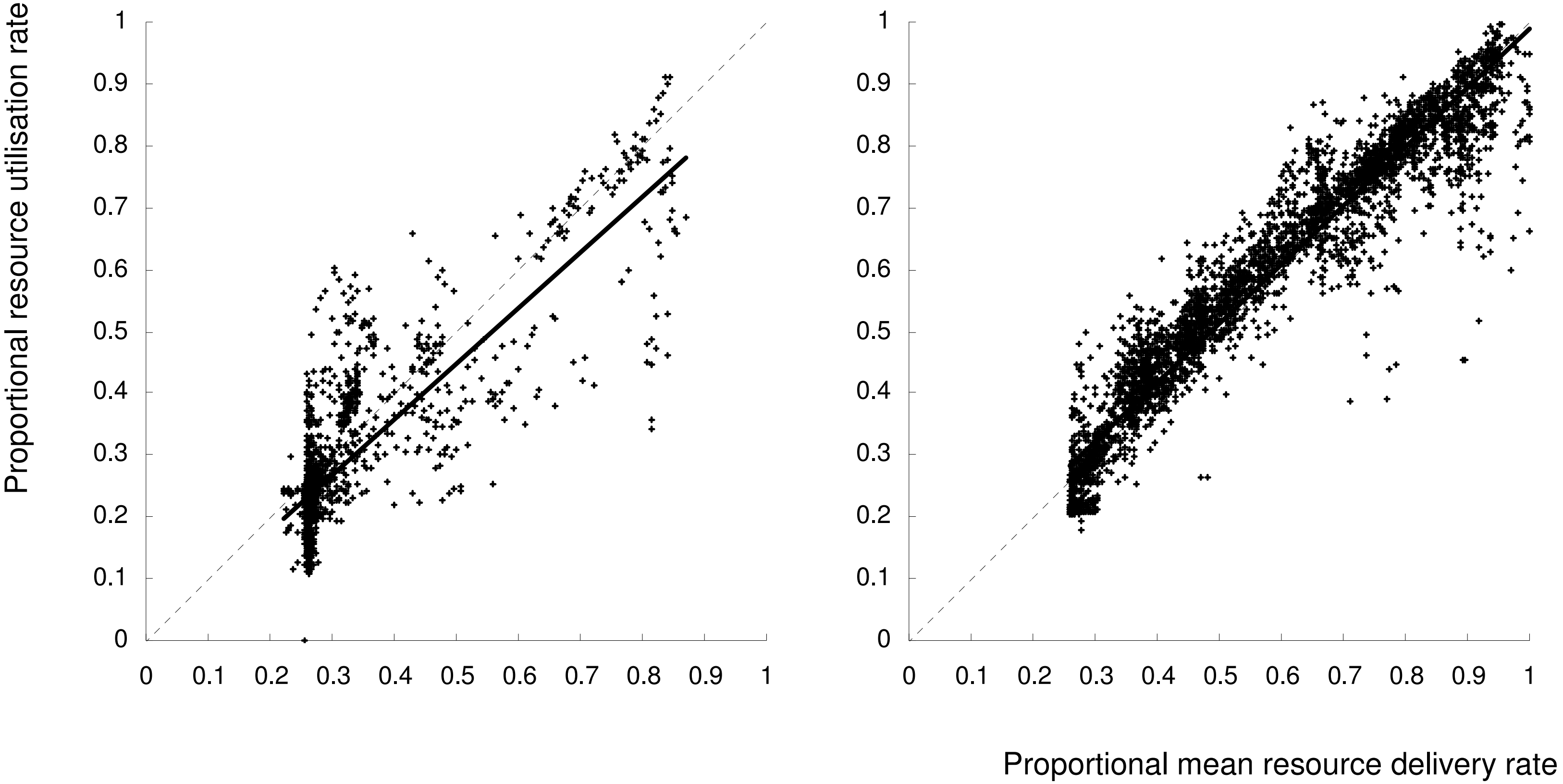
Undermatching of the IFD has been shown to occur in coarse-grained environments where animals experience difficulty in distinguishing profitable patches (Ranta *et al.* 2000), and for individual variation in the discrimination of patch profitability (Spencer *et al.* 1996). Nevertheless, the undermatching resulting here was unlikely to have been produced by failures in animal perception because of the *UBRule* (see Chapter 3, Section 3.13.11). Also, annual environmental patchiness did not differ for the replicated simulations as a result of piosphere development (pooled means = 8.99%, $t_{38} = 0.46$, $P = 0.650$). Additionally, the distance between visited cells did not cause undermatching by decreasing the capacity of the animals to differentiate cells by profitability (Kennedy & Gray 1997) as this distance (mean = 153.9 m) was less than their visual range ($F_{1,3100} = 19747.68$, $P < 0.001$).

Fig. 5.4 (*overleaf*): Deviation from IFD predictions (dotted line) shown by Generalised Linear Models (GLMs) of proportional resource utilisation rate against proportional mean resource delivery rate (solid line) for simulated dry and wet seasons with a central water point a) absent and b) present.

a)


DRY SEASON
WET SEASON
Proportional resource utilisation rate
Proportional mean resource delivery rate
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1

b)


Proportional resource utilisation rate
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Proportional mean resource delivery rate

While the mean values for energy delivery (E_{ij}^{R}) and utilisation (actual net energy intake rate) remained relatively consistent between simulations (expecting no seasonal effects on energy utilisation rate or G*, χ_1^2 = 0.33, P = 0.565), the spread in the dry season data increased by 50% for the water point simulation (standard deviations = 2.13 and 3.20). This was also reflected in the decrease in the percentage of variation accounted for by the regression fits from 89.5% to 71.6% (see R^2 values in Table 5.3).

5.4.3 Search for mechanisms

It has been established that animal production can be influenced by the presence of a piosphere inasmuch as herd biomass and state-dependent reproduction were directly limited by animal dry matter intake. The predicted reduction in daily dry matter intake during the dry season was not caused by the reallocation of available foraging time for the purposes of water-related travel; in fact, daily dry matter intake was less in the dry season than for the wet season, independent of there being a water point, also indicated by the decreases in dry season G* and mean energy utilisation rate for both simulations. Yet, it was only in the water point simulation that this limitation impacted animal foraging efficiency as indicated by undermatching of the IFD. Energy expenditure on travel was reduced or unaffected by introducing a water point, therefore changes to net energy intake rate must have resulted from variation in dry matter intake rate. This implies that a spatial mechanism operated to limit daily dry matter intake at the scale of the animal functional response. A search for that mechanism occupies the remainder of this discussion.

Whilst constraints of digestion, metabolism and time may limit total daily intake (Illius & Gordon 1993), instantaneous intake rate is the product of bite rate and bite size, the importance of each factor being determined by the spatial distribution of the forage resource. In dense resource patches with a high bite density, intake rate is mostly determined by the limiting effect of bite size on bite rate, because the time required to process previous bites delays the cropping of the next bite (Hodgson 1985, Spalinger & Hobbs 1992). For lower bite densities, bite size is less important than bite rate as previous bites may be processed whilst searching for subsequent bites (Farnsworth & Illius 1998), such that intake rate is limited by the distance between available bites. The following analysis used bite data included in the model output. In the replicated water point simulation, bite sizes were larger in the dry season than in the wet season (means = 273.02 mg DM and 167.17 mg DM, respectively, $t_{38} = 10.98$, $P < 0.001$). This was also the case for the simulation without a water point (means = 260.35 mg DM and 166.06 mg DM, $t_{38} = 8.54$, $P < 0.001$). This can be explained by the overall selection of diets in the dry season which comprised 87% fallen fruit (bite size = 300 mg DM) compared to only 29% of the diet in the wet season. The main diet component during the wet season was grass (67%, mean bite size = 112 mg DM).

Multiple regression analysis showed that bite density accounted for 90.1% of the variation in bite rate during the dry season in the water point simulation, with bite size accounting for a further 4.6% of the variation ($rate = 0.331 + 9.74\times10^{-4}\, density - 2.78\times10^{-4}\, size$, $R^2 = 0.95$, se = 0.0041, $F_{2,17} = 171.00$, $P < 0.001$). During the wet season, bite size accounted for 91.3% of the variation in bite rate, and bite density accounted for 1.4% of the variation ($rate = 0.951 - 2.23\times10^{-3}\, size - 2.89\times10^{-4}\, density$, $R^2 = 0.93$, se = 0.020, $F_{2,17} = 120.78$, $P < 0.001$). The corresponding simulation without a water point showed that bite rate was determined entirely by bite size during the wet season ($rate = 0.8005 - 0.001733\, size$, $R^2 = 0.90$, se = 0.026, $F_{1,18} = 173.68$, $P < 0.001$). Bite density accounted for 83.2% and bite size accounted for 6.2% of the variation in bite rate during the dry season ($rate = 0.450 + 9.82\times10^{-3}\, density - 8.02\times10^{-4}\, size$, $R^2 = 0.89$, se = 0.010, $F_{2,17} = 76.58$, $P < 0.001$). The water point simulation gave rise to lower dry season values for bite rate than the without water point simulation (means = 0.280 bites/s and 0.319 bites/s, respectively, $t_{38} = 3.65$, $P < 0.001$) and lower dry season bite density (means = 25.51 bites/m^2 and 67.41 bites/m^2, respectively, $t_{38} = 3.20$, $P < 0.001$). Therefore, dry season intake was primarily a function of bite density, with bite density further reduced by piosphere impacts below the levels seen for the dry season in the simulation without a water point. In terms of the Spalinger & Hobbs model (1992), dry season intake is encounter-limited (Process I and Process II), and wet season intake is handling-limited (Process III).

Bradbury *et al.* (1996) provided empirical evidence when they found exactly the same results in measurements of bite rate from Thomson's gazelles near the Maasai Mara. Bite rates in the dry season were positively correlated with dry green biomass and protein density, a prediction of the Spalinger & Hobbs (1992) model of animal functional response under conditions for their Process I and Process II. Regression fits of each version of the model accounted for 21.8% (Process I), 23.7% (Process II) and 18.4% (Process III) of the variation in dry season bite rates. Bradbury *et al.* concluded that bite rate was dictated by bite mass acting through sward height, so that short swards produced Process I and Process II-type responses, and longer swards (during the wet season) produced Process III foraging. The simulation model used in this chapter would be expected to act in the same vein. When predicting intake rate, bite mass was calculated as the volume of plant material that an animal could enclose in each bite, and was therefore constrained by the animal's incisor arcade breadth (Gordon & Illius 1988). For woody species, leaf abundance along the branch and leaf cluster overlap will determine whether each bite will weigh more than the mass of a single leaf cluster (see Chapter 4). However, for grass-like plants (graminoids) and other herbaceous vegetation, bite mass was the result of the intersection between animal buccal capacity and the vertical structure of the sward (Illius & Gordon 1999).

The switching between foraging processes across seasons is a function of standing crop, and ultimately plant growth. Additionally, bite density is sensitive to defoliation intensity because selective foragers do not uniformly utilize their forage resources. At the scale of the individual bite, the reason for this has been identified in goats elsewhere in this thesis (Chapter 4) and independently in European roe deer by Illius *et al.* (2002). It is that animals select the largest bites to eat first when distinct bites are on offer[2].

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[2] In the case of these two reported experiments, the single bites were individual leaves or leaf clusters in spinescent woody species. The model was also parameterised with a spinescent woody shrub, but the model did not presume the preferential removal of large bites, nor did it model forage biomass in greater detail than the general categories of plant parts within each cell. Bite density was simply calculated based on forage biomass and the mass of constituent plant parts, whereas, the model dynamically calculated the optimal bite size according to the available mixture of forage components.

Two depletion mechanisms act in parallel to depress local resource levels (within a patch), and switch foraging from Process III to Process II or Process I. Firstly, the removal of large bites reduces the size of subsequent bites. And, secondly, the removal of large bites increases the distance between those remaining. Hobbs *et al.* (2003) have even derived an allometric expression that relates a critical threshold distance between target plants (d^*, m) to animal body mass, below which intake rate remains under the control of bite mass, $d^* = 7.1W^{-0.06}$. The long-term mean animal mass from the 20 years simulation was 51.1 kg, which translates to $d^* = 5.61$ m between plants. However, this allometric relation was derived from measurements of animals moving between plants (feeding stations) from which they typically removed a single bite, whereas Chapter 4 reports the case for switching in foraging process within the scale of the feeding station (individual trees).

Please note that undermatching also occurred during the wet season in the water point simulation. This is most probably because, in all simulations, dry season and wet season ranges were not spatially distinct, and, therefore, bite densities within the piosphere had a slight influence on bite rate, unlike the situation for the simulation without a water point which lacked a gradient of spatial impacts.

The multiple regressions for the water point simulation describe two planes (see Fig. 5.5) which intersect along a line that can be described by vectors using the parameter t (Hamilton 1992) such that, $density = 187.17 - 1.10\text{x}10^{-4}t$, $size = 1846.41 + 0.0032t$, $rate = -0.9014\text{x}10^{-6}t$ ($t \in \mathbb{R}$). This line of intersection is a hypothetical optimum for bite rate under constant conditions (that would otherwise vary between seasons) for the determinants of bite rate. Linear transformation of the intersection upon $rate = 0$ gives $size = 317.623 - 0.647\ density$, the relationship between bite density and bite size that produces those optimal bite rates.

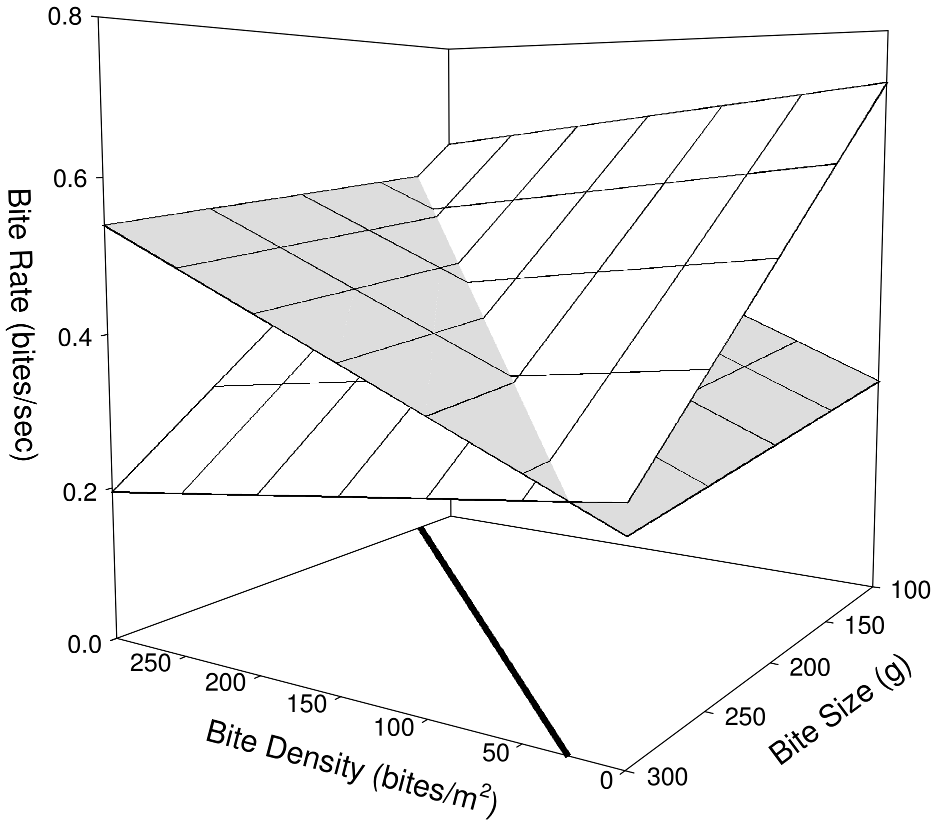

Fig. 5.5: Fitted planes from multiple regressions showing the switching of primary influences on bite rate from bite density in the dry season (shaded) to bite size in the wet season. Linear transformation of the line of intersection for the two planes reveals the relationship between bite size and bite density that produces optimal bite rates under constant conditions (dashed line).

In summary, the conflicting need to drink from a given water point meant that animals were unable to match the spatial distribution of their resources with the spatial distribution of their foraging activity in an ideal fashion. The details of the spatial mechanism that resulted in undermatching of the IFD with respect to water-related limitation of dry matter intake during the dry season concern the distribution of resources and the capacity of animals to travel between resource patches. Measures of bite density do not explicitly describe the clustering of bites to form patches. However, the accumulation of impacts in the vicinity of a water point to form a utilisation gradient, and the need for animals to return to that water point to drink, combine to reduce forage biomass, and so reduce the density of bites available to the selective forager. During the wet season the animals are free ranging, either foraging along tortuous pathways in response to the spatial distribution of their comparatively abundant forage resources, or escaping the confines of the piosphere to access supplies of additional dietary components (*e.g.*, Murray 1995, Heitkönig & Owen-Smith 1998). In the dry season, resources beyond the outer limits of the piosphere offer the greatest rewards, except, in reaching it, the profitability in net energy intake is insufficient to balance the required travel costs. But short-range movements are not inhibitory, and consequently animals only encounter depressed resource levels along their daily foraging pathway, resulting in the limitation of potential daily dry matter intake. Additionally, lower forage digestibilities during the dry season exacerbate this limitation (see Chapter 3).

5.4.4 Summary of results

Test statistic	No water	Water	Units	*P*
SR	0.028	0.020	LE/ha	***
Mortality	53.62	65.12	% herd/year	***
Fecundity	1.22		births/female/year	*NS*
Mass	7814.1	5508.9	kg	***
Diet	0.264		grass proportion	*NS*
Intake (dry season)	0.0070	0.0067	kg/ha/W^{-1}/day	*
D_{com}	3.02	1.67	km/day	***
D_{for}	1.37	1.85	km/day	***
T_{for}	8.38	8.60	hours/day	***
D_{wat}	-	0.91	km/day	-
T_{wat}	-	0.37	hours/day	-
Locations	9.2	6.9	cells/day	***
Distance	921.1		km/year	*NS*
Tortuosity	1.444	1.365	-	***

Table 5.4: Results for replicated (20 x 20 years) simulations with and without a water point. Significant variation is reported for three possible probability levels; P<0.001 (***), P<0.01 (**) and P<0.05 (*). Single values show the pooled mean for non-significant (*NS*) differences. See text for details and interpretation.

Test statistic	Season		Units	*P*
	Dry	Wet		
Recruitment	0.65	1.22	births/female/year	***
Mortality	15.31	9.44	% herd	**
Energy intake	0.725	0.851	J/s	***
Bite size	273.02	167.17	mg DM	***
Bite rate	0.280	0.319	bites/s	***
Bite density	25.51	67.41	bites/m^2	***

Table 5.5: Results from the 20 years water point simulation. Significant variation is reported for three possible probability levels; P<0.001 (***), P<0.01 (**) and P<0.05 (*). See text for details and interpretation.

5.5 Conclusions

5.5.1 Consequences of the emergence of spatial pattern

Spatially explicit population models provide a tool with which to examine spatial ecology theory and species-habitat relationships (Dunning *et al.* 1995, Turner *et al.* 1995). Ecosystem dynamics are a function of intra-species interactions plus feedback to the environment (Hunter & Price 1992, Lange 1999). Within hierarchical patch dynamic theory, the cause and effect events that drive these feedback loops operate via the interaction within and between levels of the patch hierarchy (Wu & Loucks 1995). Such event phenomena have properties that we can identify as having emerged from this patch interaction (Wu & Loucks 1995). Legitimate definitions of emergence avoid misidentification of emergent properties and their causal agents (Bergandi & Blandin 1998).

From the current example, we have seen how the selective utilisation within resource patches impacted subsequent animal energy intake rate via alterations to the resource distribution at the scale of the individual bite. At a larger scale, the accumulation of these impacts became concentrated around the location of a water point as a consequence of animal daily drinking requirements. Syntactic emergence of a piosphere resulted from this organization. Grazing pressure exerted its influence on piosphere extent via a time lag in the demographic response and animal population dynamics were regulated during the dry season via state-dependent fecundity and mortality. Energetic constraints on the range of the daily animal foraging pathway, plus constraints on the extraction of energy from their forage limited the net profitability of their diet. At the global scale, animal distributions could not achieve perfect matching of the distribution of their resources as a consequence of daily drinking requirements. Semantic emergence of a reduction in animal foraging efficiency resulted from this confined resource availability. Even when herbivore impacts are only meted through defoliation, the consequences for animal foraging efficiency are profound. The current model omitted herbivore impacts other than defoliation, but the additional negative effects on forage abundance (*e.g.*, soil compaction by trampling) would be expected to increase IFD undermatching and further limit animal intake.

5.5.2 Resource matching and ecosystem dynamics

Constraints in foraging range imply that a global measure of environmental profitability for G* may not be appropriate for descriptions of animal dry season foraging. A more localised assessment of G* also may not modify foraging behaviour (see Chapter 3). However, animals retain memories of encounters with their resources for a shorter length of time than the duration of the dry season, which indicates that GUDs should be sensitive to expectations of resource profitability assessed since the previous wet season. During the wet season, when there is sufficient surface water to allow unrestricted travel, the mean profitability remembered from previous encounters will tend towards the global average. During the dry season it may drop below the global average, thereby reducing subsequent compromises in intake rate for the sake of maintenance. If animals seasonally modify their expectations to account for the reduction in the supply rate of their dry season resources then there would be some improvement in their resource matching within the limits of dry season forage availability. If dry season resources could be sufficiently exploited, perfect matching is possible.

As a "thought experiment" it is useful to consider what would be the consequences of elevating dry season foraging efficiency (resulting in an increase in dry season intake) by increasing dry season resource levels to equal those in the wet season. In doing so it is possible to comment on an aspect of the debate about nonequilibrial dynamics currently being held in rangeland science (see Illius & O'Connor 1999 for a comprehensive discussion, but also Sullivan & Rohde 2002 and Briske *et al.* 2003). Briefly, the frequent droughts that occur in semi-arid regions are thought to decouple plant-herbivore (consumer–resource) interactions by reducing animal numbers, whilst having little influence on vegetation biomass (Ellis & Swift 1988). Nonequilibrium dynamics from this decoupling would result in low animal densities and, therefore, minimal rangeland degradation, or desertification (Scoones 1994). Included in this is the localised degradation of the piosphere pattern (Fernandez-Gimenez & Allen-Diaz 1999) plus associated feedbacks on primary productivity (Lind *et al.* 2003). Indeed, equivalent resource matching throughout the year would suggest an alternative relationship between herbivore consumers and their resources. Caughley (1979) discussed the forces attracting plants and animals towards equilibrium in terms of the 'tension' within the plant-herbivore system. Sæther (1997), Illius & O'Connor (1999, 2000), and now this thesis have identified dry season 'key resource' availability as the source of the tension. Relaxation of this tension by seasonal adaptation of marginal suitability (G*) would effectively inflate the ecological carrying capacity of the environment (*c.f.* Adler & Hall *subm.* for ET<1 in Section 1.2.11), but this would be conditional on replenishment of key resources during the growth season.

At typical intrinsic rates of increase in the absence of droughts, large herbivore population eruptions (*sensu* Caughley 1979) occur at a lower frequency than the annual regulation of population growth by limitations in dry season resource supply. When such 'boom and bust' cycles in herbivore population dynamics (*e.g.*, CluttonBrock *et al.* 1997, Desta & Coppock 2002) occur less regularly than droughts, the influence of density-independent factors (*e.g.*, rainfall variability) on population regulation would be strengthened. Gradual population growth would be punctuated by drought-induced losses (Desta & Coppock 2002) and the system would be deemed nonequilibrial. Alternative methods that also increase dry season intake (*e.g.*, supplemental feeding) would have the same effect (Illius & O'Connor 1999).

At present levels of climatic variation in semi-arid environments, where droughts occur less regularly than dry season constraints, it is clear that nonequilibrium dynamics can only originate by removal of the 'tension' in the plant-herbivore relationship, with adequate improvements being made to animal dry season foraging efficiency. However, where animal foraging efficiency is limited in each dry season by the piosphere pattern, the influence of density-independent factors must be in addition to the density dependence that animal populations have on their forage resources. This conclusion contradicts the case for nonequilibrium in semi-arid rangeland under existent management regimes.

It should be noted that an advancing view (Sullivan & Rohde 2002, Briske *et al.* 2003) argues that the decoupling does not need to be absolute, and a system's state is defined by its location at any point along an equilibrium–nonequilibrium continuum (Wiens 1984). Nonequilibrium could arise from a weak coupling between animals and their more abundant wet season resources, but, as inferred here, consumer-resource relations will produce equilibrial plant-herbivore system dynamics wherever animal survival is determined by constraints on dry season key resources.

5.5.3 Consequences for management

Insufficient preservation of dry season forage resources has been identified as a major cause of drought-related mass mortality in livestock and wildlife (*e.g.*, Sinclair & Fryxell 1985, Walker *et al.* 1987, Knight 1995b). Findings in this chapter simply echo the recommendations to maintain the supplies of dry season forage surrounding water points with which animal populations are in equilibrium (*e.g.,* Coughenour 1991). In areas with a high density of artificial water points, reducing the density of water points, perhaps leaving patterns of water points that emulate the distributions of natural water bodies (Owen-Smith 1996), will maximize dry season forage supplies. It has been proposed that minimal impact will result from clustered patterns compared to the larger effect of a single watering point (Thrash 2000), so the optimal siting of an artificial water supply would be near an existing natural water body, *e.g.*, a river (Goodman 1982). The common primary objective for managers of protected areas is to maintain or recreate the "pristine system", that is as near natural an ecosystem as possible (Goodman 1982, Pienaar *et al.* 1996). Ultimately, reliance upon distributions of naturally occurring water sources will best maintain refugia and biodiversity in protected systems (Thrash 1998a), rather than the established use of water location to increase animal access to water-less areas (see Section 1.1.7), which is still being recommended (*e.g.*, van Heezik 2003) in spite of the recent recommendations to the contrary. Towards this end, strategic water point closure plans have been initiated in both South Africa (Gaylard *et al.* 2003) and Australia (Landsberg *et al.* 1997).

Assessment of the optimal stocking rates of animal species present is often made more complicated by the transient use of watering points by herders, but often with considerably more impact on the local vegetation than permanent wildlife (Verlinden *et al.* 1998) plus an associated displacement of wildlife by livestock, possibly through competition for resources (de Leeuw *et al.* 2001). Illius & O'Connor (2000) argue that animal population size is a function of the area that defines a population's dry season range (DSR). This is by definition a difficult goal to achieve for management strategies that attempt to maintain and maximize the size of their animal populations when the size of the DSR area is essentially determined by the species' dry season foraging range. Ironically, what is better achievable is the maintenance of forage resources in the DSR by adequate preservation of the wet season range (WSR), so that the DSR is not impacted during the wet season, especially during periods of low rainfall (drought). Not doing so can lead to catastrophic population collapse (*e.g.*, Sinclair & Fryxell 1985, Walker *et al.* 1987).

Owen-Smith (1996) recommended that the WSR should be twice that of the DSR to achieve equivalent grazing pressures in each, assuming that animals spend about four months of the year near perennial water sources. To achieve this 2:1 ratio of areas, Owen-Smith (1996) estimated minimal spacing of 15 km (three times the typical potential travel distance) and 30 km (six times the typical potential travel distance) for point and linear water sources, respectively. The importance of maintaining the WSR is furthered by the need for early vegetation re-growth following the previous year's defoliation (Owen-Smith 1996). Re-growth in the DSR may be promoted by the focussing of soil water and nutrients in low-lying areas where surface water collects to create perennial drinking sources (Owen-Smith 1996), and from nutrients in animal fæces concentrated in those places by habitual watering behaviour (see thrash & Derry 1999). Additionally, the clay content of alluvial soils in river floodplains increases the retention of soil moisture favouring the growth of herbaceous vegetation over the growth of woody species, which limits bush encroachment (Brits *et al.* 2002). In arid wildlife zones, the predominance of annual plants and the comparative water independence of animal species also limit the previous year's impacts on near-water vegetation re-growth (Thrash & Derry 1999).

Real-world long-term piosphere dynamics remain an unknown. Although Landsberg *et al.* (1997) and Redfern *et al.* (2003) have been able to retrospectively analyse large scale (1:100,000 and 1 km^2, respectively) historical data, each about a decade, there are no published data sets of monitored individual watering sites. So, the relationship between piosphere dynamics and herbivore density, rainfall and rangeland 'condition' is currently limited to hypothetical modelling exercises. The most comprehensive of these is reported in this chapter. Monitoring programs need to be established in wildlife (Gaylard *et al.* 2003) and livestock (Pringle & Landsberg 2001) systems, with adequate "geomorphically and biologically intact benchmarks are critical for developing and improving understanding of the regionally specific relationships between grazing pressure and ecosystem responses" (Pringle & Landsberg 2001), where monitoring allows us to "expand our understanding through modelling and predictive exercises, thereby improving future management decisions" (Gaylard *et al.* 2003).

Management plans tend to assess the carrying capacity of rangeland in terms of their foraging potential, but without considering the moderating influence of water location on this potential. Further consideration of the consequences that watering requirements have for animal growth and survival metered by the mechanisms that moderate populations via their dry season resources will provide managers with an improved assessment of the secondary production potential of their rangeland. Partitioning of rangeland with respect to watering behaviour may prove the best approach.

CHAPTER 6 - DISCUSSION AND CONCLUSIONS

6.1 Synopsis

This thesis has set out to investigate two aspects of animal spatial foraging behaviour, both arising as a direct consequence of animal need to drink water; the concentration of animal impacts, and the response of animals to those impacts.

The foraging range of free-ranging large mammalian herbivores is constrained by the distribution of their drinking water during the dry season when temporary surface water dries up and water supplies become limited to more persistent sources. Animal impacts become concentrated around these watering sites according to the geometrical relationship between the available foraging area and the distance from water. The spatial distribution of impacts becomes organised into a utilisation gradient. Outside the season of plant growth, the temporal distribution of the impacts is determined by the day-to-day foraging behaviour of the animals. The specific conditions under which these processes operate have been identified in this thesis.

As a preliminary step to investigating animal response to resource heterogeneity, this thesis has characterised the generation of spatial pattern using spatial statistics. In a further effort to characterise utilisation gradients, contemporary ecological theory was applied with the result that piospheres have been identified as examples of emergence in natural systems.

The response of animals to this utilisation gradient involves the constraining effect that reduced resources have on animal intake. At the core of this investigation are questions asked about the response of animals to the heterogeneity of their resources. Implicated along the way are our notions of optimal foraging, scale in animal response, and resource matching. This thesis has needed to address each. In the specific context of utilisation gradients, the role of energy balance in optimal foraging has also been tested.

In the longer term, animal population dynamics were found determined by the dry season key resources present about watering points. Below there is also the proposal that piospheres exert selection pressures, and that these played a role in evolutionary time, in large mammalian herbivore diversification (see Section 6.2.7).

6.2 Synthesis of experimental findings

6.2.1 Resource heterogeneity

Landscapes are typically characterised in functional terms as a patch structure, where resource patchiness is ideally defined by a consumer's response to its environment (Wiens 1976). As no evidence was found for selection of resources at a patch scale above that of the individual feeding site (Chapter 2), a patch is empirically defined in this thesis as an individual feeding site (Chapter 4).

6.2.2 Animal assessment of resource heterogeneity

Conceptual models of animal resource assessment have assumed a hierarchy of decision making, starting with the landscape and ending with decisions at small scales about individual bites. As far as subjective categorisation of plant community allowed, this concept could not be supported by the findings here (Chapter 2). Instead, browsing animals were found to select between individual trees at the largest scale. The only obvious influence that operates daily at a larger scale, and that can be accepted with any confidence, is the need to return to drinking water[1]. These findings were used towards the simulation models of subsequent chapters (Chapter 3 and Chapter 5).

Temporal variation in selected resources and evidence of sampling imply continual assessment by animals of their resource supplies (Chapter 2). Sequential exploitation of resources is consistent with an energetic basis for this resource assessment and supports the energy intake maximisation assumptions underlying Optimal Foraging Theory. This leads to the prediction that for the conditions presented by a utilisation gradient, there should exist a distance at which animals are able to maximise their net energy gain.

6.2.3 Animal response to resource heterogeneity

Animal movements through the simulated landscape were found sensitive to the spatial distribution of their resources, revealing an adaptive foraging strategy that gave rise to tortuous foraging pathways when patch density was high (Chapter 5).

Accumulated animal activity did show how areas are used according to resource distribution (Chapter 2). At the broadest discernible scale, some areas are preferentially used for grazing while others receive most browsing activity. Spatial statistics provide a tool by which to test and visualise these patterns of animal activity. Accumulated animal activity was found related to defoliation providing a means to measure the spatial distribution of animal impacts and the response of animals to resource heterogeneity.

6.2.4 The organisation of resource heterogeneity into utilisation gradients

The simulation model developed in this thesis was very successful at simulating piosphere generation, as far as it is possible to make comparisons with real data and other model predictions (Chapter 3 and Chapter 5). At present it is not possible to validate predictions of piosphere dynamics monitored over the longer term, as there is no published data with which to do so. However, the model is an improvement on previous attempts to model the piosphere pattern. Most notable is the absence of a preconceived utilisation pressure gradient and the simplicity of the rules governing dry season spatial foraging (Chapter 3).

The gradients in resource profitability that resulted were generated by the accumulation of spatial impacts from daily foraging bouts laid out "passively" in relation to landscape geometry. Conditions in agreement with the assumptions made for Marginal Value Theorem gave rise to the most realistic gradients (Chapter 3). Within patches, it was shown that the piosphere pattern develops from preferential

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[1] Other apparent behaviour includes seeking shade.

selection of large bites, and was detected concurrently in bite size and bite density (Chapter 4).

In the absence of a water point, resource distributions are clumped, with no discernible patch structure (Chapter 2). Utilisation patterns result from modifications to patch profitability, as the accumulation of defoliation along daily foraging pathways. Distinct patterns such as the piosphere are recognised in a level of organisation at a larger spatial scale than the single patch and result from the integration of simple rules at lower levels. This level of abstraction is proving useful in testing epistemic theory (Wolfram 2002), and this thesis has contributed to the list of ecological examples by highlighting piospheres and the animal response as emergent properties of a natural system (Chapter 5).

6.2.5 Animal response to utilisation gradients

The organisation of patch profitability into a gradient, which is lowest near water, immediately implies a conflict for the free-foraging animal. Travel from water to areas of higher profitability carries with it associated energy costs. In order to maximise energy gain, the animal must therefore travel far enough "up" the utilisation gradient to reach areas sufficiently resource rich so that travel costs can be met in addition to other daily maintenance costs. The logical expectation is that optimal foraging under these conditions would depend on how far the animal is able to travel. Estimates of foraging range and foraging radius for the model animal were predicted using analytical and simulation models (Chapter 3) and were in good agreement with some literature values.

Perhaps surprising was the lack of energy balance involved in constraining animal foraging radius as indicated by piosphere extent. Yet daily intake, and the accompanying daily foraging distances, were largely constrained by the energetics underlying digestive and metabolic constraints, and the part played by travel costs may have influenced simulated piosphere dynamics if animal density had not been fixed.

Handling and encounter constraints conspire to effect a gradient in animal intake rate that mirrors the piosphere pattern detectable in resource levels (Chapter 4). The switch between the processes that determine intake rate occurs for threshold conditions of bite size and bite density which, for the coexistent gradients in these bite parameters present in a given piosphere, coincide at a threshold distance from water. The result is that within typical daily foraging radii, the rate of biting is mostly determined by encounter rate, as a function of bite density during the dry season, otherwise handling time based on bite size is more important (Chapter 5). Optimal bite rates can be achieved throughout the year for hypothetical mixtures of bite size and bite density.

6.2.6 Population response to utilisation gradients

Limited dry season foraging range directly translates into a constraint on animal intake. This reduction in resource supply regulated the animal population via mortality and state-dependent reproduction, implying that populations are in equilibrium with their dry season key resources (Chapter 5). Conversely, a delayed piosphere response in relation to animal density indicates moderation of those key resources by population size. Lower animal densities resulted from including dry season watering behaviour in the simulations.

Because of watering behaviour, animals are unable to freely access their resources to the same level that they achieve outside the dry season (Chapter 5). This was shown by application of Ideal Free Theory, which revealed seasonal differences in resource matching.

Limitations on population growth imply an optimal management strategy that aims to maintain dry season key resources immediate to watering points. Typical suggestions recommend: controls on watering point spacing (to avoid gradient overlaps), watering point rotation and cordons to allow "resting" of high impact areas, and reduced stocking rates, plus the use of physical barriers to herbivore impacts (*e.g.*, matting in the immediate vicinity of water troughs). An alternative recommendation seeks to maintain refugia by emulating the distributions of natural water bodies, rather than close-packed, evenly spaced artificial systems, which have proved deleterious to water-independent species (Owen-Smith 1996).

6.2.7 Species response to utilisation gradients

Watering point dependency has consequences for herbivore behaviour from day-to-day and season-to-season. Independently, there have been comparisons made between the water-dependencies of these species (animal papers) and the consequent impact of drinking foci on the savanna landscape (piosphere papers). If water plays such a pivotal role in the existence of the vast majority of animals, then it is conceivable that it also plays a pivotal role over a longer time scale, in their evolutionary development. To date, little emphasis has been put upon the role water requirements may have played as a driving force behind the diversification of African ruminants.

The main radiation of large mammalian herbivores in Africa took place during the Pliocene-Pleistocene (Sinclair 1983). The traditional explanation of bovid evolution relates animal adaptations to habitat change brought about by climatic variation (Janis 1989). Recent fossil-evidence from the Turkana Basin of Kenya and Ethiopia indicate 58 to 77% turnover of the mammal species between 3.0 and 1.8 million years ago (Ma) (Behrensmeyer *et al.* 2003) where species diversity increased from 3.0 to 2.0 Ma but then declined. This period was marked by fluctuating climate (with a suggested periodicity of 19,000-21,000 years, Adams 2000) and repeated cycling between forest and open grassland (savanna, the intermediate habitat type would have been present twice as long as any other, Sinclair 1983). This favoured the diversification of ruminant grazers in Africa, in contrast to the earlier rise of hind-gut fermenters in North America (Janis *et al.* 2002). So current models continue to identify habitat fragmentation as the primary cause of speciation and diversification (although the Rift Valley could be considered a combination of a physical and habitat-related barrier).

It is assumed that the small-bodied ancestral browser in Africa was relatively water independent, as are typical contemporary browsers, gaining most of their water from their diet. However, developing African grasslands would have presented herbivore populations with a strong selective pressure for conversion to grazing. Gordon & Illius (1996) have shown that this change in feeding strategy necessitated an increase in body size, and fossil records are able to confirm that there was such an increase (Janis 1989). With the adaptation of ancestral species to poorer, drier diets there was an increase in water requirements to aid digestion and thermoregulate larger body size. While small animals avoid heightened predation near water holes by being less water dependent (Ayeni 1975), there is some advantage in being large for defence against predators and for having a longer gait (Hudson 1985). But, critically, water dependency constrains the home range of free-ranging animals during the dry season and this dictates the availability of their food (*e.g.*, Weir 1971). This suggests a possible role of the watering behaviour of African ruminants in bringing about morphological adaptations and driving the diversification of their feeding strategies.

The following notes briefly suggest conditions under which the ecological consequences of animal water dependency may have played a role in their diversification and particularly the dietary adaptations of grazing.

i. Sympatric speciation Water dependence is assumed to be detrimental to animals because it restricts their foraging range during the dry season to areas degraded by high utilisation pressures. Increased water dependency is an undesirable trait associated with dietary adaptations of grazing characters (*e.g.*, large body size). It is therefore reasonable to expect a piosphere to produce opposing selection pressures; to get further away from water (Pennycuick 1979), or adapt to the consequences of the utilisation gradient and its associated compositional changes to the vegetation. This notion is supported by field observations of overlap in diet. The overlap is highest during the wet season, but declines from the start of the dry season as each animal species concentrates on a niche or "food refuge" (Sinclair 1983). In the late dry season the overlap increases again as resources are depleted to an extent that forces compromises in diet selection, suggesting that interspecific competition promotes ecological separation by food preference. Therefore, during the dry season adaptations promoting niche separation are most strongly selected (Schoener 1974)[2]. Non-overlapping watering behaviour (Ayeni 1975) and associative mating within groups specialising on vegetation at differing distances from water (Danley & Kocher 2001) may account for diversification stability under these conditions of shared geography.

ii. Allopatric speciation. Persistent watering centres, whether they comprise a single watering point or a network of watering points within travelling range, act as attractors to animal populations. A parallel may be drawn between island biogeography and the captive influence of dry season water location. Both may give rise to reproductive isolation as it is plausible that animals frequenting one of two watering centres may be isolated from animals at the other watering centres, if the watering centres are sufficiently separate. For this to occur, the waterless distance between centres would need to be further than the possible travel between drinking events and would therefore depend on species water dependency and mobility. Although models of allopatric speciation already include desert barriers, this case defines geographic isolation as a vicariance event in terms of a physiological barrier to dispersal and gene flow[3], for dry season conditions over the evolutionary time scale.

iii. Parapatric speciation where watering points are dispersed but not isolated to form distinct watering centres, sympatric speciation may be reinforced by animal populations frequenting different watering points.

The test of these hypothetical models of speciation needs to distinguish between habitat-related adaptations, utilisation gradient adaptations and water dependency

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[2] Illius & Gordon (1991) predicted that maximum daily energy intake should scale with body size as $W^{0.88}$ (*i.e.*, greater than metabolic rate, $W^{0.75}$), implying an advantage of large size for utilisation of diets with slow digestion rates, *i.e.*, larger species can subsist on poorer-quality food. The result is a selective pressure for adaptation to a poorer quality diet, as typical for depleted dry season resources, which carries with it a corresponding increase in body size (Illius & Gordon 1992). It also suggests a divergence of body size via a strong selection pressure for large body size during periods when forage is abundant but of poor quality, countered by the pressure for small size during seasons when forage is either abundant (Illius & Gordon 1992), or scarce, but of high quality (Murray & Illius 1996).

[3] Darwin (1859) only refers to drinking at one point, early on in *The Origin of Species*, but he does identify the importance of water distribution towards a mechanism for speciation later, albeit as a physical barrier, and not a physiological barrier.

isolations. The opportunity may be found in the genetic variation between animal populations spanning a known geographical barrier, such as the Rift Valley. It would be possible to test the prediction that allopatric speciation because of water dependency would cause genetic differentiation in water dependent species (and subspecies), but none in water independent species. Habitat fragmentation would not be expected to cause this difference.

Adaptations under the sympatric model may be harder to distinguish from changes in response to general environmental conditions. Undoubtedly, body size is the single whole-animal correlate best indicative of water requirement and feeding strategy. Body size relations of water and nutrient metabolism may be used to investigate historical records of animal body size. Mechanical adaptations should include increased leg length and superior water conservation (*e.g.*, blood vessels for the counter-current system of blood cooling), and fossil records may go some way to providing evidence for such adaptations. Dietary water, diet quality and forage intake are all interrelated with animal water requirements, and fossil evidence may assist in deriving an estimate of animal water dependence.

In summary, water dependency may have played a role in ungulate evolution. At the scale of the single piosphere, selection pressures are expected to promote alternative feeding strategies, morphological adaptations and avoidance behaviour. These selection pressures are present in every dry season. Over longer time periods, distinct clusters of watering points present the same evolutionary opportunities as island biogeography.

6.3 Gaps in knowledge and future research

A main gap in the literature highlighted by this investigation stems from the lack of studies that have monitored piosphere dynamics. Piosphere studies mostly measure the utilisation gradient in a number of variables, but on one occasion only. Although simulation studies such as those in this thesis are able to predict long-term piosphere dynamics, future work should be directed at validating these predictions, and relating changes in these gradients to changes in herbivore pressure, subsequent plant response and the determinants of plant growth.

Compositional piosphere effects involve so-called increaser and decreaser forage species and the associated assumptions about forage quality, or palatability. As the increaser/decreaser classifications and palatability are terms widely used in range assessment and rangeland science, finding methods for use in both science and practice to quantify these subjective measures should help define the landscape in terms of the foraging animal. The piosphere gradient is proving a useful tool.

6.3.1 Fieldwork

The above findings of this thesis are mostly based on mixed feeding in goats (Chapter 2, Chapter 3 and Chapter 5). Although Chapter 4 concentrated on browsing activity alone, these browsing-based findings are supported by the results from mixed feeding simulations in other chapters and by other literature, but this would be verified by repeating the experiment for grazing animals.

Individual chapters contain their own potential sources of error from assumptions and methods employed therein. The methodology in Chapter 2 needed to account for errors in the recording of an animal's location, plus the problems of autocorrelation. Selective Availability (National Security Council 1996) has stopped since this experiment. Therefore using GPS in conjunction with random sampling would remove such doubt.

The distance threshold hypothesis was only tested by simulation. The Runway experiment of Chapter 4 would be ideal for specialist feeders (*i.e.*, not mixed feeders who can switch diets) under dry season conditions. The experiment could be extended by manipulation of the grazing gradient, but this requires prior assessment of the associated profitability with distance from water. Alternatively, the role of travel costs could be investigated further by manipulation of the animals' energy expenditure perhaps by introduction of handicaps. More control over the gradient would be possible by constructing it artificially using feed blocks (*c.f.*, Fryxell 1998).

6.3.2 Modelling

The logistic model did not reveal fundamental relationships between the model parameters that describe the shape of the piosphere response and historical information (age, stocking rate, rainfall, etc.) when comparing real world data between different sites. It was successful when used to monitor piosphere development during simulations, and relate the piosphere (*e.g.*, extent of response) to causal factors (*e.g.*, animal density).

Simulation model development faced limitations on the parameterisation of spatial grain and iteration step imposed by computer performance (runtime), but this had little or no consequence for interpretation of simulation results. Other parameters could have been given alternative values: the amount of daily grazing time used in the models was set static at 10 hours which might have been optimal for maximisation of total daily intake. Replication of the most extensive simulations was not possible, although the effect of annual variation in rainfall was minimised and care was taken when interpreting results. Other daily input parameters were not replicated or averaged in the same way as rainfall, but were not associated with regional climatic variation.

The models did not include animal impacts other than defoliation (*e.g.*, excretion and trampling), nor did it explicitly account for plant response to that defoliation, although re-growth levels were consistent with literature values.

Assumptions were made about animal foraging behaviour. When the search algorithm failed to locate a destination, limits on nearest-neighbour searching were relaxed in preference to substituting a random walk algorithm. Variable memory would respond to resource encounter rates at differing scales, and an Exponentially Weighted Moving Average (EWMA, Hunter 1986) model of memory retention would be more sensitive to changes in environmental heterogeneity. Dependency on a watering point was identical for all years and coincided with the predetermined start of the dry season, where it is more likely determined dynamically by the accumulation of surface water in the latter part of the previous wet season. While mechanisms were tested where possible, future work should confirm the existing assumptions in comparison with these alternative solutions.

6.4 Summary of contributions and conclusion

This thesis set out to explore the mechanistic processes common to the distribution of spatial impacts through herbivory. In particular this investigation focussed on the example case of utilisation gradients. The foremost consideration involved the response of animals to their environment and this thesis has provided conclusive evidence that animals are sensitive to the heterogeneity of their resources at a small scale. In doing so, it is now clear that foraging behaviour is affected by small scale variation and the defoliation impacts accumulated at this scale are distributed such that they mirror the distribution of resources at larger scales. Because of the need to drink water, the additional influence of water location causes impacts to become arranged as utilisation gradients called piospheres. During this thesis a model was developed that is the first to simulate piosphere dynamics mechanistically, and has shown that these gradients in resource profitability are the result of landscape geometry as a function of water point location mediated by digestive constraints. A vital finding of this thesis is that below a critical threshold of food abundance, encounter rate is a more important determinant of animal intake rate than handling time. Thus, this thesis has commented widely on aspects of spatial foraging whilst explaining the consequences of piosphere phenomena for individual animal intake, population dynamics, feeding strategies and optimal management. Elsewhere, Stuth (1991) and Coppolillo (2001) have recognised that the potential distributions of animals about watering points resemble those expected for central-place foragers (Orians & Pearson 1979). Independently, the 'take home message' from this thesis is that, in effect, the combination of digestive constraints and travel costs transform free-ranging water dependent animals into central-place foragers.

APPENDICES

A1 Appendix 1: Species composition of plant communities

Vegetal communities within the paddock were identified from an orthophotograph and near infra-red image analysis (see Section 2.3.3). Six main community types were identified (ACACIA, OLIVE, ERODED, RIVERINE, ALOE and ZIZIPHUS) and 27 subtypes numbered 1,2,3,…,27. The community subtypes were identified as follows,

Main Community	Community subtype	Identifying number
ACACIA	d	1
OLIVE	e	2
ACACIA	b	3
OLIVE	g	4
ERODED	c	5
RIVERINE		6
ERODED	b	7
ERODED	e	8
ERODED	d	9
ACACIA	a	10
ACACIA	c	11
ERODED	b	12
ACACIA	c	13
OLIVE	c	14
ACACIA	b	15
ACACIA	a	16
ALOE	a	17
ACACIA	d	18
RIVERINE		19
OLIVE	b	20
ALOE	b	21
ERODED	a	22
ERODED	a	23
OLIVE	a	24
ALOE	c	25
OLIVE	c	26
ZIZIPHUS		27

Community composition was then surveyed across these communities with 53 randomly located 2x2 m quadrats (Fig A1.1, *overleaf*).

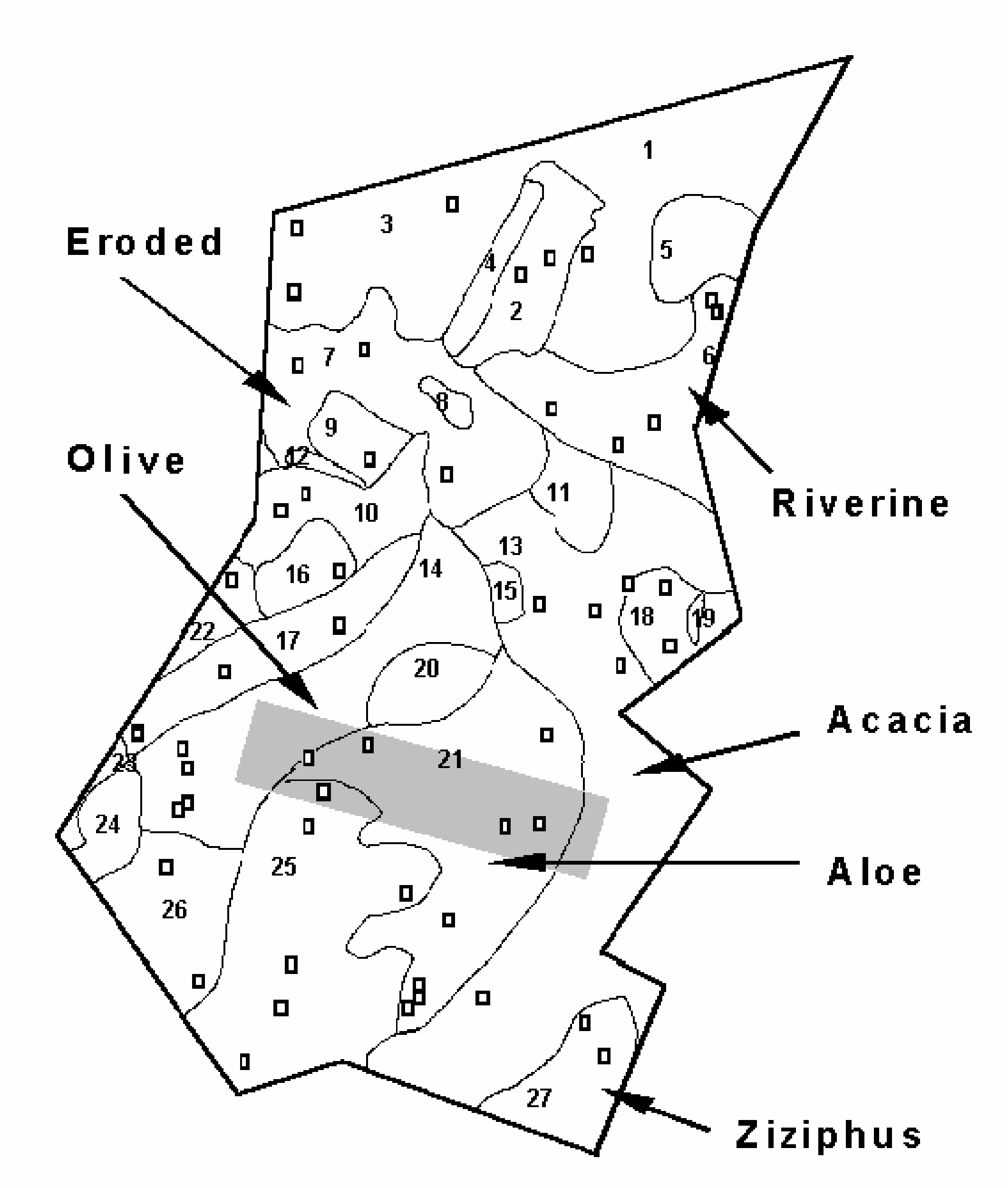

Fig. A1.1: Phytosociological community boundaries and coverage of survey quadrats for community species composition. Main community types are marked along with the 27 community subtypes (1…27) and the location of 53 species composition survey quadrats. The transect area is marked with a grey rectangle.

Species were ranked according to their estimated contribution to the total aboveground biomass within the quadrat (see Section 2.3.3 for details). Ranked species occurrence

(1 was most abundant, 2 was second most abundant, etc.) and absence (blank) for plant communities within the paddock is shown in the table overleaf (see Section 2.3.2 for species names and description of community classification).

As can be seen in the table overleaf, several species occur under more than one community type. The proportion of all shared species (n=125) that were shared between each community type combination was as follows,

	ACACIA	OLIVE	ERODED	RIVERINE	ALOE	ZIZIPHUS
ACACIA		0.112	0.096	0.056	0.112	0.032
OLIVE			0.112	0.096	0.088	0.024
ERODED				0.064	0.088	0.024
RIVERINE					0.048	0.024
ALOE						0.024
ZIZIPHUS						

It was important to consider how much of the paddock the goats had been exposed to before being able to make inferences about community selection. In the absence of a suitable statistical test that can account for temporal correlation within the sequences of community subtypes associated with the daily recorded feeding locations, and that can also make comparisons between those sequences, the statistics reported below show the course of the experiment period, progress with data collection and the cumulative daily areas traversed by the herd's foraging path. Proportional areas were calculated in terms of the whole paddock area (19.8 ha). The GPS method was introduced after trial day 4.

	Days		Observations			Community subtypes			
Trial day	from first exposure to paddock	cumulative proportion number	daily number	cumulative number	cumulative proportion number	cumulative number	cumulative proportion number	cumulative area (ha)	cumulative proportion area
1	0	0.02	38	38	0.02	9	0.36	7.10	0.358
2	2	0.07	31	69	0.04	11	0.44	10.16	0.513
3	4	0.11	33	102	0.06	13	0.52	10.50	0.530
4	7	0.18	16	118	0.07	14	0.56	12.54	0.633
5	11	0.27	205	323	0.18	21	0.84	17.44	0.881
6	14	0.34	240	563	0.32	24	0.96	19.51	0.986
7	15	0.36	115	678	0.39	24	0.96	19.51	0.986
8	16	0.39	130	808	0.46	25	1	19.73	0.997
9	17	0.41	171	979	0.56	25	1	19.73	0.997
10	21	0.50	168	1147	0.66	25	1	19.73	0.997
11	24	0.57	170	1317	0.75	25	1	19.73	0.997
12	28	0.66	175	1492	0.85	25	1	19.73	0.997
13	36	0.84	118	1610	0.92	25	1	19.73	0.997
14	43	1.00	138	1748	1.00	25	1	19.73	0.997

Quadrat number	Number of species	Species abbreviation (see Section 2.3.2 for names)																		
		ACON	AFER	AKAR	ALOE	BSAL	CASS	CDAC	CPLU	CRUD	DERI	ECAP	ECHL	ECUR	EMUT	EUPH	EURY	GOCC	HPAC	JANG
1	6				5															
2	6						1											4		
3	5		1									3								
4	5				4						2	1								
5	7			6					2		3		5							
6	9	7		2					3		5		4		6					
7	6			5					1			4	3			2				
8	2										1									
9	7				6											4				
10	3																			
11	6	2									3									
12	3				1								2							
13	6							5									3			
14	6	1		5					2		4									
15	5		2		4															
16	6									4		5								
17	9				5					4			7							
18	7				3					2										
19	7											1								6
20	4			1							3									
21	4			2							3									
22	5										2	3								
23	4								2		1	3								
24	6			4					3											
25	5			3								2								
26	7			1	3	5			6											
27	2					1														
28	4			1																
29	5				2					3	4							1		
30	3										2									
31	7				4	2			1		6									
32	3	2							1											
33	4											2								
34	2																			
35	7		1		5				2		6				4					
36	7		1		5				3				6		4					
37	7	6	1						2		6		3							
38	6					1			2		5		4							
39	7				6				3						5		2			
40	5				3					1										
41	6				4				3	1										
42	8	7	1		3						6			2						
43	8		1						7		5		3							
44	9		3		4				6		7							2		
45	8				4				2				6					3		
46	7		1		5															
47	9		1	2					7				8					3		
48	10		2						4	7		8					1		5	
49	4							3												
50	4		1																	
51	4				3															
52	4							2				1								
53	6										3	5								

Quadrat (cont...)	LFER	LJAV	LYCI	MCAF	MHET	MPOL	OEUR	OFIC	PAUR	PMAX	PVER	RLON	ROBO	RREF	SAFR	SEDG	SFIM	SISA	SMYR	TCAP	TTRI	ZCAP
1						3	4				2								1			
2			3								2											5
3										4							2					
4																	3					
5																	4				1	
6																	8				1	
7																						
8																						
9											3			2			5	1				
10											2							1				
11				1									4			5						
12																						
13						1				4	2											
14																	3					
15											1									3		
16										2	1						3					
17			3				1			6				2			8					
18				6	5					4		1										
19									3	2							4					5
20																	2					
21																	1					
22																4	1					
23																						
24													2				5				1	
25										4							1					
26										4							2					
27																						
28										2							3					
29																						
30																	1					
31																	3				5	
32																						
33										3							1					
34																					1	
35																	3					
36																					2	
37																					4	
38																	3					
39																	4				1	
40										2						4						
41										5							2					
42										5							4					
43													2	4			6					
44							1										8				5	
45															5		7		1			
46									2	4			6				3					
47		4								6							5					
48							6			9							4					
49								1	2													
50										3							2					
51										1							2					
52																	3					
53	1									4							2					

A2 Appendix 2: Sources of error in animal location measurements

A2.1 Accuracy of animal locations

The intentional modification by the US government (Selective Availability, National Security Council 1996) of the Standard Positioning Service provided via commercial satellites was terminated on May 1, 2000. Until that time (including the schedule of this experiment) this interference degraded the accuracy of triangulated positions by introduction of random signal timing and ephemeris (orbit) errors. These errors imposed a scattering effect on locations calculated by a GPS. Smaller errors in GPS positions are due to inaccuracies in satellite and receiver technology in addition to interference of satellite signals whilst passing through the troposphere and ionosphere.

		RMS (m)	CEP (m)
FENCE POSTS	Theodolite	28.9	21.7
	GPS	30.8	23.1
TRANSECT LENGTHS	Simulation	34.0	25.5

Table A2.1: Estimated error in the recordings for animal locations made with a theodolite-distance-meter survey technique and an autonomous GPS. The Root Mean Square (RMS) is equivalent to one standard deviation (Steel & Torrie 1980), giving the radius of a circle in which 68.27% of the positions will occur. Circular Error Probable (CEP) is the radius when the probability of a reading being within the circle is 0.5 (StarPal 1999).

Until its removal, it was commonplace to differentially correct for Selective Availability, either in the field or by post-processing of the captured data. However, autonomous (uncorrected) GPS was used for this study due to limitations in the data storage capacity of the GPS receiver model and the availability of suitable software with which to carry out the corrections; the recommended method when differential correction is unavailable (Casaer *et al.* 1999). Hence, estimates of the location error in GPS readings were obtained from two sources (Table A2.1). First, the recorded positions of the fence posts along the perimeter of the paddock were compared with the known positions of those fence posts extracted from the aerial photograph of the paddock. The aerial photograph was geo-referenced and the locations were extracted using the Geographical Information System (GIS) IDRISI (Clark University, Worchester, MA).

Second, the recorded distances between ends of the 50m transects used in the defoliation experiment were compared with the known transect length for the purposes of simulating the observed deviations. The sources of horizontal error that generated the observed average deviation of 44m from the known transect lengths were assumed simultaneously to act upon both ends of the transect. When ascertaining GPS accuracy, the distribution for the error along any 3-dimensional axis is assumed to be Gaussian, and the horizontal error distribution is assumed to be circular (van Diggelen 1998). Therefore the northerly and easterly co-ordinates of each transect end were varied with normally distributed random variables independently sampled from the same population to avoid sequence autocorrelation. The resulting simulated transect lengths were averaged and the deviation from the known average length was plotted against the standard deviation of the population of random variables. The polynomial relationship between average transect length and the standard deviation was solved for the observed average transect length, giving the standard deviation of random error required to produce the observed transect length deviations. These GPS error estimates agree with reported errors for autonomous GPS measurements made under similar conditions (*e.g.*, on a hilltop RMS=30m, on a hillside RMS=35m, on a valley floor RMS=45m, StarPal 1999). Theodolite-distance-meter measurement errors may be attributed to daily variation in the prism constant with temperature, in conjunction with human error. There was no difference in the deviations from known fence post positions for measurements made with the GPS and the theodolite (paired $t_{12}=1.07$). Therefore, animal locations measured by each method were not treated separately during analysis. Altitudinal estimation is more sensitive to the effects of Selective Availability and errors can be in the range of 500m. Therefore, altitude was derived from the digitization of contours on an orthophoto of the area and generation of a digital elevation model in IDRISI.

A2.2 Independence of animal locations

Statistical testing in spatial datasets is complicated by autocorrelation, which reduces the effective degrees of freedom against which t and *F* ratios should be compared (Clifford *et al.* 1989, Dutilleul 1993, Legendre 1993). Autocorrelation means that repeated samples are not independent of one another, as required by standard statistical procedures (Sokal & Rohlf 1995). However, as long as non-independence is due solely to autocorrelation, it is appropriate to modify the t-test for correlations between spatial variables simply by reducing the degrees of freedom used (Clifford *et al* 1989, Dutilleul 1993).

Ideally one would employ an analytical approach to calculate the effective degrees of freedom. This is currently only possible for simulated autocorrelated data sets (Clifford *et al.* 1989, Dutilleul 1993, Legendre 1993). The alternative approach, and the one employed here, is to choose an α probability, P (the rejection level), calculate the t or *F* ratio, and then consult statistical tables to find the minimum degrees of freedom required to reject the null hypothesis at $\alpha=0.05$, the chosen rejection level (*e.g.*, Baird 1996). An estimate is then made as to whether the effective degrees of freedom is likely to exceed this ‘conservative’ degrees of freedom, taking the sample size and autocorrelation structure (as illustrated by interpolation surfaces) into account. Although imprecise, this *ad hoc* method is straightforward, and often the required degrees of freedom are orders of magnitude smaller than the (non-independent) sample size and therefore findings of significant difference are robust. In some cases however this approach may be unsatisfactory because it does not allow confidence intervals for sample statistics to be calculated, as it is not possible to refer to a tabulated value for $t_{\alpha[v]}$ when v is equal to the effective degrees of freedom.

A3 Appendix 3: Goat diet selection from impact scores

A Generalized Linear Model (GLM) analysis was carried out on the impact scores recorded during the two surveys within the transect area. The midpoints for the categories of percentage defoliation, translated from the 6-point scale, were used as the measure of impact (`impact`). These were 5.5, 18, 38, 63 and 88%. The data forwarded as explanatory variables comprised tree species (`species`), survey number (`survey`), plant community membership (`community`), distance of the individual tree along transect (`dist`) and transect number (`vtrans`). The simplified model is presented here, omitting non-significant interaction terms (`vtrans.species` and `species.survey.vtrans`) without change to model fit (deviance, 'percentage variance accounted for' and 'standard error of observations'). The resulting GENSTAT output was as follows,

```
Response variate: impact
     Fitted terms: Constant + survey + species + vtrans + vtrans.survey +
                   survey.species + community + survey.community +
                   survey.species.community + dist
                   (FACTORIAL limit for expansion of formula = 3)

*** Summary of analysis ***

              d.f.        s.s.         m.s.      v.r.  F pr.
Regression      90      240159.       2668.4      8.00  <.001
Residual       293       97721.        333.5
Total          383      337880.        882.2

Percentage variance accounted for 62.2
Standard error of observations is estimated to be 18.3

*** Accumulated analysis of variance ***

Change                        d.f.         s.s.         m.s.      v.r.  F pr.
+ survey                         1      51401.3      51401.3    154.12  <.001
+ species                       14     116595.3       8328.2     24.97  <.001
+ vtrans                         1       6361.0       6361.0     19.07  <.001
+ vtrans.survey                  1       6864.4       6864.4     20.58  <.001
+ survey.species                14      27847.1       1989.1      5.96  <.001
+ community                      3       1727.0        575.7      1.73  0.162
+ survey.community               3       3206.4       1068.8      3.20  0.024
+ survey.species.community      52      25866.7        497.4      1.49  0.022
+ dist                           1        289.9        289.9      0.87  0.352
Residual                       293      97721.2        333.5

Total                          383     337880.2        882.2
```

The same analysis produced predicted mean percentage defoliation for each fixed term in the linear model. The interaction term `species.survey` shows at least a partial shift in goat diet preference, which was confirmed as the avoidance of some tree species and continued selection of others within the transect area during the inter-survey period (*see below*, only selected species listed. Please note that predicted means may fall outside the logical range for percentage defoliation, *i.e.*, >100% because they incorporate the standard error of the prediction). Although untested, the long-term preferred species are probably identifiable from the largest predicted mean values in the `both` column, equivalent to the mean of the two survey values,

```
*** Table of predicted means of percentage defoliation for species.survey ***
```

Species	survey 1	survey 2	both
AFER	30.4	35.3	32.8
AKAR	43.8	100.7	72.3
BSAL	13.3	47.5	30.4
CRUD	46.4	59.6	53.0
DERI	3.7	11.1	7.4
EURY	6.0	20.6	13.3
GOCC	32.6	79.9	56.2
LYCI	43.7	45.5	44.6
MPOL	10.7	16.8	13.8
OEUR	13.7	57.8	35.8
PVER	10.9	22.7	16.8
RLON	18.9	63.1	41.0
RREF	40.5	68.0	54.3
SMYR	11.8	29.1	20.4
ZCAP	78.0	103.8	90.9

```
Standard errors:   Average          33.02
```

Although the distribution of impacts changed between surveys (`vtrans` is a significant term), it can be safely concluded that the shift (or re-focussing) of diet selection between surveys is not a consequence of a clustered distribution of species abundance because neither `dist` nor `vtrans.species` are significant terms. The shift in diet selection also cannot be attributed to plant associations and the location of phytosociological communities. For example, if the goats were selecting their diet at the community level, some species would not be available because they were not represented in the selected communities. Conversely, by systematically exploiting the resources going in an uphill direction (see Section 2.4.3), the goats redistributed their defoliation impacts between surveys determined by individual tree location (the `species` and `survey` main effects are significant). This did not result from the association of tree species with vegetation communities (the `species.community` interaction is not significant). The significant effects of `survey.community` and `species.survey.community` simply show that different communities were exploited through selection of individual trees at different locations between surveys. Consequently, `community` is not a significant term because the distribution of impacts within the transect area predicted for community type was effectively uniform as shown in this REML output,

```
*** Table of predicted means of percentage defoliation for community ***

    community       ACACIA         ALOE     OLEA/ALOE      ALOE/OLEA
                    34.02        39.74        37.87          34.11

Standard error of differences:     Average            4.699
```

A4 Appendix 4: Goat diet selection from feeding duration

Diet selection by the goats for the whole paddock, recorded as the percentage of the observations of feeding duration for the entire herd (without animal locations) and for sampled individuals (with animal locations), and of the total duration for which goats were recorded feeding on the following species. For comparison, a measure of relative abundance is included taken as the percentage composition of each species calculated from quadrat data (see Section 2.3.2) by the Dry-Weight-Rank method (DWR, ‘t Mannetje and Haydock 1963).

		Herd (N=17019)	Individuals (N=1446)	
species	% composition	% observations	% observations	% duration
ACON	1.89	-	-	-
AFER	12.26	2.12	4.50	3.75
AKAR	5.09	4.12	5.88	5.58
ALOE	0.19	0.01	-	-
BSAL	3.02	3.42	5.67	6.37
CASS	1.32	0.16	0.21	0.13
CDAC	0.38	0.53	1.73	1.59
CPLU	6.98	0.04	-	0.29
CRUD	2.83	1.93	2.63	2.42
DERI	3.40	0.02	-	-
ECAP	4.15	-	-	-
ECHL	0.57	-	-	-
ECUR	0.38	-	-	-
EMUT	-	-	-	-
EUPH	0.38	0.11	1.31	1.07
EURY	1.89	3.16	3.32	4.58
GOCC	1.89	28.86	17.98	17.39
HPAC	-	-	-	-
JANG	-	0.11	0.07	0.08
KARO	7.55	1.28	6.43	5.26
LCAP	0.94	-	-	-
LFER	0.19	0.08	-	-
LJAV	-	-	-	-
LYCI	0.19	-	-	-
MCAF	0.38	-	-	-
MHET	-	3.02	4.63	4.29
MPOL	1.51	0.96	2.56	3.20
OEUR	2.64	4.57	7.68	6.94
OFIC	1.32	0.02	0.07	-
PAUR	0.94	0.61	1.18	1.05
PMAX	3.21	0.14	1.31	1.55
PROT	0.75	0.93	1.73	1.01
PVER	4.34	9.29	12.66	15.83
RLON	1.32	18.96	9.61	8.49
ROBO	0.75	0.09	-	-
RREF	0.75	2.14	3.80	3.73
SAFR	-	-	-	-
SEDG	-	-	-	-
SFIM	9.62	0.01	-	-
SISA	2.64	-	-	-
SMYR	2.64	14.19	3.60	4.53
TCAP	-	0.07	-	-
TTRI	7.17	0.11	1.24	0.67
ZCAP	-	0.20	0.21	0.17
Other	4.53	-	-	-

The DWR assumes that the three species contributing most to the total above ground biomass within each quadrat on average account for 70, 20 and 10% of that biomass. It is generally accepted that inaccuracies from this assumption are compensated for by this speedy technique, which allows the comprehensive survey of vegetation spatial heterogeneity within a brief time period. DWR was taken as a balanced estimate of abundance because savanna tree morphology was considered sufficiently consistent across species.

How representative the observations of individual goats with associated locations (N=1446) were as an estimate of diet selection by the whole herd (N=17019) was tested by application of a two-tailed paired t-test to the percentage of observations made of feeding for each species. For the 24 species appearing in both data sets, the t-test showed no difference between observations made for individuals and for the whole herd (pooled mean=4.19%, t_{23}= 0.046, P= 0.96).

The transect analysis (Appendix 3) showed a shift in diet composition between surveys. The above t-test showed that the selection of plant species within the transect area was representative of diet selection within the paddock as a whole. This implied that a similar change in diet would be expected for the paddock-wide data set because of the relationship between defoliation score and feeding duration (see Section 2.4.3). this expectation was tested using a REML analysis of the browsing duration observations recorded throughout the paddock. The explanatory variables used in the mixed model were tree species (`sel`) and trial day (`date`), and the interaction term `sel.date` that would be expected to show a temporal change in species selection.

The transect data had also been used to test the scale of diet selection by the goats. The analysis had shown that the experimental method was only ale to detect selection at the scale of the individual plants and not at a larger scale as categorised by plant association with community subtype. This finding for the transect data had been further supported in the paddock-wide data at three levels of amalgamation for community subtype (see Section 2.4.4). However, this particular analysis had summed the data across all trial days, thereby failing to account for temporal variation in selection at the community scale, which may have accompanied the temporal variation in selection at the individual scale. REML analysis was able to include the interactions between community (`com`) and `sel` and `date`, that would have descried these effects. The REML output was as follows,

```
*** Estimated Variance Components ***

Random term                Component        S.e.

goat                            0.020       0.024
```

```
*** Deviance: -2*Log-Likelihood ***

                   Deviance   d.f.

                     735.76   461


*** Wald tests for fixed effects ***

   Fixed term              Wald statistic      d.f.    Wald/d.f.    Chi-sq prob

* Sequentially adding terms to fixed model

   com                           343.87          24        14.33       <0.001
   sel                            46.96          21         2.24       <0.001
   com.sel                       518.77         225         2.31       <0.001
   sel.date                      914.83         155         5.90       <0.001
   com.date                       90.11         103         0.87        0.814
   com.sel.date                  144.65         159         0.91        0.786
```

The REML result for a significant interaction term `sel.date` supported the finding that the goats exhibited a varying preference for some species, as mentioned above. This change in diet during the course of the experiment may have been ascribed to the association of tree species with plant communities as indicated by the significant interaction term `com.sel`, however, for this to be true, it would need to have been accompanied by a temporal change in community selection, but `com.date` is not significant. More importantly, `com.sel.date` is not significant showing that the temporal variation in diet could not have been due to plant associations, or the clustering of species. The significant main effect `com` indicated that selected feeding sites receiving differing levels of feeding time were sufficiently clustered to be spatially constrained within areas bounded by identified community subtypes. This effect was irrespective of tree species and did not imply collections of tree species that matched the identified community subtype compositions. In subsequent analyses, clustering of feeding sites was confirmed in the spatial point pattern, and this indicated a patch structure (see Section 2.4.5), but given the findings here, it must be concluded that these resulted independent of the identified community distribution. Additionally, the maximum discernible patch size was in the order of 1000m^2, which was small compared to the mean community subtype area (mean=7337 m^2, standard deviation= 7483 m^2, skewness= 1.6, harmonic mean=4230 m^2, interquartile range= 8430 m^2. See Section 2.4.1 for an explanation of the advantages of alternative measures of dispersion).

A5 Appendix 5: Poster presented to IRC 2001 Pretoria, SA

1

Spatial impacts and the characterisation of resource use in a heterogeneous landscape

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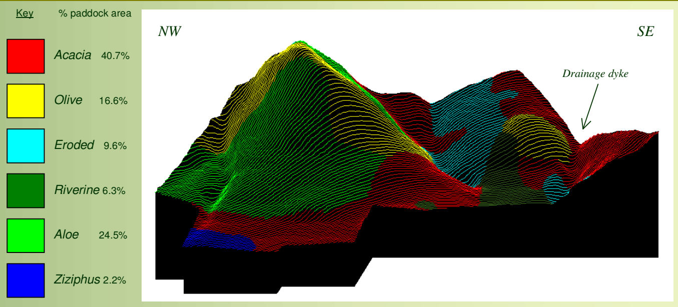
Introduction

Highly spatially variable environments pose animals with diet selection decisions that need to account for the patchy nature of their resource. Improved rangeland management would result from being able to predict patterns of animal utilisation of such vegetation. Whilst progress is being made in the comprehension of large scale influences (*e.g.*, location of drinking water, landscape topography), little is known about how these integrate with smaller scales. It is likely that animals view landscapes in differing ways, depending on the scale that processes operate. Identification of the appropriate scale at which a species is affected by the spatial heterogeneity of a resource requires characterisation of the resource spatial structure, independent of our own biases. We tend to view landscapes in terms of vegetation communities, whilst the appropriate unit for animal perception remains unclear. This poster describes a study of foraging behaviour carried out as a method by which to associate animal activity with space use as an independent estimate of spatial heterogeneity.

Method

Trials were carried out between 08/06/98 and 21/07/98 in a 19.8ha section of the Lovedale Camp, on the research farm belonging to the University of Fort Hare, in the eastern Cape, South Africa (32°47’S, 26°51’E). The long-term (1970-1996) mean annual rainfall is 620mm of which two-thirds typically falls between October and April. Only 347mm fell during 1997/8, the year preceding the experiment.

The experimental paddock was situated NW to SE across the undulating south escarpment of Sandile’s Kop, an approximately 150m-high outcrop (649.4m a.s.l.). The slope of the scarp was steepest at its NW end (20-40°) and shallowest at its SE end (5-20°). Loam soils derived from underlying shale rock were punctuated by a dolomite dyke which ran the length of the paddock, parallel to the slope, and a drainage channel which cut the SE end of the paddock, perpendicular to the slope.



Experimental paddock digital elevation model constructed from a contour plot used in conjunction with a map of plant communities showing the community types present and the percentage contribution to the paddock area.

Animals

A mixed herd of approximately 120 Nguni and Boer goats were used from which 30 individuals were marked for identification. During the course of the 6 weeks of trials, the herd was introduced into the paddock at the same entry point each day and allowed to range freely until collection, typically 6 hours later, in total accumulating an estimated 260 grazing hours per individual.

On 14 days during this period continuous animal locations for the marked individuals were recorded using a Global Positioning System (GPS).

Concurrent with the measurement of an animal location, diet selection was also recorded. The duration of feeding activity was taken as the interval between the times that were automatically associated with the GPS recordings. This is based on the assumption that the previously recorded time was an unbiased estimate of the commencement of feeding by the next animal yet to be recorded.

Diet selections and non-feeding activities (locomotive and sedentary) were recorded for all 30 experimental animals at 5 minute intervals throughout the day. In total, 118 theodolite measurements, 1630 GPS measurements, 1748 diet selections and 19930 activity observations were collected.

Vegetation

The vegetation type may be described as False Thornveld (Acocks, J.P.H., 1988, *Veld types of South Africa*. Memoirs of the Botanical Society of South Africa 57).

Phytosociological communities were identified from patterns of bush canopy cover visible in an aerial orthophotograph in combination with prior knowledge of vegetation distribution. 6 main community types were identified (*above*). Species composition was recorded, ranked by contribution to aerial cover, in 50 1x1m quadrats randomly located throughout the paddock

Animal impacts

Defoliation impacts were assessed midway through (Survey I), and at the end (Survey II) of the experiment period. A tape was used to lay 20, 50m transects, spaced 10m apart, parallel to the hill slope, on a consistent 1:4 incline. The transect ends were located using the GPS. The position of each individual shrub/tree making contact with the tape was recorded along with an assessment of defoliation damage (removal of total available browse material) up to 1.5m in height, being the typical maximum extent for goats.

Defoliation was scored using a 5-point scale as follows: 0=0%, 1=1-10%, 2=11-25%, 3=26-50%, 4=51-75% and 5=76-100%. The grass layer associated with each tree scored in this way was taken as the average of four pasture disk meter measurements, each made a metre distance from the tree trunk along a cardinal bearing.

RESULTS and ANALYSES

Relating animal activity to defoliation impact

●Browsing accounted for 97.5% of the total feeding time recorded.

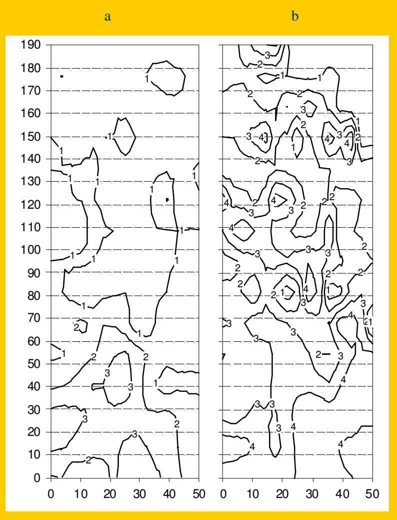
●The average time spent browsing at a feeding station ranged between 29.4 and 60.6 seconds. Average grazing activity persisted for 30.8 seconds per individual (standard deviation 46.0 seconds).

●Foraging time and defoliation impact scores both decreased with distance upslope prior to Survey I, and up to Survey II. The total minutes of foraging time accumulated for each transect before Survey I (x) showed a good correlation with the transect average defoliation impact (y) scored during Survey I (y=5.11x+2.13, R^2=0.4, *F*=10.91, P<0.01).

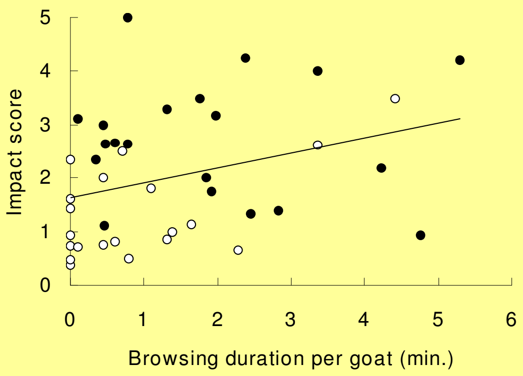
●An Olmstead-Tukey Corner Test of Association showed that defoliation impacts accumulated since Survey I were positively related with accumulated foraging time (Quadrant sum=20.0, P<0.005).

●Overall, defoliation score (*y*) was related to minutes of browsing time spent by a goat at each transect distance (*x*) by *y*=0.28*x*+1.63 (R^2=0.12, *F*=5.12, P<0.05; *right*).

●The overall average of 38.7 seconds (standard deviation 59.9 seconds) was equivalent to the 11-25% defoliation category (impact score 1).



Contour plot showing distribution of impact scores (contour labels) collected within the 200x50m transect area during a) Survey I and b) Survey II.



Relationship between defoliation impacts and total time spent foraging by goats in the transect area, before (O) and after Survey I (●).

Spatial impacts

●Analysis of the transect data using a residual maximum likelihood (REML) method showed that tree species within transects were shown to account for most of the variation in impact for either survey (*F*=23.68, df=14, P<0.001), and that there was no effect of community association (*F*=1.4, df=3, P=0.23).

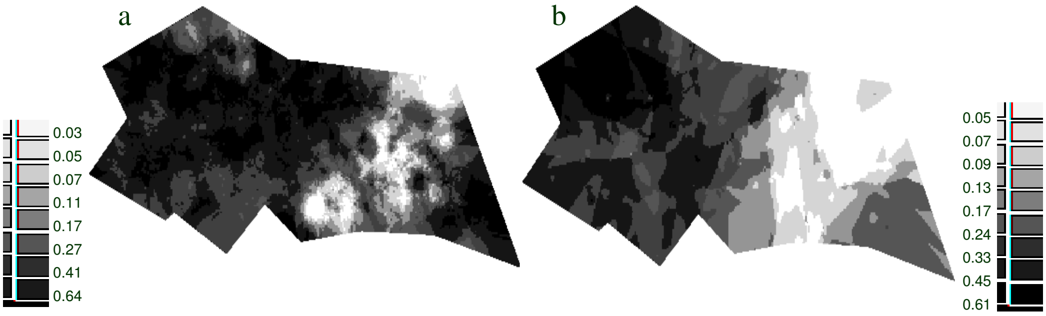
●The goats expanded the range for their foraging activity on the slope (from between 0.81m and 174.32m prior to Survey I, to 10.99m and 196.04m afterwards), giving a mean position further up the slope for Survey II both in terms of distance (means=60.5m and 101.7m, t_{96}=3.53, P<0.001) and altitude (means=540.9m and 549.6m, t_9=2.89, P<0.01).

●Diet selection within the transect area, as indicated by the distribution of defoliation impacts between tree species, shifted during the course of the experiment (*F*=7.68, df=14, P<0.001).

●Analysis of browsing activity in relation to quadrat composition showed that feeding time was also related to diet species (*F*=4.43, df=44, P<0.05). Grazing activity did not (P=0.6). Grass biomass did not differ between surveys (*F*=0.19, df=1, P=0.66).

●Average impacts for each transect were higher in Survey II than Survey I (paired t_{19}=8.58, P<0.001). Impact scores were higher and appeared to be concentrated higher up the slope in Survey II (*left*).

From the surfaces (*below*) it is possible to see that browsing activity was focused on the densely wooded slopes of the Kop, avoiding the eroded and riverine areas. Grazing was mainly at the NW end of the paddock.



Kriged interpolation of the log of goat activity duration showing the distribution of a) browsing and b) grazing in the paddock. The classes of activity duration range from high (darkest) to neglible (lightest) in minutes per individual.

CONCLUSIONS

The animals responded to the heterogeneity of their resources. Both analyses of transect and quadrat data showed that goat foraging behaviour was affected at the scale of individual tree species. Feeding activity was not related to the identified plant communities. Animal behaviour varied over time, subsequently impacting areas of lower initial defoliation. Consequently, impacts from herbivory appear to be distributed such that they mirror the distribution of the resources. Browsing results in the generation of spatially non-random impact patterns as an response to the local scale, on a tree-to-tree basis. Clumped resources in the landscape give rise to the concentration of foraging activity, and the concentration of defoliation impacts. The spatial character of these impacted regions may not be easily quantifiable, but their visualisation is achievable using geostatistical methods.

Acknowledgements

The authors would like to thank the following for their invaluable help during the experiment. Data collection was by Wellington and his team, including Mweli, MPendu and James who also assisted with GPS measurements. The Departments of Geology and Geography at the University of Fort Hare supplied GPS and surveying equipment and with advice on their use. Tony Palmer provided an aerial infrared photograph of the study site. Nick Colgrave, Trimble Navigation Europe Limited (UK), Optron (SA) and Telkom (SA) contributed towards assessment of the GPS accuracy. Craig Morris and Tony Hunter gave advise on statistical analysis. Hilary Third helped to capture the large volume of data. This work was supported by the UK Royal Society and NRF Link Programme.

A6 Appendix 6: Semi-arid grazing system model software

This is a brief, mainly diagrammatic, description of the spatial extensions to the model of a semi-arid grazing system detailed in Derry (1998), Illius *et al.* (1998), Illius & Gordon (1999) and Illius *et al.* (2000). This information is intended to explain the program architecture design based on the abiotic and biological components detailed in the main text. The following description does not conform to any industry standard, and is not a technical internal documentation. However, what is presented here should be sufficient to provide an overview of the program development and the structure of the resulting application (SimSAGS3.1), using some summarized diagrammatic inheritance diagrams which are included to highlight the spatial object pointer mechanism that was used.

A6.1 Program structure

Model 3 is a systems model of semi-arid grazing. The programming project comprised modules for each major component of the model giving adaptability of the programming code and reducing the size (footprint) of the resulting executable application. Each module was a 32-bit windows dynamic link library (DLL) containing a data class interfaced with the program hub via the following class import and export protocol contained in sagscls.defs,

```
//---------------------------------------------------------------------------
/*  _sagsclss.def
    Common definitions for pointer size and calling conventions.
*/
//---------------------------------------------------------------------------
#if !defined(___SAGSDEFS_H)
#define ___SAGSDEFS_H
//---------------------------------------------------------------------------
#    if defined(_SAGSCLASSDLL)
#      define _SAGSCLASSTYPE __declspec(dllexport)
//---------------------------------------------------------------------------
#    else
#      define _SAGSCLASSTYPE __declspec(dllimport)
//---------------------------------------------------------------------------
#    endif
//---------------------------------------------------------------------------
#endif  /* ___SAGSDEFS_H */
//---------------------------------------------------------------------------
```

This protocol allowed the necessary communication throughout the application for sharing of single instances of object data and module control via the program hub. The overall relationships between the hub and the other main components of the model are shown in Fig. A6.1.

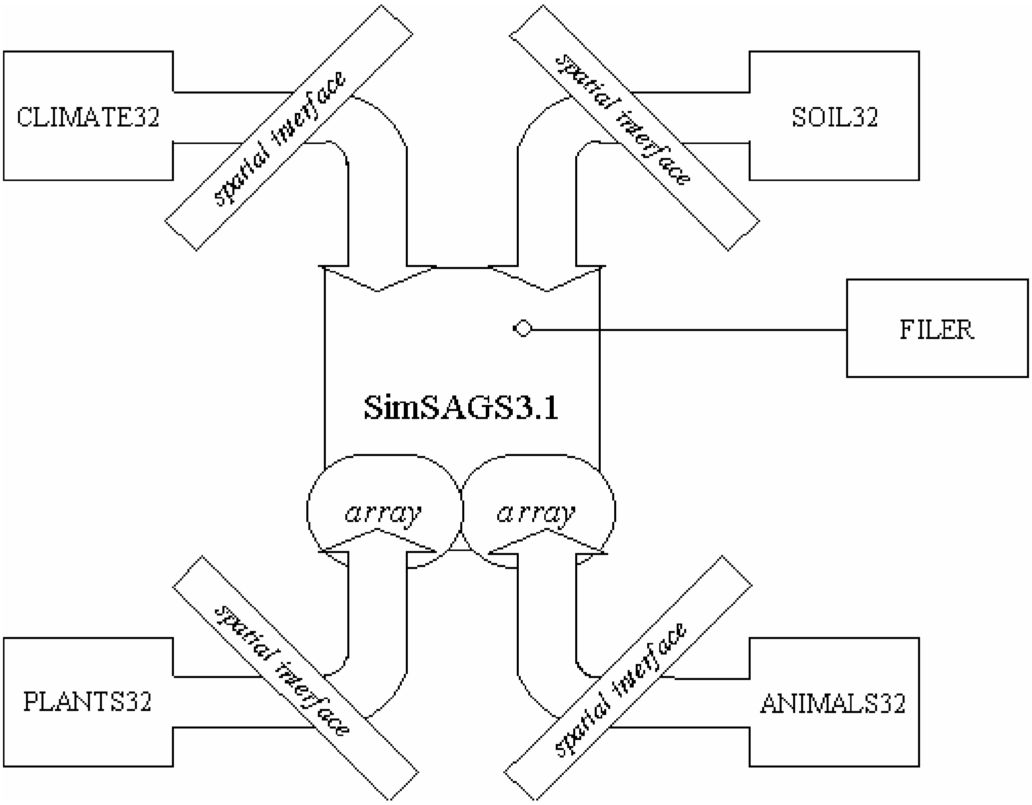


Fig. A6.1: Basic structure of the model. The *Filer* class contained utility functions for file handling. All modules were moderated by the program hub to share a single instance of the filer object. More details of the array structures used to house differing instances of the plants and animals modules can be found in Derry (1998).

The spatial interface between each module and the program hub was based on the same spatial class specification *spatial* inherited from an implementation of a grid-based data storage template, *spGrid*.

```
//---------------------------------------------------------------------------
#ifndef SPATIAL_H
#define SPATIAL_H
//---------------------------------------------------------------------------
#include "spGrid.h"
#include "sagscls.defs"
//---------------------------------------------------------------------------
template <class T>
class _SAGSCLASSTYPE spatial : public spGrid<T> {
public:
spatial(int, int, …);
~spatial();
T* cell(int, int);
...
};
//---------------------------------------------------------------------------
#include "spatial.cpp"
//---------------------------------------------------------------------------
#endif
//---------------------------------------------------------------------------
```

A class template (also called a generic class or class generator) allows definition of a pattern for class definitions of undefined data type T. This allowed great flexibility when handling many different data types as the occupying data type need not be declared until runtime. s*pGrid* used this flexibility to allow generation of grids for all the spatial data types in the model. Pointers to individual objects of each type were stored in the C++ Standard Template Library (STL) container class called a vector.

```
//---------------------------------------------------------------------------
#ifndef SPGRID_H
#define SPGRID_H
//---------------------------------------------------------------------------
#include <vector>
#include "sagscls.defs"
//---------------------------------------------------------------------------
using std::vector;
//---------------------------------------------------------------------------
template <class T>
class _SAGSCLASSTYPE spGrid {
private:
vector<T*> vt;
public:
spGrid();
spGrid(…);
~spGrid();
int rows;
int columns;
bool create(int, int);
T* element(int, int);
...
};
//---------------------------------------------------------------------------
#include "spGrid.cpp"
//---------------------------------------------------------------------------
#endif
//---------------------------------------------------------------------------
```

Vectors are a sequence that supports random access iterators. That is, any element could be referred to, and the data retrieved, without iterating through the complete data structure. Dereferencing a vector element returned a const T&, which was the stored object pointer. Thus a grid of cells was a 2-dimensional map of object pointers allowing individual grid cells to be referenced by column and row, by translation from a 2-dimensional coordinate system into the unidimensional memory index of the linear data storage array underlying the spatial grid,

```
template <class T>
T* spGrid<T>::element(int column, int row)
        {
         return &(*vt[row*columns+column]);
        }
```

A6.2 Climate and Soil modules

The *Climate* and *Soil* modules were extended using the spatial template class *spatial*. Geographical variations in rainfall could be achieved by adjustment of the input rainfall data according to the modifiers in a text 'flat file' or a raster GIS map. Similarly, soil topography could be defined by writing to a single altitude class member within each soil object.

A6.3 Plant module

There were also few modifications to the vegetation component of the model. Using *spatial*, each cell was simply populated with a single object pointer to an object of each modelled plant type. Plant growth per cell (and therefore woody-grass ratio) was determined by soil moisture, and spatial variation in growth between cells arose from surface water runoff according to landscape topography. Seed dispersal, incidence and shading were not tackled explicitly, nor fire, therefore competition was for soil moisture alone. This is in contrast to the rules for colonization used by Jeltsch *et al.* (1997), where introduction of any new vegetation was prohibited until extinction of the occupying species. This suggests that the rules for interspecies competition of moisture within two soil layers are partially nullified and only influence homogenous grid cells by interaction with neighbouring grid cells. Furthermore, there is little evidence that competition for soil moisture outside topsoil has an appreciable influence on vegetation dynamics (Scholes & Walker 1993, Seghieri 1995, Mordelet *et al.* 1997). Rainfall intensity and soil properties determine the ratio of water in the topsoil, as compared to that in the subsoil, and this has been suggested as an explanation of the balance between herbaceous and woody species (Knoop & Walker 1985).

A6.4 Animal module

To incorporate spatial features of animal foraging, the existing herbivore class was repackaged and extended with a spatial foraging module that dealt with the assessment and selection of spatially distributed forage resources (*Foraging*), and the associated herd movements entailed in accessing those locations (*Commuting*).

Because the animal herds were free to travel across the grid and were not constrained to any single grid cell, it was not appropriate to adopt the same object pointer mechanism as used for the other model components. Instead, a single spatial grid for each animal type was populated with a forage parameter that was used to differentiate between grid cells, as a basis for diet selection (*CommutingCells*). Because of its cursory similarity to a popular video game, this module was nicknamed *PACMAN.*

The assumptions discussed above, based on the fieldwork described in Chapter 2, suggested a natural organization of these processes into a nested format such that the spatial diet dictated herd movement as a function of diet selection and as a facet of spatial foraging (see Fig. A6.2).

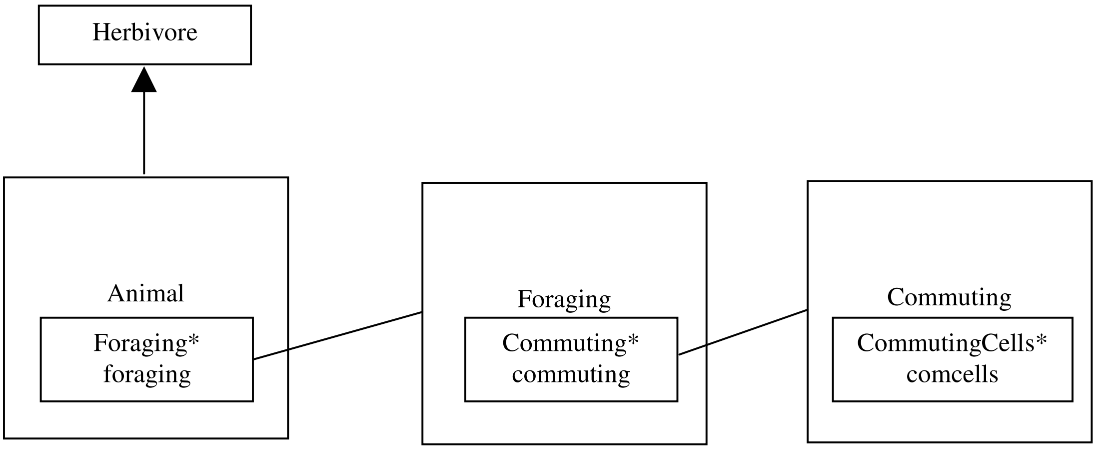


Fig. A6.2: Nested relationships in the animal spatial foraging module (*PACMAN*).

PACMAN also contained the programming code for animal watering behaviour. The location of a single watering point was defined, typically central in the landscape, from which the herd would start each foraging bout during the dry season. Travel from the watering point to the first selected diet grid cell (not necessarily the same as the watering point nor a neighbour cell), and return travel to the watering point at the end of the day involved time and energy costs. Both were included in the time and energy costs for the whole day. During the wet season there were no water-related costs, as the herd would continue their foraging from the last cell visited during the previous day's foraging bout.

A6.5 Module structure

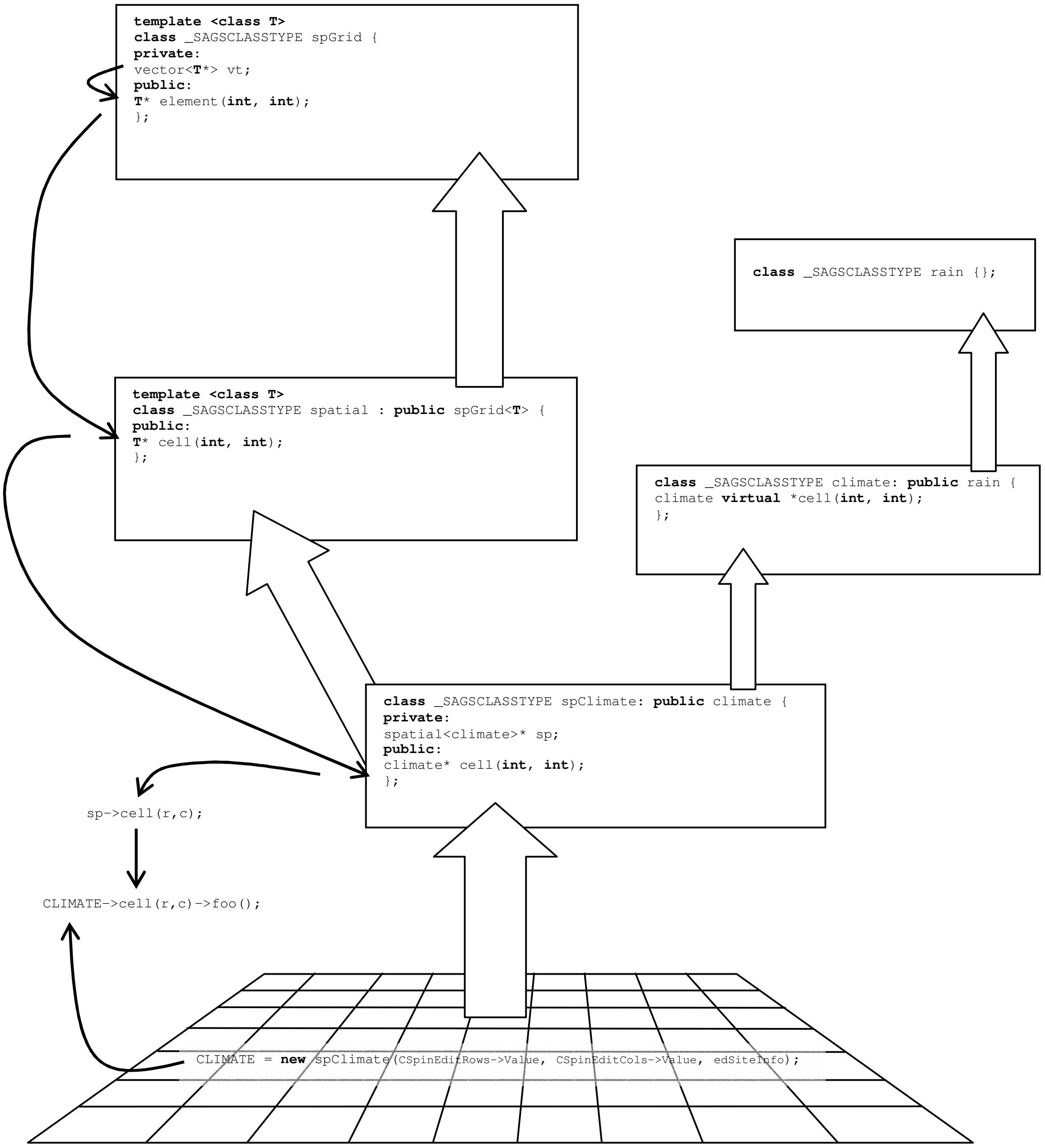
The structure of each module and, where appropriate, their associated container classes (arrays), follow in a series of diagrammatic class diagrams and object class hierarchy diagrams. A hierarchy diagram illustrates the parent/child inheritance and sibling relationships between classes. Public members and methods are inherited down the inheritance tree (which is denoted by a reverse arrow meaning "inherited from"). For simplification, all classes are shown the same; so base classes, abstract classes and their pure virtual methods are not highlighted. The series of figures is as follows,

Fig. A6.3	Spatial climate object
Fig. A6.4	Spatial soil object
Fig. A6.5	Vegetation container object
Fig. A6.6	Spatial plant container (array) object
Fig. A6.7	Plant object
Fig. A6.8	Spatial plant object
Fig. A6.9	Spatial herbivores container (array) object
Fig. A6.10	Herbivores object
Fig. A6.11	Spatial herbivores object
Fig. A6.12	Spatial commuting object
Fig. A6.13	Spatial foraging object
Fig. A6.14	Spatial objects in "foraging path" (*PACMAN*)

SimSAGS3.1

Fig. A6.3: *SPATIAL* CLIMATE OBJECT

CLASS HIERACHY



```
template <class T>
class _SAGSCLASSTYPE spGrid {
private:
vector<T*> vt;
public:
T* element(int, int);
};
```

```
class _SAGSCLASSTYPE rain {};
```

```
template <class T>
class _SAGSCLASSTYPE spatial : public spGrid<T> {
public:
T* cell(int, int);
};
```

```
class _SAGSCLASSTYPE climate: public rain {
climate virtual *cell(int, int);
};
```

```
class _SAGSCLASSTYPE spClimate: public climate {
private:
spatial<climate>* sp;
public:
climate* cell(int, int);
};
```

```
sp->cell(r,c);
```

```
CLIMATE->cell(r,c)->foo();
```

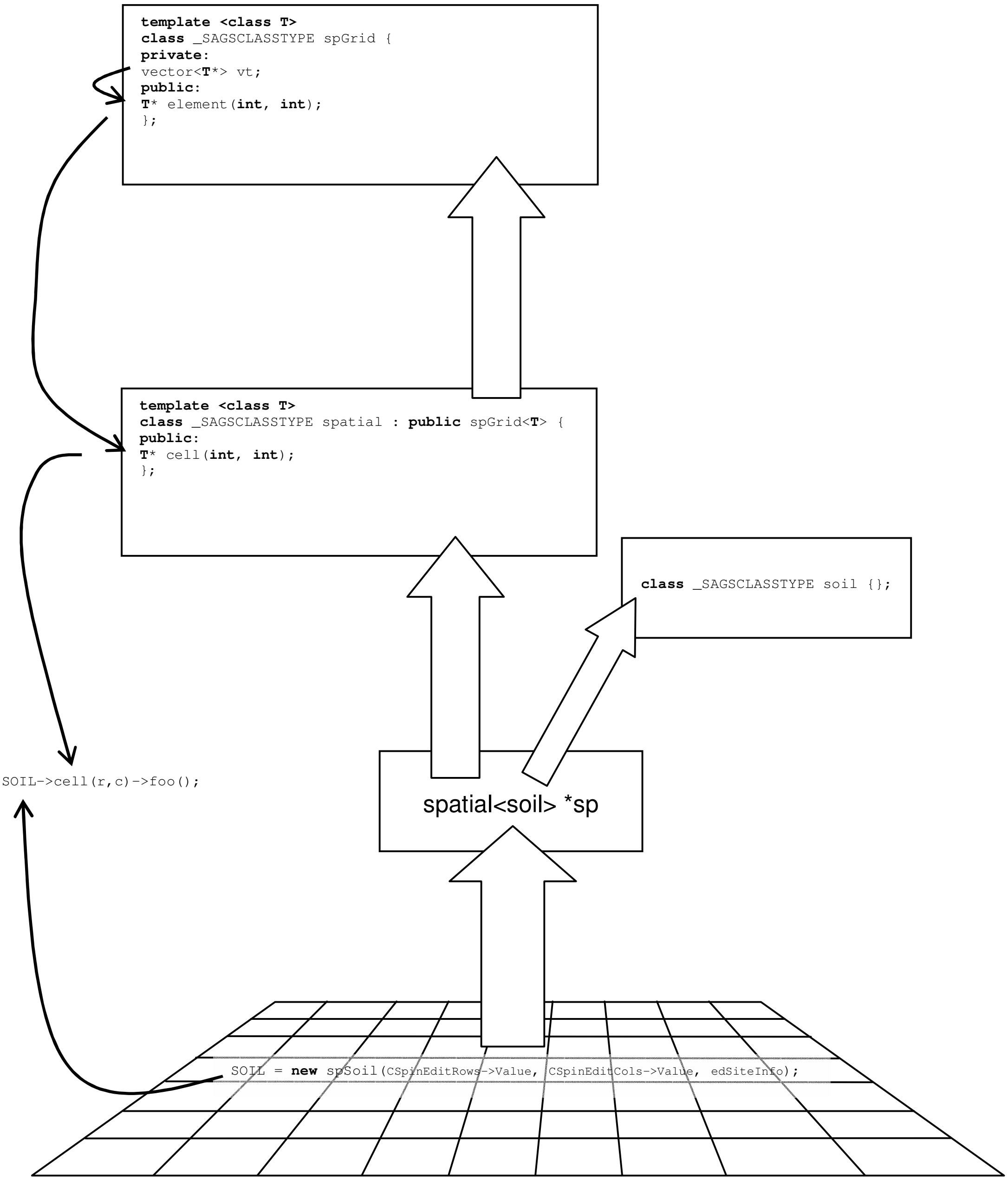
```
CLIMATE = new spClimate(CSpinEditRows->Value, CSpinEditCols->Value, edSiteInfo);
```

SimSAGS3.1 spatial CLIMATE grid

SimSAGS3.1

Fig. A6.4: *SPATIAL* SOIL OBJECT

CLASS HIERACHY



```
template <class T>
class _SAGSCLASSTYPE spGrid {
private:
vector<T*> vt;
public:
T* element(int, int);
};
```

```
template <class T>
class _SAGSCLASSTYPE spatial : public spGrid<T> {
public:
T* cell(int, int);
};
```

```
class _SAGSCLASSTYPE soil {};
```

```
spatial<soil> *sp
```

```
SOIL->cell(r,c)->foo();
```

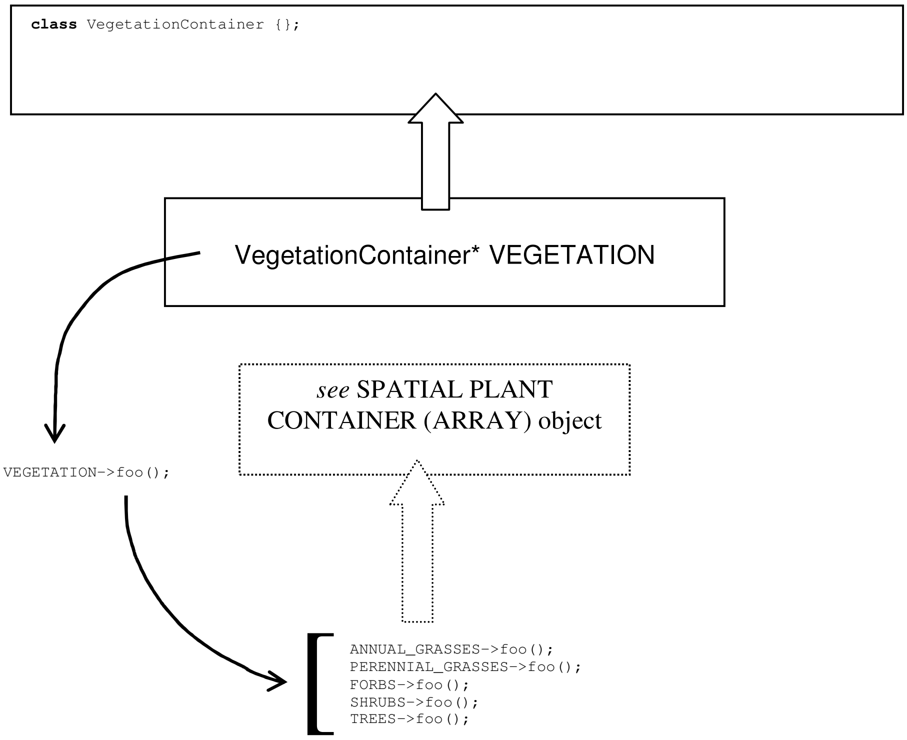
```
SOIL = new spSoil(CSpinEditRows->Value, CSpinEditCols->Value, edSiteInfo);
```

SimSAGS3.1 spatial SOIL grid matrix

SimSAGS3.1

Fig. A6.5: VEGETATION CONTAINER OBJECT

CLASS HIERACHY



```
class VegetationContainer {};
```

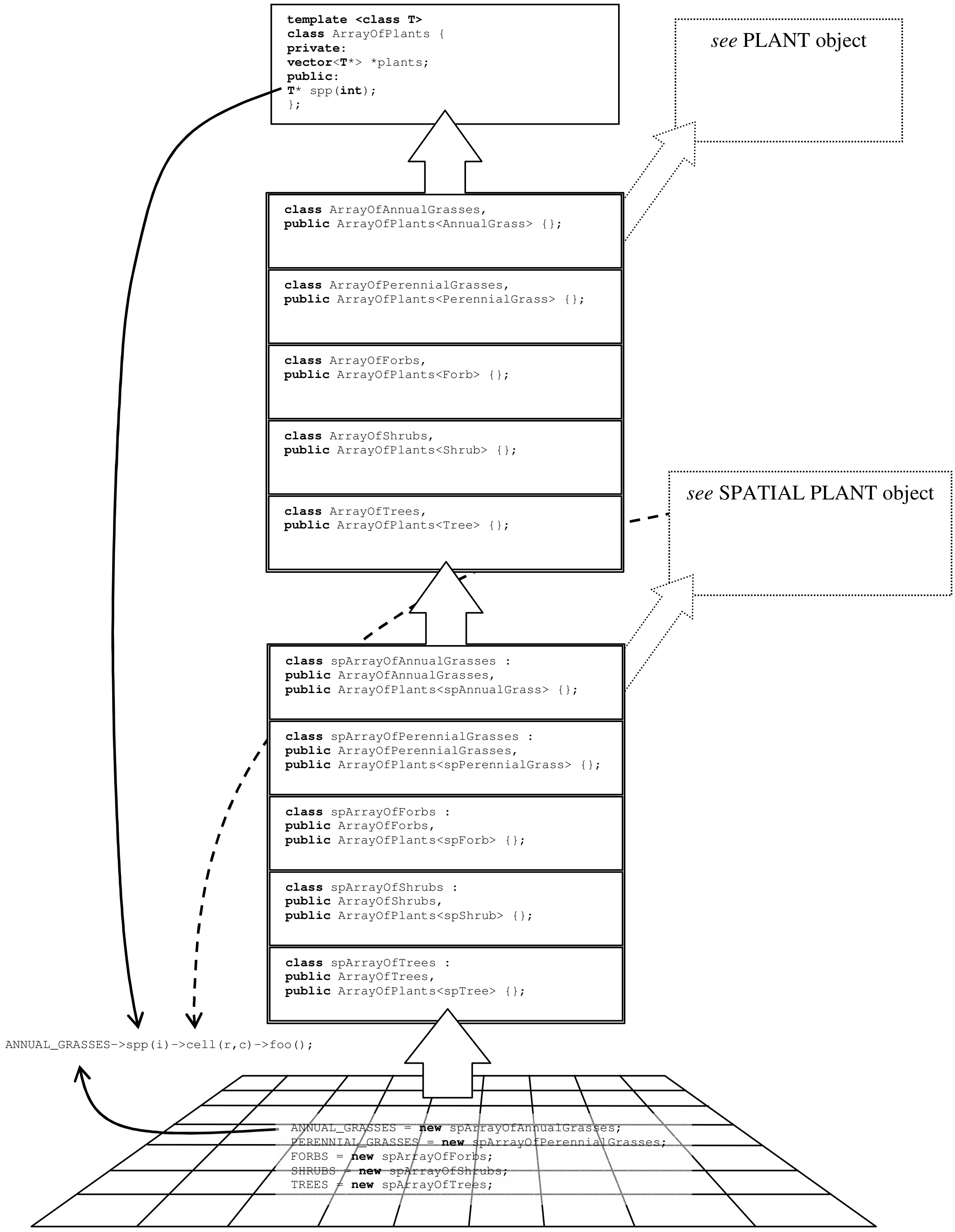
```
VEGETATION->foo();
```

```
ANNUAL_GRASSES->foo();
PERENNIAL_GRASSES->foo();
FORBS->foo();
SHRUBS->foo();
TREES->foo();
```

SimSAGS3.1

Fig. A6.6: *SPATIAL* PLANT CONTAINER (ARRAY) OBJECT

CLASS HIERACHY



```
template <class T>
class ArrayOfPlants {
private:
vector<T*> *plants;
public:
T* spp(int);
};
```

```
class ArrayOfAnnualGrasses,
public ArrayOfPlants<AnnualGrass> {};

class ArrayOfPerennialGrasses,
public ArrayOfPlants<PerennialGrass> {};

class ArrayOfForbs,
public ArrayOfPlants<Forb> {};

class ArrayOfShrubs,
public ArrayOfPlants<Shrub> {};

class ArrayOfTrees,
public ArrayOfPlants<Tree> {};
```

```
class spArrayOfAnnualGrasses :
public ArrayOfAnnualGrasses,
public ArrayOfPlants<spAnnualGrass> {};

class spArrayOfPerennialGrasses :
public ArrayOfPerennialGrasses,
public ArrayOfPlants<spPerennialGrass> {};

class spArrayOfForbs :
public ArrayOfForbs,
public ArrayOfPlants<spForb> {};

class spArrayOfShrubs :
public ArrayOfShrubs,
public ArrayOfPlants<spShrub> {};

class spArrayOfTrees :
public ArrayOfTrees,
public ArrayOfPlants<spTree> {};
```

```
ANNUAL_GRASSES->spp(i)->cell(r,c)->foo();
```

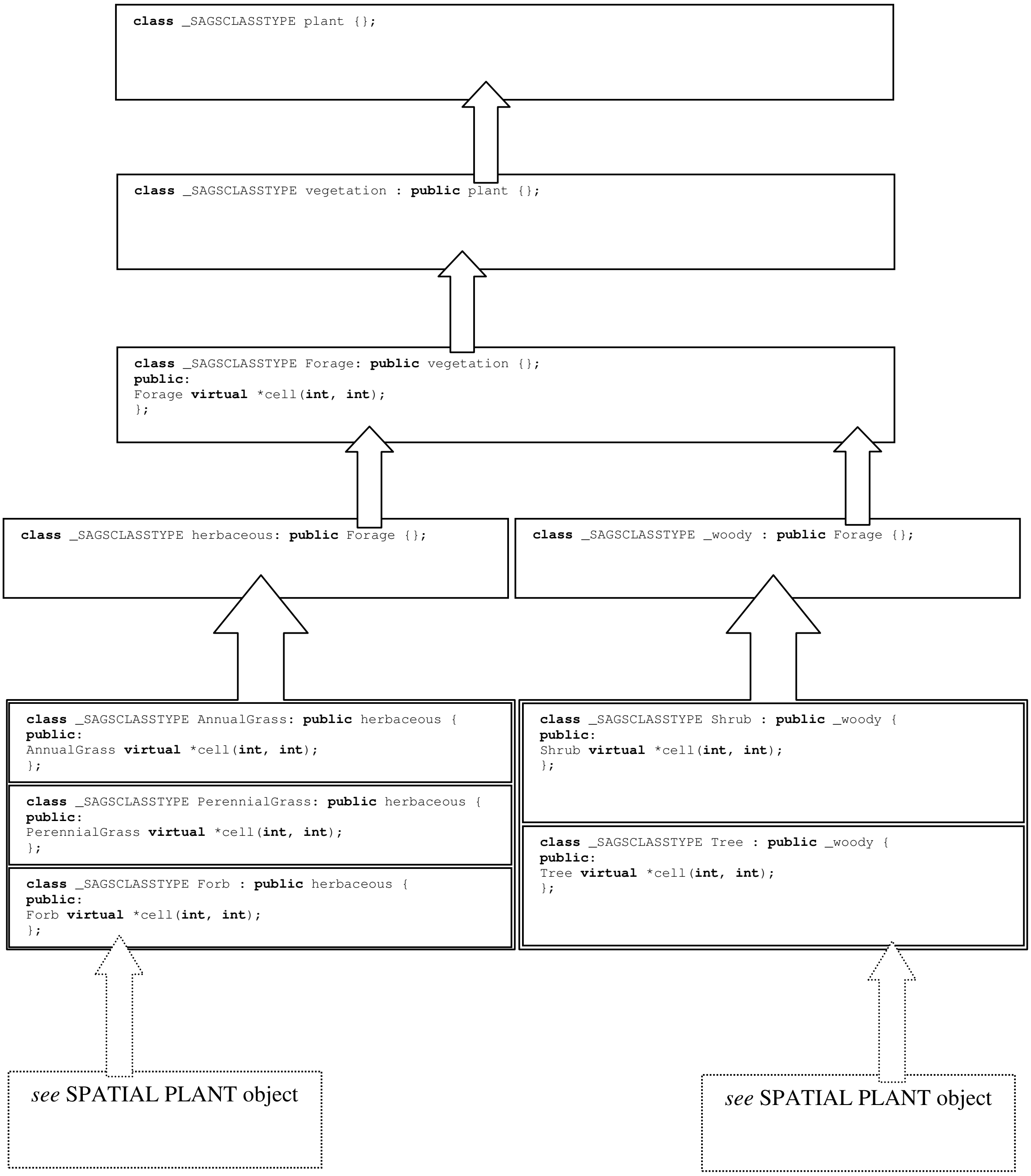
```
ANNUAL_GRASSES = new spArrayOfAnnualGrasses;
PERENNIAL_GRASSES = new spArrayOfPerennialGrasses;
FORBS = new spArrayOfForbs;
SHRUBS = new spArrayOfShrubs;
TREES = new spArrayOfTrees;
```

SimSAGS3.1 spatial PLANT CONTAINER grid

SimSAGS3.1

Fig. A6.7: PLANT OBJECT

CLASS HIERACHY



```
class _SAGSCLASSTYPE plant {};
```

```
class _SAGSCLASSTYPE vegetation : public plant {};
```

```
class _SAGSCLASSTYPE Forage: public vegetation {};
public:
Forage virtual *cell(int, int);
};
```

```
class _SAGSCLASSTYPE herbaceous: public Forage {};
```

```
class _SAGSCLASSTYPE _woody : public Forage {};
```

```
class _SAGSCLASSTYPE AnnualGrass: public herbaceous {
public:
AnnualGrass virtual *cell(int, int);
};
```

```
class _SAGSCLASSTYPE PerennialGrass: public herbaceous {
public:
PerennialGrass virtual *cell(int, int);
};
```

```
class _SAGSCLASSTYPE Forb : public herbaceous {
public:
Forb virtual *cell(int, int);
};
```

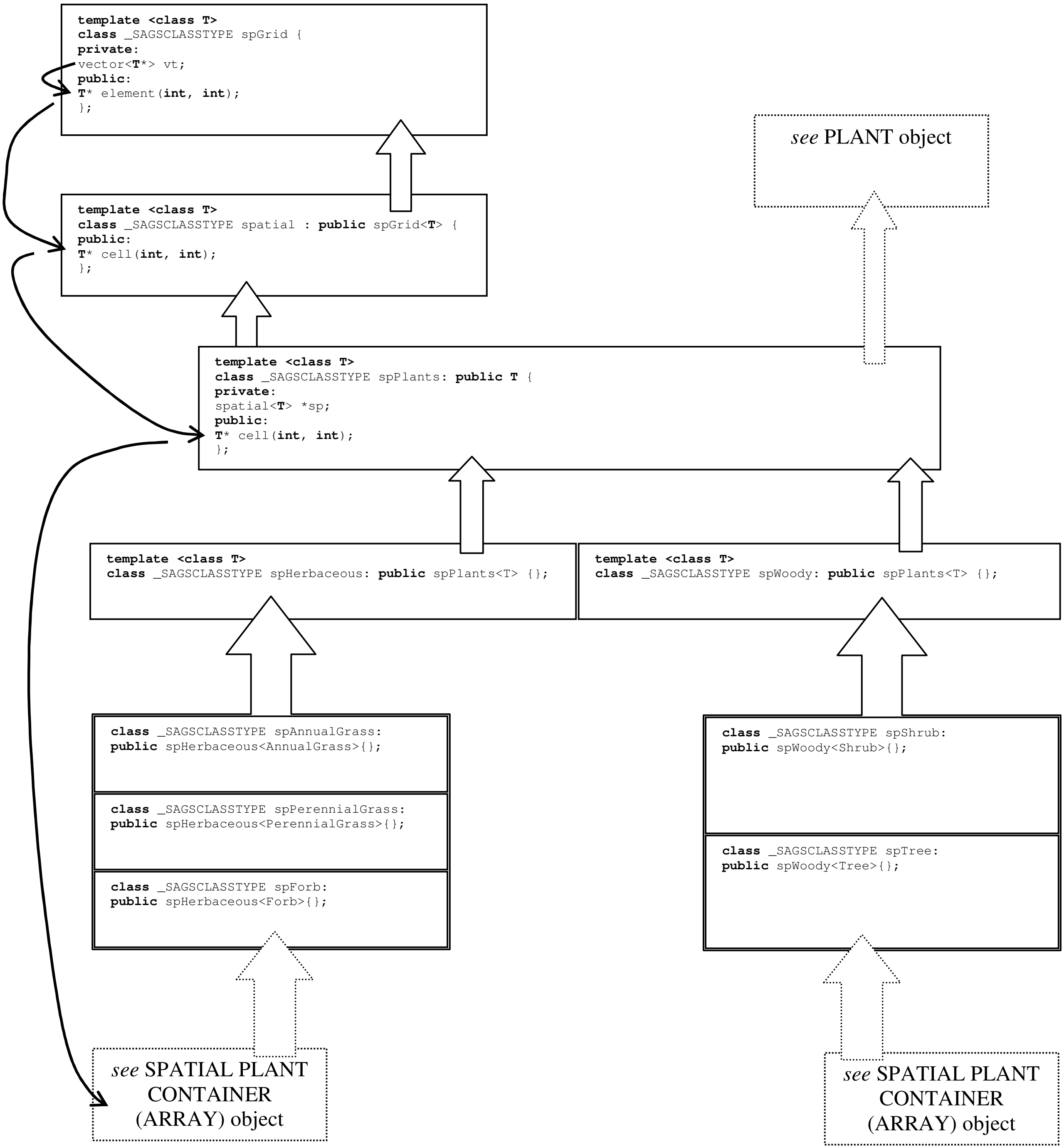
```
class _SAGSCLASSTYPE Shrub : public _woody {
public:
Shrub virtual *cell(int, int);
};
```

```
class _SAGSCLASSTYPE Tree : public _woody {
public:
Tree virtual *cell(int, int);
};
```

SimSAGS3.1

Fig. A6.8: *SPATIAL* PLANT OBJECT

CLASS HIERACHY



```
template <class T>
class _SAGSCLASSTYPE spGrid {
private:
vector<T*> vt;
public:
T* element(int, int);
};
```

```
template <class T>
class _SAGSCLASSTYPE spatial  : public spGrid<T> {
public:
T* cell(int, int);
};
```

```
template <class T>
class _SAGSCLASSTYPE spPlants: public T {
private:
spatial<T> *sp;
public:
T* cell(int, int);
};
```

```
template <class T>
class _SAGSCLASSTYPE spHerbaceous: public spPlants<T> {};
```

```
template <class T>
class _SAGSCLASSTYPE spWoody: public spPlants<T> {};
```

```
class _SAGSCLASSTYPE spAnnualGrass:
public spHerbaceous<AnnualGrass>{};
```

```
class _SAGSCLASSTYPE spPerennialGrass:
public spHerbaceous<PerennialGrass>{};
```

```
class _SAGSCLASSTYPE spForb:
public spHerbaceous<Forb>{};
```

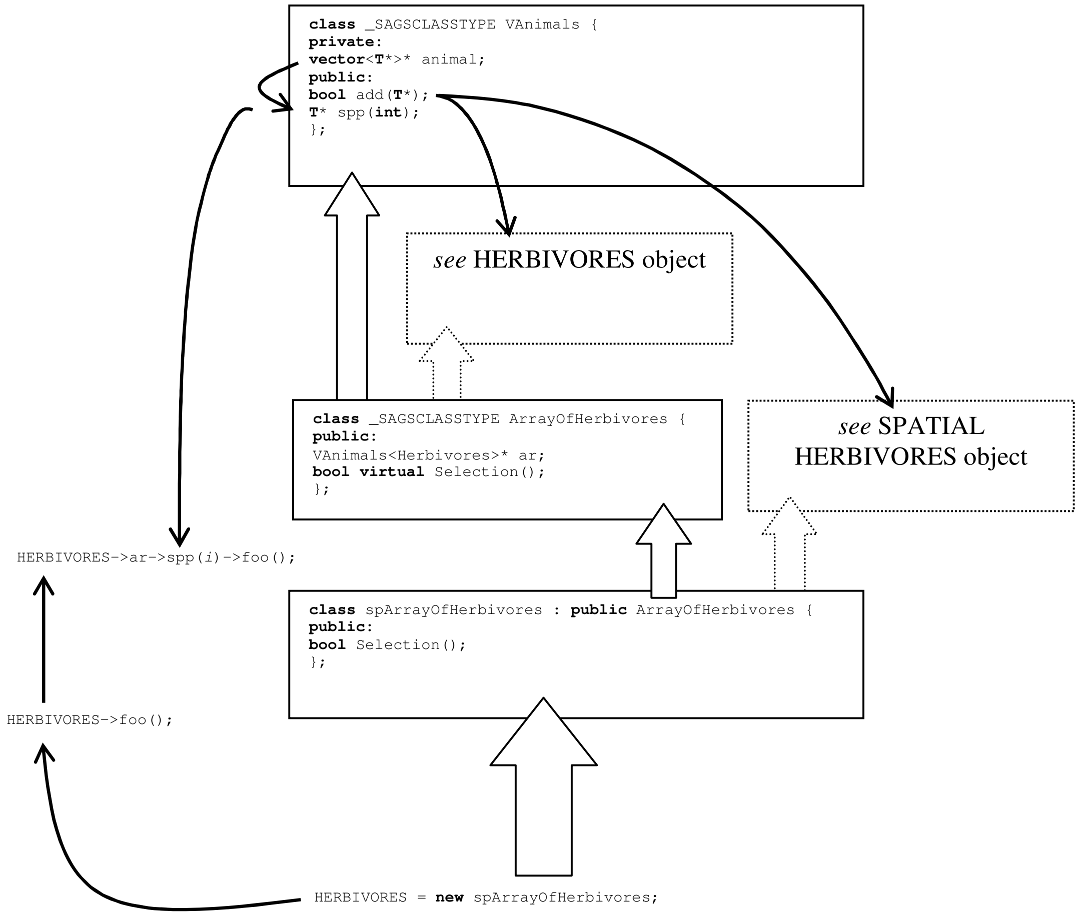
```
class _SAGSCLASSTYPE spShrub:
public spWoody<Shrub>{};
```

```
class _SAGSCLASSTYPE spTree:
public spWoody<Tree>{};
```

SimSAGS3.1

Fig. A6.9: *SPATIAL* HERBIVORES CONTAINER (ARRAY) OBJECT

CLASS HIERACHY



```
class _SAGSCLASSTYPE VAnimals {
private:
vector<T*>* animal;
public:
bool add(T*);
T* spp(int);
};
```

```
class _SAGSCLASSTYPE ArrayOfHerbivores {
public:
VAnimals<Herbivores>* ar;
bool virtual Selection();
};
```

```
class spArrayOfHerbivores : public ArrayOfHerbivores {
public:
bool Selection();
};
```

```
HERBIVORES->ar->spp(i)->foo();
```

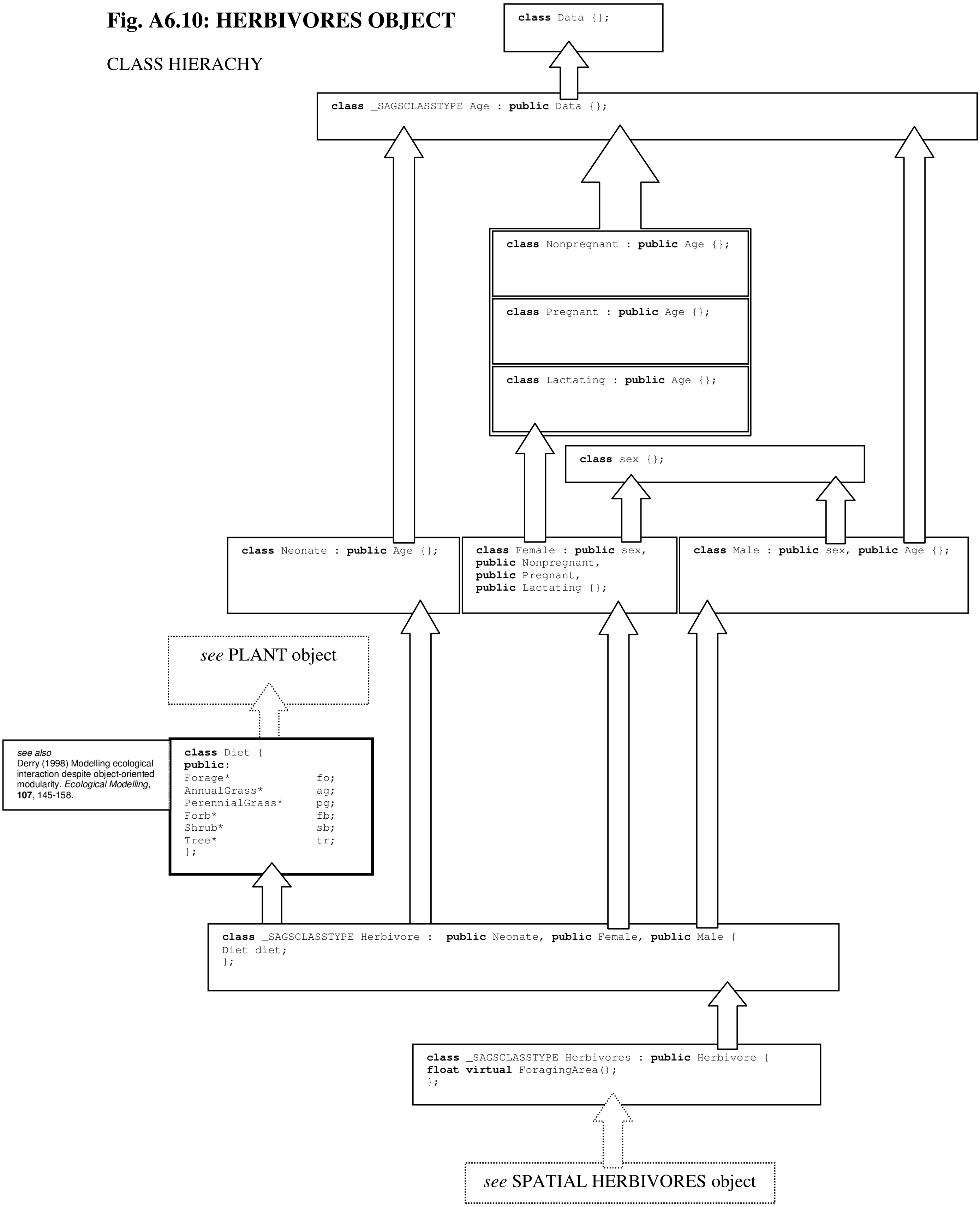
```
HERBIVORES->foo();
```

```
HERBIVORES = new spArrayOfHerbivores;
```

SimSAGS3.1

Fig. A6.10: HERBIVORES OBJECT

CLASS HIERACHY



```
class Data {};
```

```
class _SAGSCLASSTYPE Age : public Data {};
```

```
class Nonpregnant : public Age {};
```

```
class Pregnant : public Age {};
```

```
class Lactating : public Age {};
```

```
class sex {};
```

```
class Neonate : public Age {};
```

```
class Female : public sex,
public Nonpregnant,
public Pregnant,
public Lactating {};
```

```
class Male : public sex, public Age {};
```

see also
Derry (1998) Modelling ecological interaction despite object-oriented modularity. *Ecological Modelling*, **107**, 145-158.

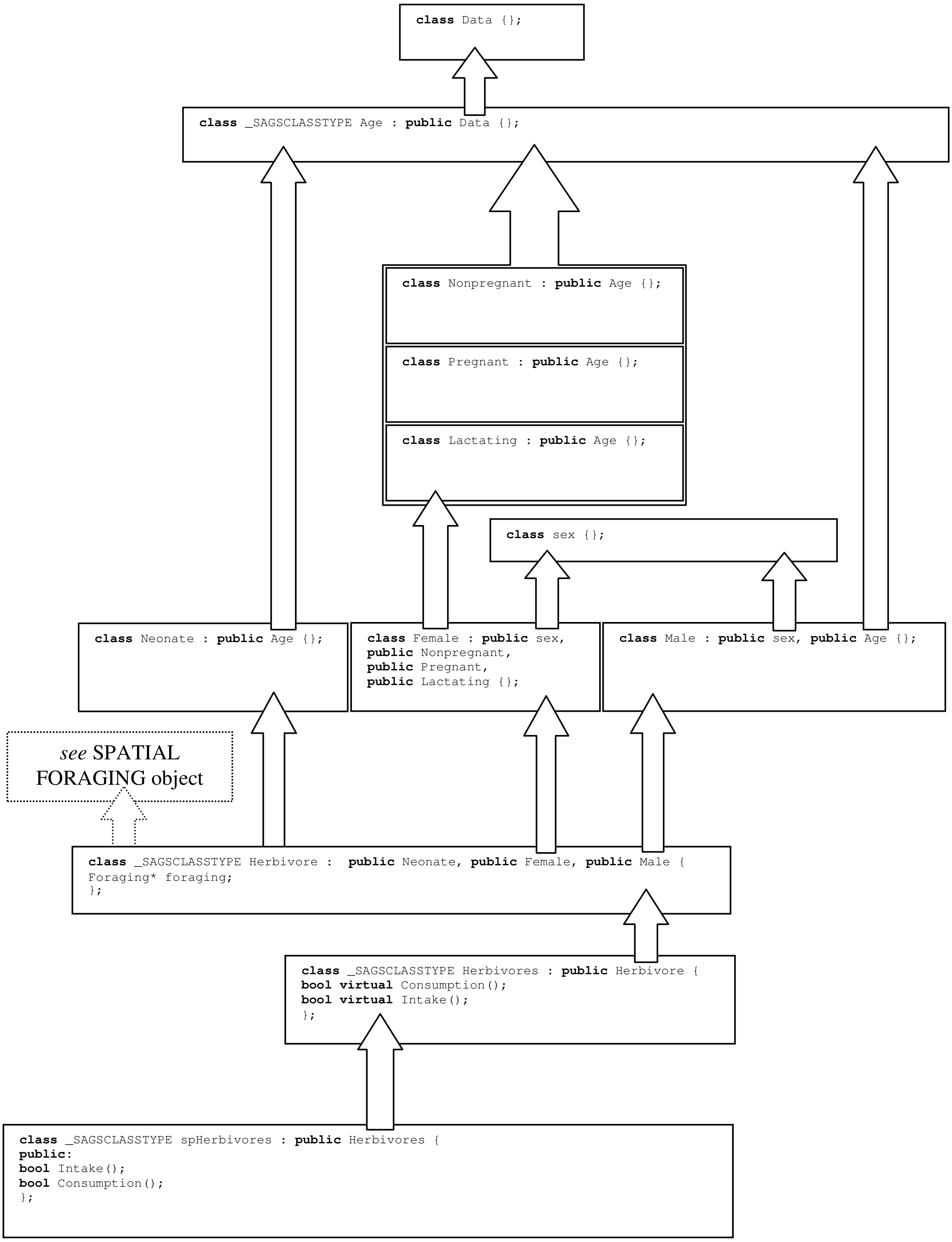
```
class Diet {
public:
Forage*              fo;
AnnualGrass*         ag;
PerennialGrass*      pg;
Forb*                fb;
Shrub*               sb;
Tree*                tr;
};
```

```
class _SAGSCLASSTYPE Herbivore :  public Neonate, public Female, public Male {
Diet diet;
};
```

```
class _SAGSCLASSTYPE Herbivores : public Herbivore {
float virtual ForagingArea();
};
```

Fig. A6.11: *SPATIAL* HERBIVORES OBJECT

CLASS HIERACHY



```
class Data {};
```

```
class _SAGSCLASSTYPE Age : public Data {};
```

```
class Nonpregnant : public Age {};
```

```
class Pregnant : public Age {};
```

```
class Lactating : public Age {};
```

```
class sex {};
```

```
class Neonate : public Age {};
```

```
class Female : public sex,
public Nonpregnant,
public Pregnant,
public Lactating {};
```

```
class Male : public sex, public Age {};
```

```
class _SAGSCLASSTYPE Herbivore :  public Neonate, public Female, public Male {
Foraging* foraging;
};
```

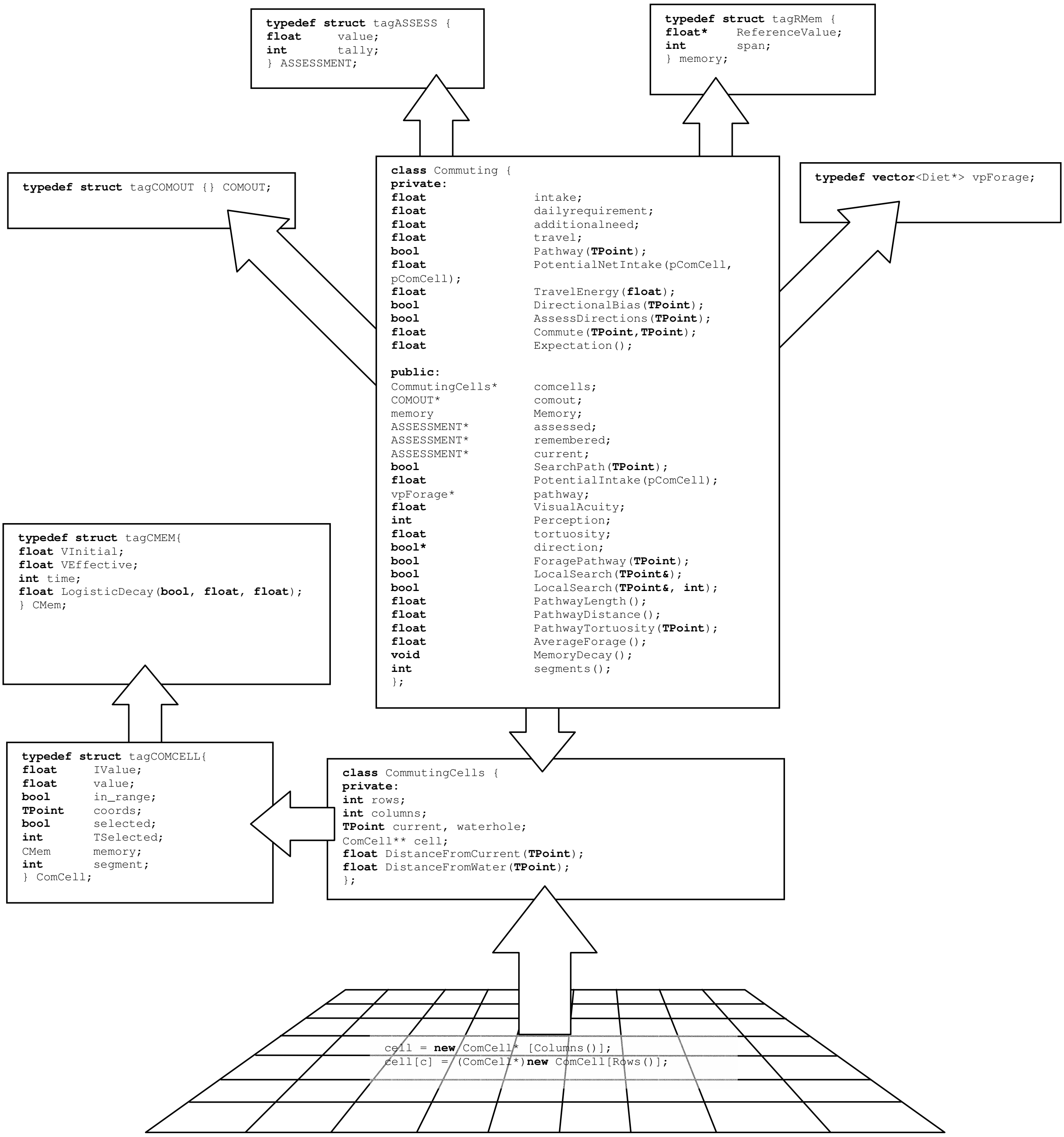
```
class _SAGSCLASSTYPE Herbivores : public Herbivore {
bool virtual Consumption();
bool virtual Intake();
};
```

```
class _SAGSCLASSTYPE spHerbivores : public Herbivores {
public:
bool Intake();
bool Consumption();
};
```

SimSAGS3.1

Fig. A6.12: *SPATIAL* COMMUTING OBJECT

CLASS HIERACHY



```
typedef struct tagASSESS {
float      value;
int        tally;
} ASSESSMENT;
```

```
typedef struct tagRMem {
float*     ReferenceValue;
int        span;
} memory;
```

```
typedef struct tagCOMOUT {} COMOUT;
```

```
class Commuting {
private:
float                  intake;
float                  dailyrequirement;
float                  additionalneed;
float                  travel;
bool                   Pathway(TPoint);
float                  PotentialNetIntake(pComCell,
pComCell);
float                  TravelEnergy(float);
bool                   DirectionalBias(TPoint);
bool                   AssessDirections(TPoint);
float                  Commute(TPoint,TPoint);
float                  Expectation();

public:
CommutingCells*        comcells;
COMOUT*                comout;
memory                 Memory;
ASSESSMENT*            assessed;
ASSESSMENT*            remembered;
ASSESSMENT*            current;
bool                   SearchPath(TPoint);
float                  PotentialIntake(pComCell);
vpForage*              pathway;
float                  VisualAcuity;
int                    Perception;
float                  tortuosity;
bool*                  direction;
bool                   ForagePathway(TPoint);
bool                   LocalSearch(TPoint&);
bool                   LocalSearch(TPoint&, int);
float                  PathwayLength();
float                  PathwayDistance();
float                  PathwayTortuosity(TPoint);
float                  AverageForage();
void                   MemoryDecay();
int                    segments();
};
```

```
typedef vector<Diet*> vpForage;
```

```
typedef struct tagCMEM{
float VInitial;
float VEffective;
int time;
float LogisticDecay(bool, float, float);
} CMem;
```

```
typedef struct tagCOMCELL{
float      IValue;
float      value;
bool       in_range;
TPoint     coords;
bool       selected;
int        TSelected;
CMem       memory;
int        segment;
} ComCell;
```

```
class CommutingCells {
private:
int rows;
int columns;
TPoint current, waterhole;
ComCell** cell;
float DistanceFromCurrent(TPoint);
float DistanceFromWater(TPoint);
};
```

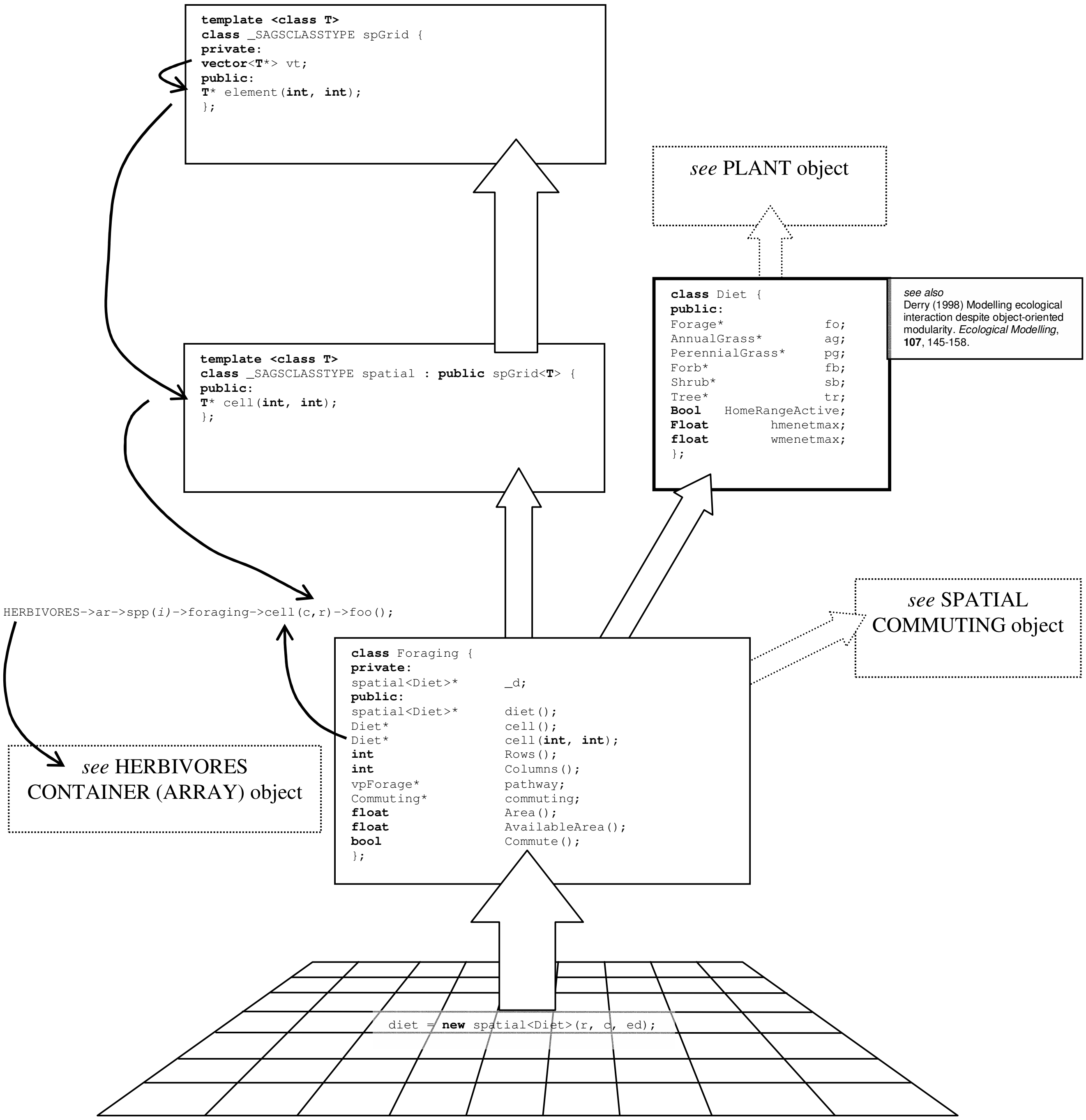
```
cell = new ComCell* [Columns()];
cell[c] = (ComCell*)new ComCell[Rows()];
```

SimSAGS3.1 spatial COMMUTING CELLS

SimSAGS3.1

Fig. A6.13: *SPATIAL* FORAGING OBJECT

CLASS HIERACHY



```
template <class T>
class _SAGSCLASSTYPE spGrid {
private:
vector<T*> vt;
public:
T* element(int, int);
};
```

```
template <class T>
class _SAGSCLASSTYPE spatial : public spGrid<T> {
public:
T* cell(int, int);
};
```

```
class Diet {
public:
Forage*                 fo;
AnnualGrass*            ag;
PerennialGrass*         pg;
Forb*                   fb;
Shrub*                  sb;
Tree*                   tr;
Bool    HomeRangeActive;
Float          hmenetmax;
float          wmenetmax;
};
```

see also
Derry (1998) Modelling ecological interaction despite object-oriented modularity. *Ecological Modelling*, **107**, 145-158.

```
HERBIVORES->ar->spp(i)->foraging->cell(c,r)->foo();
```

```
class Foraging {
private:
spatial<Diet>*       _d;
public:
spatial<Diet>*       diet();
Diet*                cell();
Diet*                cell(int, int);
int                  Rows();
int                  Columns();
vpForage*            pathway;
Commuting*           commuting;
float                Area();
float                AvailableArea();
bool                 Commute();
};
```

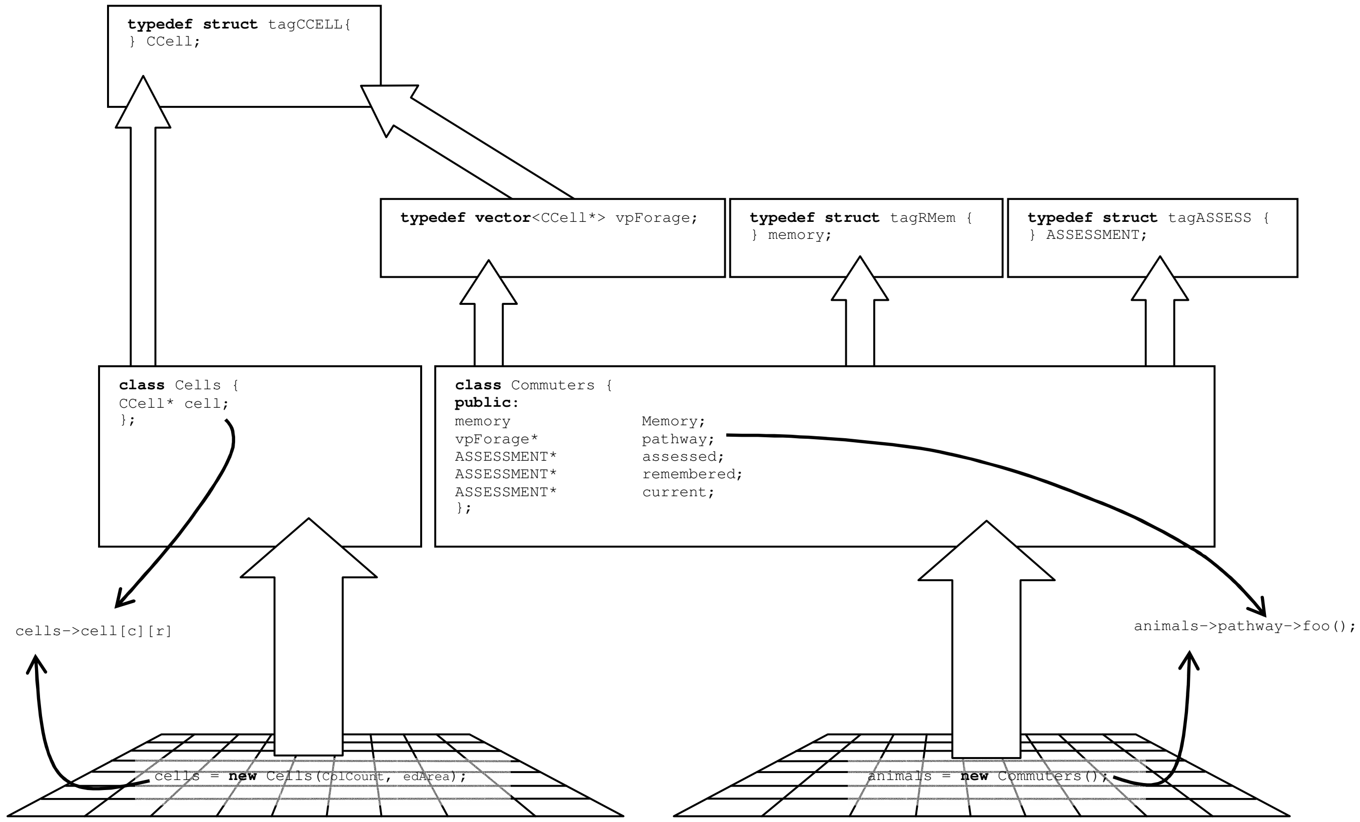
```
diet = new spatial<Diet>(r, c, ed);
```

SimSAGS3.1 spatial DIET grid matrix

SimSAGS3.1

Fig. A6.14: *SPATIAL* OBJECTS IN "FORAGING PATH" (*PACMAN*)

CLASS HIERACHY



```
typedef struct tagCCELL{
} CCell;
```

```
typedef vector<CCell*> vpForage;
```

```
typedef struct tagRMem {
} memory;
```

```
typedef struct tagASSESS {
} ASSESSMENT;
```

```
class Cells {
CCell* cell;
};
```

```
class Commuters {
public:
memory                  Memory;
vpForage*               pathway;
ASSESSMENT*             assessed;
ASSESSMENT*             remembered;
ASSESSMENT*             current;
};
```

```
cells->cell[c][r]
```

```
animals->pathway->foo();
```

```
cells = new Cells(ColCount, edArea);
```

```
animals = new Commuters();
```

PACMAN spatial CELLS grid matrix

PACMAN spatial COMMUTERS grid matrix

A7 Appendix 7: Use Biomass Rule

To provide an alternative conversion from the grid currency of potential energy intake rate into actual biomass consumed, a contingency rule was developed that could operate under low levels of resource grid heterogeneity. It also needed to be independent of energy intake rate. The solution was to redefine the grid currency in terms of forage biomass by simply allocating a portion of a cell's forage biomass for consumption if there was insufficient grid heterogeneity. This contingency conversion mechanism was called the "Use Biomass Rule", or *UBRule* for short.

To ensure that the *UBRule* would not unduly bias model performance, a sensitivity analysis using 100 day long simulations was carried out to investigate the elasticity of the threshold parameter for CV of grid heterogeneity (h) and the parameter for the fraction of biomass consumed (n).

To test the effect of the *UBRule* on dry matter intake moderated by digestive constraints, comparisons were made of model response using the ratio between daily intake and predicted intake for the herd as a measure of foraging efficiency (Table A7.1). To test the effect of the *UBRule* on metabolic energy intake moderated by metabolic constraints, comparisons were made of model response using the ratio between daily metabolic energy intake and predicted metabolic energy intake for the herd as a measure of foraging efficiency (Table A7.2). Both tables show that foraging efficiency is unaffected (highest values) for h ≥ 1% and maximal n. The *UBRule* was implemented using h = 1% and n = 50%.

	n%				
h%	0	0.01	1	10	50
0	0.952*	0.952	0.952	0.952	0.952
0.01	0.952	0.859	0.989	0.993	0.992
1	0.952	0.247	0.985	1.000	1.000
10	0.952	0.201	0.983	0.999	1.000
50	0.952	0.200	0.987	1.000	1.000

* Equation 3.8 conversion factor exclusive

Table A7.1: Effect of *UBRule* parameters on foraging efficiency of dry matter intake. The *UBRule* was inactive for h=0 and n=0. The *UBRule* was exclusive for h=0 (shaded).

	n%				
h%	0	0.01	1	10	50
0	0.208*	0.208	0.208	0.208	0.208
0.01	0.208	0.149	0.232	0.241	0.248
1	0.208	0.021	0.222	0.251	0.271
10	0.208	0.013	0.217	0.246	0.270
50	0.208	0.013	0.220	0.248	0.272

* Equation 3.8 conversion factor exclusive

Table A7.2: Effect of *UBRule* parameters on foraging efficiency of metabolic energy intake. The *UBRule* was inactive for h=0 and n=0. The *UBRule* was exclusive for h=0 (shaded).

A8 Appendix 8: *BiteRate* software

Tailor-made software (*BiteRate*, J..F.Derry, *unpublished*) was written to capture the animal bite rate data from the field tape recordings to a computer. The programming language was C++, compiled in Borland's C++ Builder 4 (Borland 1999). There was already software that could have been used (*KeyPress*, John Deag, University of Edinburgh) but it offered too detailed an interface for this simple task.

Upon listening to the tape playback, keys on the computer keyboard were pressed in correspondence with voice markers for the start and end of the sampling sequence, individual bites, and for starting and stopping travel between feeding sites. Default settings for the corresponding keys could be defined for convenience.

BiteRate wrote the time from the start of the sequence for each event to a text file along with the event code, although all that was needed for analysis was the total sequence duration and the number of bites, and bite intervals were not used.

The code is presented here in its entirety as a useful data utility.

BiteRate.h

```
//---------------------------------------------------------------------------
#ifndef BiteRateH
#define BiteRateH
//---------------------------------------------------------------------------
#include <Classes.hpp>
#include <Controls.hpp>
#include <StdCtrls.hpp>
#include <Forms.hpp>
//---------------------------------------------------------------------------
class TForm1 : public TForm
{
__published:    // IDE-managed Components
private:        // User declarations
public:         // User declarations
        __fastcall TForm1(TComponent* Owner);
};
//---------------------------------------------------------------------------
extern PACKAGE TForm1 *Form1;
//---------------------------------------------------------------------------
#endif
```

BiteRate.cpp

```
//---------------------------------------------------------------------------
#include <vcl.h>
#pragma hdrstop
USERES("BiteRate.res");
USEFORM("frmMain.cpp", MainForm);
USEFORM("frmKeys.cpp", frmDefine);
USEUNIT("Keys.cpp");
USEUNIT("Utils.cpp");
//---------------------------------------------------------------------------
WINAPI WinMain(HINSTANCE, HINSTANCE, LPSTR, int)
{
        try
        {
                Application->Initialize();
                Application->CreateForm(__classid(TMainForm), &MainForm);
```

```
                Application->CreateForm(__classid(TfrmDefine), &frmDefine);
                Application->Run();
        }
        catch (Exception &exception)
        {
                Application->ShowException(&exception);
        }
        return 0;
}
//---------------------------------------------------------------------------
```

KeyCodes.def

```
#define START VK_SPACE
#define BITEP3 VK_3
#define BITEP1 VK_1
#define TRAVP1 VK_4
#define BITEP2 VK_2
#define STOP VK_RETURN
```

frmMain.h

```
//---------------------------------------------------------------------------
#ifndef frmMainH
#define frmMainH
//---------------------------------------------------------------------------
#include <Classes.hpp>
#include <Controls.hpp>
#include <StdCtrls.hpp>
#include <Forms.hpp>
//---------------------------------------------------------------------------
class TMainForm : public TForm
{
__published:   // IDE-managed Components
        TButton *btnStart;
        TButton *btnBiteP3;
        TButton *btnStop;
        TButton *btnTravelP1;
        TButton *btnBiteP1;
        TButton *btnBiteP2;
        void __fastcall FormKeyDown(TObject *Sender, WORD &Key, TShiftState Shift);
        void __fastcall btnStartClick(TObject *Sender);
        void __fastcall btnStopClick(TObject *Sender);
        void __fastcall btnBiteP3Click(TObject *Sender);
        void __fastcall btnBiteP1Click(TObject *Sender);
        void __fastcall btnTravelP1Click(TObject *Sender);
        void __fastcall btnBiteP2Click(TObject *Sender);
private:        // User declarations
        void __fastcall BiteProcess3();
        void __fastcall BiteProcess1();
        void __fastcall TravelProcess1();
        void __fastcall BiteProcess2();
        void __fastcall StartRun();
        void __fastcall StopRun();
        int KeyCode(WORD);
public:         // User declarations
        __fastcall TMainForm(TComponent* Owner);
};
//---------------------------------------------------------------------------
extern PACKAGE TMainForm *MainForm;
//---------------------------------------------------------------------------
#endif
```

frmMain.cpp

```
//---------------------------------------------------------------------------
#include <fstream.h>
#include <time.h>
#include <vcl.h>
#pragma hdrstop
```

```
#include "frmMain.h"
#include "frmKeys.h"
#include "VK.h"
#include "KeyCodes.def"
//---------------------------------------------------------------------------
#pragma package(smart_init)
#pragma resource "*.dfm"
TMainForm *MainForm;
//---------------------------------------------------------------------------
AnsiString GetRegistryEntry(AnsiString, AnsiString, AnsiString);
//---------------------------------------------------------------------------
clock_t tStart;
//---------------------------------------------------------------------------
WORD Start;
WORD BiteP3;
WORD BiteP1;
WORD TravelP1;
WORD BiteP2;
WORD Stop;
//---------------------------------------------------------------------------
ofstream of;
AnsiString ofPath = "c:\\temp\\BiteRate.txt";
//---------------------------------------------------------------------------
__fastcall TMainForm::TMainForm(TComponent* Owner) : TForm(Owner)
{
GetRegistryEntry("Key Codes", "Start", START);
GetRegistryEntry("Key Codes", "BiteP3", BITEP3);
GetRegistryEntry("Key Codes", "BiteP1", BITEP1);
GetRegistryEntry("Key Codes", "TravelP1", TRAVP1);
GetRegistryEntry("Key Codes", "BiteP2", BITEP2);
GetRegistryEntry("Key Codes", "Stop", STOP);

btnStart->Enabled=true;
btnStop->Enabled=false;
btnBiteP3->Enabled=false;
btnBiteP1->Enabled=false;
btnTravelP1->Enabled=false;
btnBiteP2->Enabled=false;
}
//---------------------------------------------------------------------------
void __fastcall TMainForm::FormKeyDown(TObject *Sender, WORD &Key, TShiftState Shift)
{
if (Key==Start) StartRun();
else
if (Key==BiteP3) BiteProcess3();
else
if (Key==BiteP1) BiteProcess1();
else
if (Key==TravelP1) TravelProcess1();
else
if (Key==BiteP2) BiteProcess2();
else
if (Key==Stop) StopRun();
else
if (Key==VK_F12)
{
Hide();
frmDefine = new TfrmDefine(this);
frmDefine->ShowModal();
Show();
}
}
//---------------------------------------------------------------------------
void __fastcall TMainForm::StartRun()
{
Start = StrToInt(GetRegistryEntry("Key Codes", "Start", START));
BiteP3 = StrToInt(GetRegistryEntry("Key Codes", "BiteP3", BITEP3));
BiteP1 = StrToInt(GetRegistryEntry("Key Codes", "BiteP1", BITEP1));
```

```
TravelP1 = StrToInt(GetRegistryEntry("Key Codes", "TravelP1", TRAVP1));
BiteP2 = StrToInt(GetRegistryEntry("Key Codes", "BiteP2", BITEP2));
Stop = StrToInt(GetRegistryEntry("Key Codes", "Stop", STOP));

btnStart->Enabled=false;
btnStop->Enabled=true;
btnBiteP3->Enabled=true;
btnBiteP1->Enabled=true;
btnTravelP1->Enabled=true;
btnBiteP2->Enabled=true;

of.open(ofPath.c_str());
tStart = clock();
of << "Start\t" << ofPath.c_str() << "\n";
}
//---------------------------------------------------------------------------
void __fastcall TMainForm::BiteProcess3()
{
of << "B3\t" << ((clock()-tStart)/CLK_TCK) << "\n";
}
//---------------------------------------------------------------------------
void __fastcall TMainForm::BiteProcess1()
{
of << "B1\t" << ((clock()-tStart)/CLK_TCK) << "\n";
}
//---------------------------------------------------------------------------
void __fastcall TMainForm::TravelProcess1()
{
of << "T1\t" << ((clock()-tStart)/CLK_TCK) << "\n";
}
//---------------------------------------------------------------------------
void __fastcall TMainForm::BiteProcess2()
{
of << "B2\t" << ((clock()-tStart)/CLK_TCK) << "\n";
}
//---------------------------------------------------------------------------
void __fastcall TMainForm::StopRun()
{
of << "End\t" << ((clock()-tStart)/CLK_TCK) << "\n";
of.close();
WinExec(("Notepad " + ofPath).c_str(), SW_RESTORE);
btnStart->Enabled=true;
btnStop->Enabled=false;
btnBiteP3->Enabled=false;
btnBiteP1->Enabled=false;
btnTravelP1->Enabled=false;
btnBiteP2->Enabled=false;
}
//---------------------------------------------------------------------------
void __fastcall TMainForm::btnStartClick(TObject *Sender)
{
StartRun();
}
//---------------------------------------------------------------------------
void __fastcall TMainForm::btnStopClick(TObject *Sender)
{
StopRun();
}
//---------------------------------------------------------------------------
void __fastcall TMainForm::btnBiteP3Click(TObject *Sender)
{
BiteProcess3();
}
//---------------------------------------------------------------------------
void __fastcall TMainForm::btnBiteP1Click(TObject *Sender)
{
BiteProcess1();
}
```

```
//---------------------------------------------------------------------------
void __fastcall TMainForm::btnTravelP1Click(TObject *Sender)
{
TravelProcess1();
}
//---------------------------------------------------------------------------
void __fastcall TMainForm::btnBiteP2Click(TObject *Sender)
{
BiteProcess2();
}
//---------------------------------------------------------------------------
```

Utils.cpp

```
//---------------------------------------------------------------------------
#include <vcl.h>
#include <Registry.hpp>
#pragma hdrstop
//---------------------------------------------------------------------------
AnsiString rootKey = "Software\\Bite Rate\\" ;
//---------------------------------------------------------------------------
void PutRegistryEntry(AnsiString key, AnsiString label, AnsiString value)
{
TRegistry *Reg;
Reg = new TRegistry;
try
{
Reg->RootKey = HKEY_LOCAL_MACHINE;
if (Reg->OpenKey(rootKey+key, true))
{
Reg->WriteString(label, value);
Reg->CloseKey();
}
}
__finally
{
delete Reg;
}
}
//---------------------------------------------------------------------------
AnsiString GetRegistryEntry(AnsiString key, AnsiString label, AnsiString _default)
{
AnsiString S;
TRegistry *Reg;
Reg = new TRegistry;
try
{
Reg->RootKey = HKEY_LOCAL_MACHINE;
if (Reg->OpenKey(rootKey+key, true))
{
S=Reg->ReadString(label);
if (!S.Length())
{
S=_default;
Reg->WriteString(label, S);
}
Reg->CloseKey();
}
}
__finally
{
delete Reg;
}
return S;
}
//---------------------------------------------------------------------------
```

frmKeys.h

```
//---------------------------------------------------------------------------
#ifndef frmKeysH
#define frmKeysH
//---------------------------------------------------------------------------
#include <Classes.hpp>
#include <Controls.hpp>
#include <StdCtrls.hpp>
#include <Forms.hpp>
#include <Buttons.hpp>
//---------------------------------------------------------------------------
class TfrmDefine : public TForm
{
__published:   // IDE-managed Components
        TLabel *lblStart;
        TLabel *lblBiteP3;
        TLabel *lblTravelP1;
        TLabel *lblBiteP1;
        TLabel *lblBiteP2;
        TLabel *lblStop;
        TBitBtn *btnStart;
        TBitBtn *btnBiteP3;
        TBitBtn *btnBiteP1;
        TBitBtn *btnTravelP1;
        TBitBtn *btnStop;
        TBitBtn *btnBiteP2;
        void __fastcall tnStartClick(TObject *Sender);
        void __fastcall tnBiteP3Click(TObject *Sender);
        void __fastcall tnTravelP1Click(TObject *Sender);
        void __fastcall tnBiteP1Click(TObject *Sender);
        void __fastcall tnBiteP2Click(TObject *Sender);
        void __fastcall tnStopClick(TObject *Sender);
        void __fastcall FormKeyDown(TObject *Sender, WORD &Key,
          TShiftState Shift);
private:       // User declarations
        void Reset();
        WORD ScanKey(WORD);
public:        // User declarations
        __fastcall TfrmDefine(TComponent* Owner);
};
//---------------------------------------------------------------------------
extern PACKAGE TfrmDefine *frmDefine;
//---------------------------------------------------------------------------
#endif
```

frmKeys.cpp

```
//---------------------------------------------------------------------------
#include <vcl.h>
#include <time.h>
#pragma hdrstop
#include "frmKeys.h"
#include "KeyCodes.def"
#include "VK.h"
//---------------------------------------------------------------------------
#pragma package(smart_init)
#pragma resource "*.dfm"
TfrmDefine *frmDefine;
//---------------------------------------------------------------------------
void PutRegistryEntry(AnsiString, AnsiString, AnsiString);
AnsiString GetRegistryEntry(AnsiString, AnsiString, AnsiString);
//---------------------------------------------------------------------------
int KeyCode(WORD);
AnsiString KeyName(WORD);
//---------------------------------------------------------------------------
bool scanning = false;
WORD KeySel;
//---------------------------------------------------------------------------
```

```
__fastcall TfrmDefine::TfrmDefine(TComponent* Owner) : TForm(Owner)
{
Reset();
lblStart->Caption = KeyName(StrToInt(GetRegistryEntry("Key Codes", "Start", START)));
lblBiteP3->Caption = KeyName(StrToInt(GetRegistryEntry("Key Codes", "BiteP3", BITEP3)));
lblTravelP1->Caption = KeyName(StrToInt(GetRegistryEntry("Key Codes", "TravelP1",
BITEP1)));
lblBiteP1->Caption = KeyName(StrToInt(GetRegistryEntry("Key Codes", "BiteP1", TRAVP1)));
lblBiteP2->Caption = KeyName(StrToInt(GetRegistryEntry("Key Codes", "BiteP2", BITEP2)));
lblStop->Caption = KeyName(StrToInt(GetRegistryEntry("Key Codes", "Stop", STOP)));
}
//---------------------------------------------------------------------------
void TfrmDefine::Reset()
{
btnStart->Font->Color = clBlack;
btnBiteP3->Font->Color = clBlack;
btnBiteP2->Font->Color = clBlack;
btnBiteP1->Font->Color = clBlack;
btnTravelP1->Font->Color = clBlack;
btnStop->Font->Color = clBlack;

scanning = false;

btnStart->Enabled=true;
btnStop->Enabled=true;
btnBiteP3->Enabled=true;
btnBiteP1->Enabled=true;
btnTravelP1->Enabled=true;
btnBiteP2->Enabled=true;
}
//---------------------------------------------------------------------------
void __fastcall TfrmDefine::tnStartClick(TObject *Sender)
{
Reset();
btnStop->Enabled=false;
btnBiteP3->Enabled=false;
btnBiteP1->Enabled=false;
btnTravelP1->Enabled=false;
btnBiteP2->Enabled=false;
btnStart->Font->Color = clRed;
WORD wKey = ScanKey(KeyCode(StrToInt(GetRegistryEntry("Key Codes", "Start", START))));
lblStart->Caption = KeyName(wKey);
PutRegistryEntry("Key Codes", "Start", KeyCode(wKey));
Reset();
}
//---------------------------------------------------------------------------
void __fastcall TfrmDefine::tnBiteP3Click(TObject *Sender)
{
Reset();
btnStart->Enabled=false;
btnStop->Enabled=false;
btnBiteP1->Enabled=false;
btnTravelP1->Enabled=false;
btnBiteP2->Enabled=false;
btnBiteP3->Font->Color = clRed;
WORD wKey = ScanKey(StrToInt(GetRegistryEntry("Key Codes", "BiteP3", BITEP3)));
lblBiteP3->Caption = KeyName(wKey);
PutRegistryEntry("Key Codes", "BiteP3", KeyCode(wKey));
Reset();
}
//---------------------------------------------------------------------------
void __fastcall TfrmDefine::tnTravelP1Click(TObject *Sender)
{
Reset();
btnStart->Enabled=false;
btnStop->Enabled=false;
btnBiteP3->Enabled=false;
btnBiteP1->Enabled=false;
```

```
btnBiteP2->Enabled=false;
btnTravelP1->Font->Color = clRed;
WORD wKey = ScanKey(StrToInt(GetRegistryEntry("Key Codes", "TravelP1", TRAVP1)));
lblTravelP1->Caption = KeyName(wKey);
PutRegistryEntry("Key Codes", "TravelP1", KeyCode(wKey));
Reset();
}
//---------------------------------------------------------------------------
void __fastcall TfrmDefine::tnBiteP1Click(TObject *Sender)
{
Reset();
btnStart->Enabled=false;
btnStop->Enabled=false;
btnBiteP3->Enabled=false;
btnTravelP1->Enabled=false;
btnBiteP2->Enabled=false;
btnBiteP1->Font->Color = clRed;
WORD wKey = ScanKey(StrToInt(GetRegistryEntry("Key Codes", "BiteP1", BITEP1)));
lblBiteP1->Caption = KeyName(wKey);
PutRegistryEntry("Key Codes", "BiteP1", KeyCode(wKey));
Reset();
}
//---------------------------------------------------------------------------
void __fastcall TfrmDefine::tnBiteP2Click(TObject *Sender)
{
Reset();
btnStart->Enabled=false;
btnStop->Enabled=false;
btnBiteP3->Enabled=true;
btnBiteP1->Enabled=false;
btnTravelP1->Enabled=false;
btnBiteP2->Font->Color = clRed;
WORD wKey = ScanKey(StrToInt(GetRegistryEntry("Key Codes", "BiteP2", BITEP2)));
lblBiteP2->Caption = KeyName(wKey);
PutRegistryEntry("Key Codes", "BiteP2", KeyCode(wKey));
Reset();
}
//---------------------------------------------------------------------------
void __fastcall TfrmDefine::tnStopClick(TObject *Sender)
{
Reset();
btnStart->Enabled=false;
btnBiteP3->Enabled=false;
btnBiteP1->Enabled=false;
btnTravelP1->Enabled=false;
btnBiteP2->Enabled=false;
btnStop->Font->Color = clRed;
WORD wKey = ScanKey(StrToInt(GetRegistryEntry("Key Codes", "Stop", STOP)));
lblStop->Caption = KeyName(wKey);
PutRegistryEntry("Key Codes", "Stop", KeyCode(wKey));
Reset();
}
//---------------------------------------------------------------------------
void __fastcall TfrmDefine::FormKeyDown(TObject *Sender, WORD &Key, TShiftState Shift)
{
KeySel = Key;
scanning = false;
}
//---------------------------------------------------------------------------
WORD TfrmDefine::ScanKey(WORD oldSel)
{
KeySel = oldSel;
scanning = true;
bool timeout = false;
clock_t stTime = clock();
while (scanning && !timeout)
{
Application->ProcessMessages();
```

```
timeout = (((clock() - stTime) / CLK_TCK) > 5);
}
return KeySel;
}
//---------------------------------------------------------------------------
```

VK.h

```
//---------------------------------------------------------------------------
#ifndef _VIRTUAL_KEY_CODES_H
#define _VIRTUAL_KEY_CODES_H
//---------------------------------------------------------------------------
//Virtual Key Codes
/*
The following table shows the symbolic constant names, hexadecimal values, and keyboard
equivalents for the virtual-key codes used
by the Windows operating system version 3.1. The codes are listed in numeric order.
*/
//---------------------------------------------------------------------------
#define VK_LBUTTON     0x0001         // Left mouse button
#define VK_RBUTTON     0x0002         // Right mouse button
#define VK_CANCEL      0x0003         // Used for control-break processing
#define VK_MBUTTON     0x0004         // Middle mouse button (three-button mouse)
//--                   0x0005-0x0007     Undefined
#define VK_BACK                0x0008 // BACKSPACE key
#define VK_TAB         0x0009         // TAB key
//--                   0x000A-0x000B     Undefined
#define VK_CLEAR       0x000C         // CLEAR key
#define VK_RETURN      0x000D         // ENTER key
//--                   0x000E-0x000F     Undefined
#define VK_SHIFT       0x0010         // SHIFT key
#define VK_CONTROL     0x0011         // CTRL key
#define VK_MENU                0x0012 // ALT key
#define VK_PAUSE       0x0013         // PAUSE key
#define VK_CAPITAL     0x0014         // CAPS LOCK key
//--                   0x0015-0x0019     Reserved for Kanji systems
//--                   0x001A            Undefined
#define VK_ESCAPE      0x001B         // ESC key
//--                   0x001C-0x001F     Reserved for Kanji systems
#define VK_SPACE       0x0020         // SPACEBAR
#define VK_PRIOR       0x0021         // PAGE UP key
#define VK_NEXT                0x0022 // PAGE DOWN key
#define VK_END         0x0023         // END key
#define VK_HOME                0x0024 // HOME key
#define VK_LEFT                0x0025 // LEFT ARROW key
#define VK_UP          0x0026         // UP ARROW key
#define VK_RIGHT       0x0027         // RIGHT ARROW key
#define VK_DOWN                0x0028 // DOWN ARROW key
#define VK_SELECT      0x0029         // SELECT key
//--                   0x002A            OEM specific
#define VK_EXECUTE     0x002B         // EXECUTE key
#define VK_SNAPSHOT    0x002C         // PRINT SCREEN key for Windows 3.0 and later
#define VK_INSERT      0x002D         // INS key
#define VK_DELETE      0x002E         // DEL key
#define VK_HELP                0x002F // HELP key
#define VK_0           0x0030         // 0 key
#define VK_1           0x0031         // 1 key
#define VK_2           0x0032         // 2 key
#define VK_3           0x0033         // 3 key
#define VK_4           0x0034         // 4 key
#define VK_5           0x0035         // 5 key
#define VK_6           0x0036         // 6 key
#define VK_7           0x0037         // 7 key
#define VK_8           0x0038         // 8 key
#define VK_9           0x0039         // 9 key
//--                   0x003A-0x0040     Undefined
#define VK_A           0x0041         // A key
#define VK_B           0x0042         // B key
#define VK_C           0x0043         // C key
```

```
#define VK_D           0x0044         // D key
#define VK_E           0x0045         // E key
#define VK_F           0x0046         // F key
#define VK_G           0x0047         // G key
#define VK_H           0x0048         // H key
#define VK_I           0x0049         // I key
#define VK_J           0x004A         // J key
#define VK_K           0x004B         // K key
#define VK_L           0x004C         // L key
#define VK_M           0x004D         // M key
#define VK_N           0x004E         // N key
#define VK_O           0x004F         // O key
#define VK_P           0x0050         // P key
#define VK_Q           0x0051         // Q key
#define VK_R           0x0052         // R key
#define VK_S           0x0053         // S key
#define VK_T           0x0054         // T key
#define VK_U           0x0055         // U key
#define VK_V           0x0056         // V key
#define VK_W           0x0057         // W key
#define VK_X           0x0058         // X key
#define VK_Y           0x0059         // Y key
#define VK_Z           0x005A         // Z key
//--                   0x005B-0x005F     Undefined
#define VK_NUMPAD0     0x0060         // Numeric keypad 0 key
#define VK_NUMPAD1     0x0061         // Numeric keypad 1 key
#define VK_NUMPAD2     0x0062         // Numeric keypad 2 key
#define VK_NUMPAD3     0x0063         // Numeric keypad 3 key
#define VK_NUMPAD4     0x0064         // Numeric keypad 4 key
#define VK_NUMPAD5     0x0065         // Numeric keypad 5 key
#define VK_NUMPAD6     0x0066         // Numeric keypad 6 key
#define VK_NUMPAD7     0x0067         // Numeric keypad 7 key
#define VK_NUMPAD8     0x0068         // Numeric keypad 8 key
#define VK_NUMPAD9     0x0069         // Numeric keypad 9 key
#define VK_MULTIPLY    0x006A         // Multiply key
#define VK_ADD         0x006B         // Add key
#define VK_SEPARATOR   0x006C         // Separator key
#define VK_SUBTRACT    0x006D         // Subtract key
#define VK_DECIMAL     0x006E         // Decimal key
#define VK_DIVIDE      0x006F         // Divide key
#define VK_F1          0x0070         // F1 key
#define VK_F2          0x0071         // F2 key
#define VK_F3          0x0072         // F3 key
#define VK_F4          0x0073         // F4 key
#define VK_F5          0x0074         // F5 key
#define VK_F6          0x0075         // F6 key
#define VK_F7          0x0076         // F7 key
#define VK_F8          0x0077         // F8 key
#define VK_F9          0x0078         // F9 key
#define VK_F10         0x0079         // F10 key
#define VK_F11         0x007A         // F11 key
#define VK_F12         0x007B         // F12 key
#define VK_F13         0x007C         // F13 key
#define VK_F14         0x007D         // F14 key
#define VK_F15         0x007E         // F15 key
#define VK_F16         0x007F         // F16 key
#define VK_F17         0x0080H        // F17 key
#define VK_F18         0x0081H        // F18 key
#define VK_F19         0x0082H        // F19 key
#define VK_F20         0x0083H        // F20 key
#define VK_F21         0x0084H        // F21 key
#define VK_F22         0x0085H        // F22 key
#define VK_F23         0x0086H        // F23 key
#define VK_F24         0x0087H        // F24 key
//--                   0x0088-0x008F     Unassigned
#define VK_NUMLOCK     0x0090         // NUM LOCK key
#define VK_SCROLL      0x0091         // SCROLL LOCK key
//--                   0x0092-0x00B9     Unassigned
```

```
//--                   0x00BA-0x00C0     OEM specific
//--                   0x00C1-0x00DA     Unassigned
//--                   0x00DB-0x00E4     OEM specific
//--                   0x00E5            Unassigned
//--                   0x00E6            OEM specific
//--                   0x00E7-0x00E8     Unassigned
//--                   0x00E9-0x00F5     OEM specific
//--                   0x00F6-0x00FE     Unassigned
#endif
//----------------------------------------------------------------------------
```

Keys.cpp

```
//----------------------------------------------------------------------------
#include <vcl.h>
#pragma hdrstop
#include "VK.h"
//----------------------------------------------------------------------------
int KeyCode(WORD key)
{
switch (key)
{
case VK_LBUTTON: return 0x0001;       // Left mouse button
case VK_RBUTTON: return 0x0002;       // Right mouse button
case VK_CANCEL: return 0x0003;        // Used for control-break processing
case VK_MBUTTON: return 0x0004;       // Middle mouse button (three-button mouse)
//-- : return 0x0005-0x0007           Undefined
case VK_BACK: return 0x0008;          // BACKSPACE key
case VK_TAB: return 0x0009;           // TAB key
//-- : return 0x000A-0x000B           Undefined
case VK_CLEAR: return 0x000C;         // CLEAR key
case VK_RETURN: return 0x000D;        // ENTER key
//-- : return 0x000E-0x000F           Undefined
case VK_SHIFT: return 0x0010;         // SHIFT key
case VK_CONTROL: return 0x0011;       // CTRL key
case VK_MENU: return 0x0012;          // ALT key
case VK_PAUSE: return 0x0013;         // PAUSE key
case VK_CAPITAL: return 0x0014;       // CAPS LOCK key
//-- : return 0x0015-0x0019           Reserved for Kanji systems
//-- : return 0x001A                  Undefined
case VK_ESCAPE: return 0x001B;        // ESC key
//-- : return 0x001C-0x001F           Reserved for Kanji systems
case VK_SPACE: return 0x0020;         // SPACEBAR
case VK_PRIOR: return 0x0021;         // PAGE UP key
case VK_NEXT: return 0x0022;          // PAGE DOWN key
case VK_END: return 0x0023;           // END key
case VK_HOME: return 0x0024;          // HOME key
case VK_LEFT: return 0x0025;          // LEFT ARROW key
case VK_UP: return 0x0026;            // UP ARROW key
case VK_RIGHT: return 0x0027;         // RIGHT ARROW key
case VK_DOWN: return 0x0028;          // DOWN ARROW key
case VK_SELECT: return 0x0029;        // SELECT key
//-- : return 0x002A                  OEM specific
case VK_EXECUTE: return 0x002B;       // EXECUTE key
case VK_SNAPSHOT: return 0x002C;      // PRINT SCREEN key for Windows 3.0 and later
case VK_INSERT: return 0x002D;        // INS key
case VK_DELETE: return 0x002E;        // DEL key
case VK_HELP: return 0x002F;          // HELP key
case VK_0: return 0x0030;             // 0 key
case VK_1: return 0x0031;             // 1 key
case VK_2: return 0x0032;             // 2 key
case VK_3: return 0x0033;             // 3 key
case VK_4: return 0x0034;             // 4 key
case VK_5: return 0x0035;             // 5 key
case VK_6: return 0x0036;             // 6 key
case VK_7: return 0x0037;             // 7 key
case VK_8: return 0x0038;             // 8 key
case VK_9: return 0x0039;             // 9 key
//-- : return 0x003A-0x0040           Undefined
```

```
case VK_A: return 0x0041;             // A key
case VK_B: return 0x0042;             // B key
case VK_C: return 0x0043;             // C key
case VK_D: return 0x0044;             // D key
case VK_E: return 0x0045;             // E key
case VK_F: return 0x0046;             // F key
case VK_G: return 0x0047;             // G key
case VK_H: return 0x0048;             // H key
case VK_I: return 0x0049;             // I key
case VK_J: return 0x004A;             // J key
case VK_K: return 0x004B;             // K key
case VK_L: return 0x004C;             // L key
case VK_M: return 0x004D;             // M key
case VK_N: return 0x004E;             // N key
case VK_O: return 0x004F;             // O key
case VK_P: return 0x0050;             // P key
case VK_Q: return 0x0051;             // Q key
case VK_R: return 0x0052;             // R key
case VK_S: return 0x0053;             // S key
case VK_T: return 0x0054;             // T key
case VK_U: return 0x0055;             // U key
case VK_V: return 0x0056;             // V key
case VK_W: return 0x0057;             // W key
case VK_X: return 0x0058;             // X key
case VK_Y: return 0x0059;             // Y key
case VK_Z: return 0x005A;             // Z key
//-- : return 0x005B-0x005F            Undefined
case VK_NUMPAD0: return 0x0060;       // Numeric keypad 0 key
case VK_NUMPAD1: return 0x0061;       // Numeric keypad 1 key
case VK_NUMPAD2: return 0x0062;       // Numeric keypad 2 key
case VK_NUMPAD3: return 0x0063;       // Numeric keypad 3 key
case VK_NUMPAD4: return 0x0064;       // Numeric keypad 4 key
case VK_NUMPAD5: return 0x0065;       // Numeric keypad 5 key
case VK_NUMPAD6: return 0x0066;       // Numeric keypad 6 key
case VK_NUMPAD7: return 0x0067;       // Numeric keypad 7 key
case VK_NUMPAD8: return 0x0068;       // Numeric keypad 8 key
case VK_NUMPAD9: return 0x0069;       // Numeric keypad 9 key
case VK_MULTIPLY: return 0x006A;      // Multiply key
case VK_ADD: return 0x006B;           // Add key
case VK_SEPARATOR: return 0x006C;     // Separator key
case VK_SUBTRACT: return 0x006D;      // Subtract key
case VK_DECIMAL: return 0x006E;       // Decimal key
case VK_DIVIDE: return 0x006F;        // Divide key
case VK_F1: return 0x0070;            // F1 key
case VK_F2: return 0x0071;            // F2 key
case VK_F3: return 0x0072;            // F3 key
case VK_F4: return 0x0073;            // F4 key
case VK_F5: return 0x0074;            // F5 key
case VK_F6: return 0x0075;            // F6 key
case VK_F7: return 0x0076;            // F7 key
case VK_F8: return 0x0077;            // F8 key
case VK_F9: return 0x0078;            // F9 key
case VK_F10: return 0x0079;           // F10 key
case VK_F11: return 0x007A;           // F11 key
case VK_F12: return 0x007B;           // F12 key
case VK_F13: return 0x007C;           // F13 key
case VK_F14: return 0x007D;           // F14 key
case VK_F15: return 0x007E;           // F15 key
case VK_F16: return 0x007F;           // F16 key
//-- : return 0x0088-0x008F            Unassigned
case VK_NUMLOCK: return 0x0090;       // NUM LOCK key
case VK_SCROLL: return 0x0091;        // SCROLL LOCK key
//-- : return 0x0092-0x00B9            Unassigned
//-- : return 0x00BA-0x00C0            OEM specific
//-- : return 0x00C1-0x00DA            Unassigned
//-- : return 0x00DB-0x00E4            OEM specific
//-- : return 0x00E5                   Unassigned
//-- : return 0x00E6                   OEM specific
```

```
//-- : return 0x00E7-0x00E8           Unassigned
//-- : return 0x00E9-0x00F5           OEM specific
//-- : return 0x00F6-0x00FE           Unassigned
default: MessageBeep(0); return 0x00F6-0x00FE;}
}
//---------------------------------------------------------------------------
AnsiString KeyName(WORD key)
{
switch (key)
{
case VK_LBUTTON: return "Left mouse button";
case VK_RBUTTON: return "Right mouse button";
case VK_CANCEL: return "Used for control-break";
case VK_MBUTTON: return "Middle mouse button";
case VK_BACK: return "BACKSPACE";
case VK_TAB: return "TAB";
case VK_CLEAR: return "CLEAR";
case VK_RETURN: return "ENTER";
case VK_SHIFT: return "SHIFT";
case VK_CONTROL: return "CTRL";
case VK_MENU: return "ALT";
case VK_PAUSE: return "PAUSE";
case VK_CAPITAL: return "CAPS LOCK";
case VK_ESCAPE: return "ESC";
case VK_SPACE: return "SPACEBAR";
case VK_PRIOR: return "PAGE UP";
case VK_NEXT: return "PAGE DOWN";
case VK_END: return "END";
case VK_HOME: return "HOME";
case VK_LEFT: return "LEFT ARROW";
case VK_UP: return "UP ARROW";
case VK_RIGHT: return "RIGHT ARROW";
case VK_DOWN: return "DOWN ARROW";
case VK_SELECT: return "SELECT";
case VK_EXECUTE: return "EXECUTE";
case VK_SNAPSHOT: return "PRINT SCREEN";
case VK_INSERT: return "INS";
case VK_DELETE: return "DEL";
case VK_HELP: return "HELP";
case VK_0: return "0";
case VK_1: return "1";
case VK_2: return "2";
case VK_3: return "3";
case VK_4: return "4";
case VK_5: return "5";
case VK_6: return "6";
case VK_7: return "7";
case VK_8: return "8";
case VK_9: return "9";
case VK_A: return "A";
case VK_B: return "B";
case VK_C: return "C";
case VK_D: return "D";
case VK_E: return "E";
case VK_F: return "F";
case VK_G: return "G";
case VK_H: return "H";
case VK_I: return "I";
case VK_J: return "J";
case VK_K: return "K";
case VK_L: return "L";
case VK_M: return "M";
case VK_N: return "N";
case VK_O: return "O";
case VK_P: return "P";
case VK_Q: return "Q";
case VK_R: return "R";
case VK_S: return "S";
```

```
case VK_T: return "T";
case VK_U: return "U";
case VK_V: return "V";
case VK_W: return "W";
case VK_X: return "X";
case VK_Y: return "Y";
case VK_Z: return "Z";
case VK_NUMPAD0: return "Numeric pad 0";
case VK_NUMPAD1: return "Numeric pad 1";
case VK_NUMPAD2: return "Numeric pad 2";
case VK_NUMPAD3: return "Numeric pad 3";
case VK_NUMPAD4: return "Numeric pad 4";
case VK_NUMPAD5: return "Numeric pad 5";
case VK_NUMPAD6: return "Numeric pad 6";
case VK_NUMPAD7: return "Numeric pad 7";
case VK_NUMPAD8: return "Numeric pad 8";
case VK_NUMPAD9: return "Numeric pad 9";
case VK_MULTIPLY: return "Multiply";
case VK_ADD: return "Add";
case VK_SEPARATOR: return "Separator";
case VK_SUBTRACT: return "Subtract";
case VK_DECIMAL: return "Decimal";
case VK_DIVIDE: return "Divide";
case VK_F1: return "F1";
case VK_F2: return "F2";
case VK_F3: return "F3";
case VK_F4: return "F4";
case VK_F5: return "F5";
case VK_F6: return "F6";
case VK_F7: return "F7";
case VK_F8: return "F8";
case VK_F9: return "F9";
case VK_F10: return "F10";
case VK_F11: return "F11";
case VK_F12: return "F12";
case VK_F13: return "F13";
case VK_F14: return "F14";
case VK_F15: return "F15";
case VK_F16: return "F16";
case VK_NUMLOCK: return "NUM LOCK";
case VK_SCROLL: return "SCROLL LOCK";
default: MessageBeep(0); return "None";
}
}
//---------------------------------------------------------------------------
```

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