The Role of Resource Competition in Ungulate Diversity and Community Structure in Africa

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ABSTRACT

Resource competition theory (RCT), also known as resource ratio theory, was developed in the 1980's by plant community ecologists and became a highly successful description of inter-specific competition and community structure. The theory never achieved popularity among animal ecologists, with only one experimental test reported. An important factor in the reluctance of animal ecologists to use the theory was its description of resources, which is very different to the traditional way animal resources have been described in classical competition theory (CCT). RCT is, nevertheless, a theory with very general applicability, and with a highly flexible description of resources. The major aim of this thesis is to develop, apply, and test resource competition theory in the ungulate communities of Africa. Ungulates were chosen because RCT requires a great deal of information about the foraging ecology of the species to be modelled, and foraging ecology in ungulates has probably been subjected to more detailed research than any other animal group.

The first chapter reviews the literature on competition in ungulates. Chapter 2 then develops a description of ungulate resources within the RCT framework. This new description efficiently encapsulates many well known features of ungulate foraging ecology. Several ungulate foraging scenarios are then described within the RCT framework in a series of conceptual models. A strong prediction that stable co-existence is possible between species that are sufficiently, but not too much, different in body size, emerges. One of these models, describing competition between topi and wildebeest, is developed more fully and tested using data from the literature. The model predicts the resource supply conditions under which each species can be expected to exclude the other. Co-existence is shown to be promoted by environmental heterogeneity that is generated by the foraging activity of the animals themselves.

The modelling approach is developed in chapter 3, with a generic model of resource competition between two species differing in body size. The effect of body size on energetic requirements, intake rate, digestive capacity, and selective ability are integrated within the model. Despite the large literature on ungulate foraging ecology, there remain areas of insufficient knowledge, in particular a quantitative description of the relationship between body size and selective ability. The model predicts that stable co-existence is possible between two species competing for resources. Given a list of species and a description of the environment (i.e. of resource supply characteristics), the model has the potential to predict which species can co-exist, and which will be competitively excluded.

Chapter 4 examines the evidence that grazing communities in Africa are structured by competition - whether the body sizes of co-existing species shows evidence of limiting similarity. A Monte Carlo method is developed based on the methods commonly used in the literature to test for limiting similarity. The conclusion is that competitive structuring of grazer communities is very rare. One ecosystem where the evidence is strong is the Serengeti.

The Serengeti is investigated in chapter 5 using a rich database of monthly aerial surveys carried out between 1969 and 1972 by the Serengeti Ecological Monitoring Programme (SEMP). These data have not been analysed to date, except to describe the wildebeest migration, and indeed the data were almost lost in the

1980's. Data were extracted from the database for the south-east short-grass plains in the wet season, which is the destination of the major annual migration of wildebeest, zebra and other species. Bell's (1982) prediction that ungulate biomass will be concentrated in large body size classes in areas where productivity is high and vegetation quality is low was tested and supported. This hypothesis has been tested using comparisons between ecosystems, but not so far within a single community. Facilitation was also demonstrated, with the presence of smaller species on tall swards promoted by the presence of larger species. Facilitation has been used to explain sequential patch occupancy by species of different body sizes, but has not been tested for simultaneous patch occupancy. Some evidence in support of RCT is also presented - the relationship between productivity and species richness is unimodal. However, this observation can only provide weak support, as the pattern is subject to various explanations. A direct test of RCT using the database is possible and is described, but could not be carried out using the subset of data analysed in this thesis.

The final two chapters use satellite data to examine patterns in ungulate diversity at the continental scale. Chapter 6 describes the use of satellite imagery to measure primary productivity. The imagery is then analysed to provide measures of mean productivity, spatial heterogeneity, and a variety of indices of temporal variability. These data are then used in chapter 7 to test whether the RCT explanation of the relationship between diversity and productivity is supported. RCT predicts that species richness should follow a unimodal pattern, rising with productivity over the lower part of the productivity gradient, before reaching a maximum and then falling again over the upper part of the gradient. Diversity falls because of an assumption that spatial variability falls at high productivity. This assumption is tested for the first time in an animal community, and found to be partly true. Ungulate diversity is also shown to follow a unimodal pattern, and therefore the RCT mechanism is supported.

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1. INTRODUCTION TO COMPETITION IN AFRICAN UNGULATE COMMUNITIES

HISTORICAL NOTE ON COMPETITION THEORY

Evolutionary ecology developed initially with a strong expectation of finding extensive evidence of competition in most communities (Murray & Illius 2000). The evolutionary paradigm of Darwin, with its all pervasive influence of competition as an explanation for patterns in evolutionary time, was applied to ecological situations without much discussion of the difference between evolutionary and ecological time scales (Abrams 1990).

Theory

Schoener (1982) summarised the major features of competition theory in six propositions. These were

1. competitive exclusion (demonstrated by Gause's experiments and modelled by the Lotka-Volterra equations)
2. resource partitioning among coexisting species
3. character displacement
4. allopatry of potential competitors (competition determines a community's species composition)
5. the possibility of interference competition (as well as exploitation competition) in some circumstances
6. the idea that competition could be experimentally detected by measuring the response of a population of one species to the introduction or removal of individuals of another species sharing the same resources.

Early theoretical workers described various patterns that could be expected in communities that are strongly influenced by competitive interactions. A fundamental feature of the theory was that the mechanism of competition is resource mediated. Logistic population models (Volterra 1926, Lotka 1932, Gause 1934, 1935) predicted strong negative interactions between species that share resources. These population models were developed and applied to multiple species competing for resources that vary along a resource character axis such as seed size. MacArthur & Levins (1967) estimated the competition coefficients of the Lotka-Volterra model by measuring the similarity in resource use of pairs of species, and May & MacArthur (1972) predicted the degree of similarity in resource use permissible between coexisting species. Logistic models consistently predicted the exclusion of one species by another when resources were shared.

Fundamentally however, these models were all descriptive rather than predictive (Tilman 1982, Grover 1997). They were unable to predict which of a pair of species would turn out to be the stronger competitor unless the model was previously calibrated by measurements or *ad hoc* estimations of the competition coefficient. They also generally avoided modelling the resource exploitation mechanism assumed to underlie most competitive interactions. Lack of knowledge about the mechanisms of exploitative competition has been a long-standing fundamental problem for theoretical community ecology (Tilman 1987). Such field and experimental evidence as existed during the early development of theory more often than not identified interference as the competitive mechanism, not resource exploitation, and the role of competition in general and resources in particular in structuring communities came under increased criticism from the mid 1970's onwards (Schoener 1982).

The strength of the exclusionary prediction led to the equilibrium model of island diversity (MacArthur & Wilson 1963, 1967, MacArthur 1972), in which immigration rates of new species are balanced at equilibrium by extinction rates due to competition among resident species. Exclusion of species was also expected to complement evolutionary character shifts in forming communities of competitors with regular, relatively large character differences, in the theory of limiting similarity (Hutchinson 1959, MacArthur & Levins 1967, May 1973, Abrams 1983). A further application of the exclusionary principle came in Diamond's (1975) description of 'checkerboard' patterns of species occupancy of islands in an archipelago. In this pattern, islands are occupied by one or other of a pair of ecologically similar species, sometimes neither, but never both.

Empiricism

Early empirical work tended to support the competition theories, and widespread competition in extant communities became the dominant paradigm of community ecology. Connell (1983) and Schoener (1983) reviewed the evidence from field studies and found widespread agreement with the competitive predictions of the exclusionary principle tradition. Population sizes of species that shared resources were negatively related where the species occurred in sympatry, and experimental perturbations of the population sizes of suspected competitors often produced the predicted response.

However, there were also many cases where competition was not supported. Both authors also pointed out that there is a strong reporting bias in their literature review studies. Significant results (that support competition when compared to a null hypothesis of no competition) were much more likely to be submitted to journals, and accepted by editors, than non-significant results (failing to reject the no-competition null hypothesis). In fact, non-significant results tended to be reported only as part of larger studies that examined several localities or combinations of species, usually finding enough significant results to 'justify' publication.

Evidence of limiting similarity in the distribution of character values among coexisting competitors appeared to be widespread, until the review and re-analysis of Simberloff & Boecklen (1981). These authors were concerned at the lack of statistical testing in the literature up to that point. They identified appropriate tests from the statistical literature. The Irwin (1955) test identifies whether the smallest observed difference in character values in a set of species is larger than might be expected at random. The Barton & David (1954) test examines whether size ratios from a community are more regular than expected. Simberloff & Boecklen (*ibid.*) found that only four of the 21 claims of ratio constancy were strongly supported. A further three were supported in a minority of the cases reported by the original paper. Only one of 18 claims of an unexpectedly large minimum difference was supported for all cases described by the original paper. A further six studies' claims of large minimum differences were supported in some, but not all, cases.

Aspects of the methodology of Simberloff & Boecklen (*ibid.*) have been criticised. In particular, their methods for combining statistical tests are likely to be excessively conservative (although they attempted to ameliorate this by repeating their analyses with a threshold of $P < 0.3$ rather than $P < 0.05$). For instance, requiring all or a majority of individual cases reported by a paper to be supported by the statistical tests is very conservative. Losos, Naeem & Colwell (1989) re-analysed the data of Simberloff & Boecklen (*ibid.*), using Fisher's log sum of probabilities to combine tests from different localities within a broader study. They found more cases of limiting similarity (almost 50%), but nevertheless, the expectation of finding widespread evidence of competitive structure in ecological communities had been significantly reduced.

Conclusions

Schoener (1982) summarised several important issues in the development of competition theory. Firstly, mathematical ecologists tended to be sympathetic to the general resource competition thesis. Models with different assumptions and basic structure proliferated, but the focus on resource exploitation remained. However, detailed studies investigating resource exploitation itself were rare (Tilman 1987).

Secondly, reanalyses of previous field observations, which had been used to support various aspects of the resource competition paradigm (particularly limiting similarity and patterns of sympatry and allopatry), suggested that non-random, competitive structuring was in fact rare. These studies (e.g. Simberloff & Boecklen 1981, Connor & Simberloff 1984) depended on the construction of statistical null hypotheses that in many cases turned out to be indistinguishable from the observed pattern.

A third strand of debate argued that the magnitude of environmental variability experienced by most species would swamp any competitive interactions most of the time. Species rarely exist at close to carrying capacity, and therefore resources are usually in excess and competition for resources cannot occur. Only very occasionally are populations able to outstrip resources and become susceptible to resource depletion by a competitor. But even then, outside factors (typically climate) soon reduce the population size so that it escapes from competition, and any evolutionary or ecological consequences are short lived and unlikely to be observed. However, Schoener's (1983) review of field experiments revealed that competition was frequently observed in nature. Fluctuations either in the intensity of competition or in the supply of resources were not such that competition was extremely rare.

The fourth major criticism of the importance of competition in natural communities is that predation is much more important. In some situations, predation has been shown to regulate prey species populations, which therefore are not in competition for resources. Hairston, Smith & Slobodkin (1960) and Slobodkin, Smith & Hairston (1967) produced a logical argument that predators and producers should normally be resource limited (and therefore in competition), whereas herbivores are limited by predators and therefore generally are not in competition with one another. This argument has been criticised by Sinclair (1975), who points out that the resources available to herbivores are a very small proportion of the vegetation biomass. Most primary productivity is entirely indigestible to herbivores. Furthermore, primary productivity typically varies seasonally, and the important stage for competition and resource limitation among a herbivore guild may be a short but severe period each year.

The early expectation that competition would emerge as the dominant force structuring biological communities has given way to the reality of ecological complexity. More stringent testing of hypotheses has led to the rejection of many claims that competitive mechanisms are responsible for observed patterns of community structure. Nevertheless, some claims of the structuring power of competition have been supported. The focus of community biology has shifted from the search for patterns that can be interpreted as competitive structure, to the search for the factors that are present in those communities for which a competitive hypothesis is supported. The key to this programme will come from detailed studies of resource use in different groups. One important group whose resource ecology has been studied in considerable depth is the ungulates.

UNGULATE FORAGING ECOLOGY AND RESOURCE COMPETITION

Over the past three decades, a large body of both theory and fieldwork has developed describing the physiological ecology and inter-specific interactions of wild ungulate feeding (*e.g.* Gwynne & Bell 1968, Bell 1970, Jarman 1974, Owen-Smith 1982, 1985, Demment & van Soest 1985, Belovsky 1986, Illius & Gordon 1987, 1992, Hofmann 1989, Alexander 1991, Murray 1991, 1993, Murray and Brown 1993, Murray and Illius 1996, 2000, van Soest 1994, Prins & Olff 1998, Wilmshurst, Fryxell & Bergman 2000). This fundamental database has provided the basis for an expanding literature investigating ungulate community structure. Species-area relationships (Soulé, Wilcox & Holtby 1979, East 1981, 1983, 1985, Burkey 1995), total carrying capacity (McNaughton *et al.* 1989, Oesterheld, Sala & McNaughton 1992, Fritz & Duncan 1993, 1994) and the relative carrying capacities of species in different size classes (Bell 1982, 1984, East 1984), the productivity-diversity relationship (Western 1991, Rosenzweig 1995, Ritchie & Olff 1999), and species packing and body size distributions (Prins & Olff 1998, Ritchie & Olff 1999) have all received attention.

The basic relationship underlying niche differentiation in ungulates of different body sizes is the difference between metabolic requirements and digestive capacity (Bell 1970, Jarman 1974, Demment & van Soest 1985). Metabolic requirements scale allometrically with body size, with an exponent of about 0.75 for interspecific comparisons. Gut capacity is isometric with body weight (Demment & van Soest 1985). This suggests that larger animals have a greater digestive capacity relative to their requirements than do smaller animals. On the same forage (with unrestricted intake), larger animals are expected to do better than smaller animals.

However, forage characteristics vary, and intake is often limited. In particular, the fibre content of forages increases with the standing biomass of vegetation (McNaughton 1984, Demment & van Soest 1985). To achieve a sufficient intake to meet requirements, larger ungulates must accept a lower quality (higher fibre content) diet (Jarman 1974, Demment & Van Soest 1985). Incorporating these sources of environmental variability into models of ungulate foraging allowed detailed, experimentally testable descriptions of ungulate feeding niches to be made (*e.g.* Owen-Smith 1985, Illius & Gordon 1987, 1992, Gordon & Illius 1996).

These models describe the dependence of food intake rates on both forage and herbivore characteristics. They predict the nutrient assimilation rates achieved by different ungulates on different forages through detailed models of the digestion process in both ruminants and non-ruminants. The models show how ungulates of similar body size coexist through differing digestive strategies, such as the ruminant/hind-gut fermenter dichotomy (Illius & Gordon 1992), or through specialising on different components of the vegetation as grazers, browsers or mixed feeders (Owen-Smith 1985, Gordon & Illius 1996). Ungulates of differing body size, sharing the same digestive strategy and foraging on the same vegetation component, can coexist because they utilise different qualities of vegetation (Illius & Gordon 1992).

This description of ungulate resource use provides the fundamental model for interspecific, resource-based interactions in ungulate communities. The next section reviews the evidence from field studies that competition is in fact an important factor determining the structure (patterns in the characteristics of co-existing species) of ungulate communities.

EVIDENCE OF COMPETITION IN UNGULATE COMMUNITIES

Much of the research on African ungulate communities of the past four decades has taken place in the context of a widespread assumption of the prevalence of competition in ecological communities. Interpretations of field studies have often been based on competitive explanations. However, the practical focus of field research has been on the description of ungulate niches, particularly their foraging ecology, rather than the quantification of interactions between putative competitors. This has led to the development of an impressive body of knowledge on resource exploitation by individual species of ungulate, perhaps more detailed than in any other vertebrate group.

In this section, the various strands of evidence from a variety of field studies for and against a hypothesis of competitive structuring of African ungulate communities are reviewed.

Population interactions

The classical method of assessing whether species are competitors is to perturb the density of one species and observe the responses of the other(s) (see reviews by Connell (1983) and Schoener (1983)). Experimental manipulation of ungulate numbers is difficult (and generally unethical) in natural communities, but natural and anthropogenic perturbations can and have been used by alert field biologists.

One of the earliest studies to take advantage of a management perturbation monitored the large ungulate populations on a peninsula in Rwenzori National Park.

In 1957-58, one third of the population of hippopotamus were shot to control overgrazing (Eltringham 1974), and in the region of the peninsula all hippo were culled. None were allowed to return until after 1966. As a direct result of the reduction in grazing pressure, the vegetation on the peninsula recovered and populations of elephant, waterbuck and particularly, buffalo, all increased.

Poaching activity has also provided artificial manipulations of population sizes. Prins (1996) observed an increase in the population growth rate of buffalo in Lake Manyara National Park, Tanzania, when elephant were removed by poaching.

Novellie & Knight (1994) and Prins & Olff (1998) have reviewed the impacts and success of species re-introductions, using these interventions as *de facto* experimental manipulations. The re-introduction of white rhino to Kruger National Park in South Africa was successful, despite the presence of hippo in the same weight class. However, these species occupy very different ecological niches and are unlikely to compete for resources in most situations. The re-introduction of oribi to the Kruger was unsuccessful, which may have been due to the presence of klipspringer and steenbok in the same weight class. The re-introduction of common reedbuck to Bontebok National Park in South Africa also failed, with blesbok already present in the same weight class. The re-introduction of eland to Mountain Zebra National Park in South Africa was successful, with no other species present in its weight class.

In a rare experimental study, Hobbs *et al.* (1996a, b) manipulated elk population density in 32 *ha* pastures, and measured cattle population responses over four years. The elk foraged within the pastures from January to April each year, then were replaced with seven cow/calf pairs and one heifer each May. Body mass of cows and calves was strongly controlled by vegetation biomass, and vegetation biomass was reduced by elk grazing. Where vegetation biomass was less than 45 $g.m^{-2}$ after the elk grazing period, calf growth rates and body sizes were negatively correlated to elk density. Above this threshold, competition was not evident.

Distribution interactions

Sinclair (1985) used inter-animal and inter-herd distances in the Serengeti to test hypotheses of competition and anti-predation in multi-species feeding situations.

Evidence of resource separation had been used to support a hypothesis of interspecific competition, but in fact many species forage together without obvious interference. In addition, although the range of habitats used by buffalo contracts when the wildebeest herds arrive, it also contracts in parts of the ecosystem that the wildebeest do not migrate into. A further anomaly is that although wildebeest numbers have increased markedly since their recovery from the rinderpest epidemics, zebra populations have remained static, suggesting that competition with wildebeest for resources (which are limiting to wildebeest) was not occurring. Some other factor seemed to be regulating the zebra population. In order to investigate whether resource competition was occurring, Sinclair (1985) separated out the extent to which species share the same habitats from the amount of time they spend in physically close association with one another.

The arrival of the wildebeest herds in the northern Serengeti/Mara in the dry season provides a natural perturbation experiment. Compared to the wildebeest-free wet season, overlap in resource use between pairs of species *not* including wildebeest tended to decrease in the dry season (17/28 comparisons for habitat types, and 18/28 for grass height use). Overlap in resource use between each species and wildebeest did *not* decrease (14/16 comparisons). When the wildebeest arrive, other species do not reduce their use of wildebeest-preferred habitat. Impala is an exception, decreasing their use of wildebeest habitat when the wildebeest arrive, suggesting competition. For a number of species (Thompson's gazelle, topi, waterbuck and warthog), habitat overlap in fact increased, suggesting either facilitation or an anti-predation strategy.

Despite the reduction in habitat use overlap, impala (along with Grant's and Thompson's gazelle) spent an unexpectedly large amount of time in close proximity to the wildebeest herds, strongly suggesting a predator avoidance advantage for these species.

The association between zebra and wildebeest is particularly interesting. During the wet season, on the short grass plains in the southern Serengeti, zebra are found on the leading edge of the wildebeest herds. Wildebeest therefore do not facilitate zebra. Zebra also do not facilitate wildebeest, because most wildebeest do not follow the zebra. The zebra appear to obtain an anti-predator advantage by associating with the wildebeest herds, but they must stay ahead of the herds because wildebeest consume 80% of the vegetation biomass (competition).

Although the extra eyes and sheer numbers of the wildebeest herds provide other species with protection from predators, the fringes of wildebeest herds can be dangerous places, because that is where the predators gather. If both predation and competition influence the distribution of other species, then a bimodal distribution is predicted, with these species gathering either close to or within the wildebeest herds, or else at some distance away. Topi, waterbuck and warthog show such a bimodal distribution with respect to the wildebeest herds in the dry season (tall grass, Mara), and zebra in the wet season (short grass southern plains). Zebra have to move further from the wildebeest herds in the dry season because of the food limitation, removing the bimodality.

These interplays between competition and predation, with the strategies of different species changing in different seasons and locations and in response to each other's strategies, illustrate the complexity and subtlety of both ungulate community structure, and the studies required to describe and explain such structure.

Allopatric distribution

It has been suggested (Kingdon 1992) that the distribution and diversity of the smaller forest antelopes is consistent with a hypothesis of competition leading to allopatric speciation. Among the larger grazers, Bauer, McMorrow & Yalden (1994) have documented a sequence where *Equus africanus* (African wild ass), *E. grevyi* (Grevy's zebra) and *E. burchelli* (common zebra) replaced one another from north to south in north east Africa, along a gradient of decreasing temperature and aridity and increasing primary productivity. Their ranges had narrow regions of overlap, and their similarities of morphology and digestive anatomy would predict strong competition in sympatry (if resources were limiting).

Shared resources

Sharing of resources is a prerequisite for resource competition. Much of the literature on African ungulate foraging ecology presents data that illustrate various degrees of overlap in the diets of co-existing species. Measuring the importance of such overlap has been more difficult - how much diet overlap is necessary before two species have a negative impact on one another?

Sinclair (1985) solved this relativist problem by showing that many ungulates have greater overlap with wildebeest than with other species, and that the degree of habitat and diet overlap changes with the arrival of the wildebeest on their annual migration. This pseudo-experimental approach allowed him to measure overlap before and after the wildebeest herds were present, and therefore to infer that resource competition was responsible for a shift in the diet of impala (away from resources preferred and depleted by wildebeest).

Changes in habitat and forage use in other species could not be related to competition with wildebeest, and in several species supported instead a hypothesis of protection against predation. Despite their large impact on forage standing biomass, wildebeest did not have measurable negative, competitive impacts on most co-existing ungulate populations.

Depletion of resources

Demonstrating that resources are shared is only the first step towards testing a hypothesis of resource competition. Potential competitors must also be capable of reducing, by consumption, the availability of shared resources.

Eltringham (1974) showed that the removal of a large population of hippopotamus from Rwenzori National Park allowed vegetation standing biomass to increase, and population sizes of other ungulates grew.

Migrating herds of ungulates, particularly wildebeest, are capable of reducing vegetation biomass almost to nothing, typically consuming about 80% of the vegetation standing biomass (McNaughton 1976, Sinclair 1985), up to 94% (McNaughton 1985) and leaving virtually no edible material for other species. Sedentary species consume a much smaller proportion of the vegetation.

Changing resource characteristics

Grazing produces a flush of new, high quality grass growth in the growing season (Vesey-Fitzgerald 1965, McNaughton 1976, 1984, 1985), and increases the patchiness or variance of primary productivity (Vesey-Fitzgerald 1965, McNaughton

1985, 1994). At moderate intensity, the stimulating effect of grazing can increase total primary productivity (McNaughton 1984, 1985, 1994). Changes to the characteristics of resources makes them more palatable to some ungulates (facilitation), and less palatable to others (competition).

Facilitation was first described by Vesey-Fitzgerald (1960, 1965) in the Rukwa Valley in Tanzania. The valley is flooded annually, and the tall *Vossia* grasses that grow in the swamp region are first grazed and trampled down by the largest animals. The re-growth of this grass is then available to smaller bodied ungulates. On the drier perimeter plains, the higher concentration of animals maintains the vegetation in a shorter, actively growing stage that is unsuitable to the largest ungulates, and they are competitively excluded.

Bell (1970, 1971), Pennycuick (1975), and Maddock (1979) described another facilitation scenario in the annual migrations of ungulates in the Serengeti. The large-bodied, roughage specialist zebra are the first to leave the depleted dry season range, as the availability of forage falls below their requirements. They arrive on the short grass plains in the south east of the ecosystem at the beginning of the rainy season, where they break down the remaining, mature standing vegetation and help stimulate the new growth that comes with the rains. Zebra are followed in turn by wildebeest and then gazelle. McNaughton (1976) showed that gazelle benefit from the new growth promoted by wildebeest grazing.

Population limitation by resources

Several studies have reported that the ecosystem carrying capacity for ungulates is directly dependent upon primary productivity. McNaughton *et al.* (1989) compiled data for a range of world-wide natural ecosystems, and showed that primary productivity predicts herbivore biomass, consumption, and secondary productivity. The same relationship held, but with an enhanced Y-intercept, for ecosystems receiving a basic level of agricultural management in South America (Oesterheld, Sala & McNaughton 1992). Elementary agricultural practices increase secondary productivity by about an order of magnitude. Resources control ungulate productivity, with other modifying factors.

Fritz and Duncan (1993, 1994) carried out a similar analysis for African pastoral systems, and found that primary productivity and soil nutrient availability (SNA) predicted secondary productivity, but agricultural practices did not. Although their measure of SNA was crude, and their data organised by country rather than ecosystem (McNaughton, Oesterheld & Sala 1993), it seems that the most important predictor of ungulate biomass is resource availability, and that other factors are secondary.

Hairston, Smith & Slobodkin (1960) and Slobodkin, Smith & Hairston (1967) argued that less than 10% of primary productivity is typically consumed by herbivores, and that therefore the herbivore trophic level is generally not resource limited. Although the 10% figure is typical of most terrestrial ecosystems, migratory herds of ungulates are capable of consuming a huge proportion of the available biomass in grazing systems (McNaughton 1976, 1985, Sinclair 1985). Furthermore, typically most vegetation biomass is unavailable to herbivores as food. Seasonal changes in all terrestrial systems mean that there is a period when most vegetation biomass is unavailable. In forests, lignification removes most vegetation biomass from the diets of herbivores, and even the green leaves accumulate secondary compounds such as tannins and become indigestible as they mature.

Sinclair (1975) developed these ideas for herbivore guilds in the Serengeti. Arguing that smaller herbivores would be more sensitive to periods of resource limitation than larger animals, he censused populations of invertebrate herbivores (mainly grasshoppers), small mammals, and ungulates, in three different habitats: long grass, kopjes (rocky outcrops), and short grass areas. In all three habitats, food requirements fell below requirements for all three herbivore groups during at least part of the dry season.

The food deficit lasted the longest in the short grass plains. In these areas, invertebrate biomass was low and small mammal biomass almost zero. Smaller animals are most susceptible to resource limitation. In the kopjes the food deficit was much shorter, and small mammals and invertebrates were more important herbivores. In all three habitats, food was deficient for a period, and it is therefore likely that the herbivore trophic level in the Serengeti is food limited.

Insularisation can intensify the effects of seasonally limiting food supplies by preventing the animals from moving away in search of less depleted areas. Lake Nakuru National Park in Kenya was enclosed by fencing in 1987. The park is small (188 km^2), with a higher biomass of ungulates than typically supported by similar, non-enclosed savanna. The seasonal supply of food fluctuates widely, with very low protein levels and low biomass during the dry season (October to February). These fluctuations are responsible for periodic loss of body condition and mass die-offs of ungulates observed in the park (Mwangi & Western 1998).

A model incorporating spatial and temporal variability in resource supply (Illius & O'Connor 2000) has shown that grazer populations are in a form of long-term equilibrium with dry season resources, because resources are limiting in the dry season. Super-abundance of resources during the wet season can not support higher population densities if the dry season is severe.

Limitation by resources can also be demonstrated if an increase in the food supply leads to an increase in herbivore populations. In a series of papers, Sinclair and co-workers monitored the population dynamics of wildebeest in the Serengeti (Sinclair & Norton-Griffiths 1982, Sinclair, Dublin & Borner 1985, Dublin *et al.* 1990, Mduma, Sinclair & Hilborn 1999). In the early 1970's, the food supply in the Serengeti increased as a result of higher than average dry season rainfall. The increase in the food supply led to a rapid increase in the wildebeest population. The wildebeest population stabilised in the late 1970's as food became limiting (intra-specific competition), and then fell after a reduction in the food supply after a drought in 1993. Stabilisation of the population occurred when density was high relative to food availability. Dry season mortality was also high at these times. Population growth occurred when density was low relative to the food supply.

Resource partitioning

Descriptions of the resources selected and habitats occupied by different ungulate species form the basic database of ungulate foraging ecology. Much of this data has been collected not with the goal of elucidating competition, but of understanding the requirements of species requiring management or protection, and of understanding the impacts that wild ungulates have on their habitats. However, this data can be used to assess the similarity in resource use of different species, therefore identifying at least the potential for competitive interactions (see *Shared resources* above). Conversely, the same data have often been used to characterise the differences in resource use of co-existing species. These differences have been interpreted as evidence for resource partitioning.

Few studies have actually quantified changes in resource use of several species either in the presence or absence of each. One such study (Sinclair 1985) was discussed above (*Shared resources*). There was little evidence that patterns of resource use changed in response to competition for resources, except for the interaction between wildebeest and impala.

The observation that different ungulate species consume different foods came early in ungulate field ecology. Lamprey (1963) in the Tarangire Game Reserve, Tanzania, and Jarman (1971) in the Kariba Basin of the Zambezi Valley, observed food selection and habitat use of ungulate communities throughout the seasonal cycle. In the Kariba Basin, the large mammals were forced to occupy a restricted area of woodland when the Basin was flooded. Most herbivores were browsers. In the wet season, food was abundant and diets overlapped because the animals showed less selectivity. In the dry season, food was restricted and diets also overlapped, despite increased selectivity, because food was rare. However, despite this overlap in part of the diet, the most common species were also able to exploit resources that the other species did not take. In the Tarangire, Lamprey (*ibid.*) documented a similar situation, with species diverging in at least part of their diet. Additionally, a broader range of habitat types were available, and different species occupied different habitats in the same season, and the same habitats in different seasons.

Ferrar & Walker (1974) applied more sophisticated statistical techniques to the measurement of ungulate habitat choice. Using a multivariate ordination technique (discriminant function analysis), they found that three environmental gradients predicted herbivore distribution in Kyle National Park, Zimbabwe. These were: 1) a gradient from shrubby, wooded, patchy habitat towards open grassland, 2) a gradient from rocky outcrops with minimal herbaceous layer, to open, flat country with a stronger herbaceous component, and 3) a gradient from a tall, dense herbaceous layer to a short, sparse layer. Together these axes (discriminant functions) explained 65% of the variance in their dataset of 14 herbivore species and 20 habitat variables. Vegetative structure predicts herbivore distribution.

In a similar study in a private nature reserve in South Africa, Ben-Shahar & Skinner (1988) used multiple regression and correspondence analysis to measure the habitat preferences of 10 ungulate species. Their data showed a measure of habitat separation according to vegetation structure and topography, although the interpretation of the ordination axes was less clear.

These studies illustrate ecological separation, but can say less about what is causing it. Different species end up in different places, but are they selecting these places in direct response to the measured variables, or is there something else correlated to these variables? Ordination techniques are useful in that they can combine measurements from a number of precisely defined, but perhaps not directly relevant variables, generating a much less precise, but hopefully more relevant set of environmental gradients that predict ungulate distribution. The general finding is that vegetation structure and landscape topography predict herbivore distribution. These gradients may be related to differences in resource use, but will also be affected by different anti-predator adaptations and strategies and other autecological factors.

Ben-Shahar (1991) carried out a more focussed study, comparing the diets of wildebeest and zebra in a semi-arid private nature reserve bordering Kruger National Park in South Africa. Wildebeest and zebra are both classed as roughage feeders, and occur in similar habitat types. Both are generalist grazers, showing limited selectivity for grass species. Over a two year period, the time spent feeding on different grass species was measured, and related to the availability of that species. Wildebeest were more selective than zebra, leading to dietary separation during part of the year. When forage quality fell, wildebeest, a fore-gut fermenter, became more selective whereas zebra, a hind-gut fermenter, increased their intake.

The main characteristic separating ungulate diets is their body size. Smaller animals require a higher quality diet (more protein, less indigestible fibre) than larger animals, as described above (*Ungulate foraging ecology and resource competition*). Gwynne & Bell (1968) and Bell (1970) observed that selectivity operates not just at the level of plant species taken, but also, and perhaps even more importantly, at the level of the parts of the plants that are taken. Young shoots and leaves have higher protein content and lower indigestible fibre and secondary compounds. Body size imposes constraints on the ability of animals to be selective at such a detailed level, potentially leading to resource partitioning correlated to body size.

Owen-Smith (1985) modelled the digestive capacities of different sized ungulates, and also incorporated the differing digestive strategies of ruminants (fore-gut fermentation) and non-ruminants (hind-gut fermenters). Resource partitioning was indicated by the larger animals having lower optimal quality forages than smaller animals (because high quality food was rare). Additionally, the model indicated that the range of acceptable quality food was narrower for ruminants than for hind-gut fermenters. The feeding niches of ruminants are relatively narrow. This may explain why ruminants are much more species rich in African grazing systems than non-ruminants. Owen-Smith (*ibid.*) also suggested that co-existing, browsing bovids tend to have graded body sizes, whereas co-existing, grazing bovids have much more similar body sizes.

In testing his model, Owen-Smith (*ibid*) found that small changes in the vegetation parameters led to relatively large changes in the characteristics of the optimal forager (*e.g.* body size, selectivity, intake rates, digestive parameters). This suggests that the selective pressures on ungulates to fit their foraging environment may be strong, and therefore capable of causing patterns of evolutionary change and selective extinction of similar species from ungulate communities.

Jarman & Sinclair (1979) and McNaughton & Georgiadis (1986) summarised the range of strategies that ungulates may be using to partition resources. Different species have characteristic proportions of grass and/or browse in their diets. Ungulates may select only a subset of the available plant species, and may only select specific parts of those plants they do eat. They may occupy only a subset of the available habitats, and they may use the same habitats at different times. All of these observations can be interpreted as being caused by competition, but it is very difficult to demonstrate this experimentally.

Morphological adaptations

Ungulate characteristics, especially those related to foraging and digestion, have been widely interpreted as evolutionary responses to competition, with different species becoming adapted for different niches.

Feeding strategy and gut morphology are closely related (Hofmann 1989). Grass and roughage feeders have a large rumen and complex omasum. The rumen allows an extended fermentation of the cellulose particles, and the omasum is thought to control the selective retention of the larger particles until they are completely fermented. Concentrate selectors have a higher turnover or throughput rate, with a lower efficiency of cellulose digestion. Their rumen is smaller and the omasum simpler, but the absorptive surfaces of their guts are densely papillated for rapid uptake of nutrients. Mixed feeders have intermediate gut morphology.

Optimal gut morphology varies with the proportion of easily digestible cell contents and indigestible (but fermentable) cell wall in the diet. The relative sizes of ruminant gut chambers suggests that their guts are optimised for a poor quality diet. The equid arrangement, with no foregut fermentation chamber, is optimised for intermediate quality diets (Alexander 1991).

Body size as a fundamental ungulate adaptation to diet has been discussed above (*Ungulate foraging ecology and resource competition*). The relatively high metabolic requirements of small bodied animals require a high quality diet, entailing high selectivity. The small mouthparts and low absolute requirements of smaller animals are pre-adapted to the rarity of high quality food. Larger animals require bulkier food, and their large guts and mouthparts are pre-adapted to digesting and rapidly harvesting their low quality but abundant food.

Limiting similarity

Owen-Smith (1985) made several suggestions about the body sizes of sympatric and allopatric African ungulates, but unfortunately did not provide any data to test these ideas. He suggested that the widely-distributed browsing ungulates of Africa form a discretely graded body-size series with a size ratio of 2.0 to 2.5. He also stated that similar-sized browsers do not occur sympatrically. Finally, he argued that grazers of similar body size do exist, and that this allopatry is mediated by detailed specialisations in mouth dimensions.

Prins & Olff (1998) attempted to test whether sympatric grazers in African national parks have a regular weight ratio. Note that this is the opposite hypothesis to Owen-Smith (1985). Their analysis provided strong support for the hypothesis that African grazer assemblages are structured by body size, with co-existing species in a community differing in size by a constant ratio. Unfortunately, their methodology was flawed. The new analysis presented in this thesis (chapter 4) explains the problem, and shows that in fact competitive structuring of African grazer assemblages is very rare, only being observed in the Serengeti-Mara ecosystem.

Limiting difference

Facilitation occurs when a larger species grazes down the sward, stimulating regrowth that is suitable for a smaller species. Prins & Olff (1998) pointed out that facilitation will only occur where the two species are not too dissimilar in body size. Facilitation fails when body sizes are too divergent because the larger animal abandons the sward when it is still too tall and of too poor quality for the smaller animal to use. This scenario also appears naturally in the resource competition models presented in this thesis (chapter 2). In fact, the models make the prediction that coexistence is not possible if the two species body sizes are too different, introducing the possibility of a limiting difference for ungulate coexistence.

Patterns of extinction related to insularization

The theory of island biogeography (MacArthur & Wilson 1967) shows how an equilibrium species richness develops on an island. The equilibrium depends in part on the size of the island, with smaller islands supporting fewer species. This model can be applied to other insularized habitats, such as national parks, and predicts a loss of species when ecosystems or parts of ecosystems become isolated from the surrounding geography (Soulé, Wilcox & Holtby 1979, Burkey 1995). Extinctions occur partly as a result of stochasticity (random fluctuations leading to local extinction of a species, which can not become re-established by immigrants from outside the isolated region). Extinctions also occur due to increased competition, because populations are restricted in their ability to respond to competition by temporarily leaving the area.

Prins & Olff (1998) reviewed extinctions in ecosystems that had recently become insularized. In two national parks (Waza-Lagone in northern Cameroon, and Lake Manyara in Tanzania), a number of species went extinct in body size classes that had 2 or more representatives. In other words, one species disappeared while the other(s) survived or even thrived. These extinctions were not related to body size (they occurred in several body size classes in each park), and were not caused by hunting. It appears that competitive exclusion mediated by resource competition was responsible for the selective extinction of these species.

Conclusions: the evidence for competition in African ungulate communities

In many of the studies discussed above, competition is used to help in the interpretation of results. Competition is rarely treated as a falsifiable hypothesis to be tested in its own right. The attraction of competition for resources as an organising principle for understanding ungulate communities is natural, but it is important to evaluate the strength of the evidence that supports this view. To this end, these studies may be discussed under three headings.

1. Is competition possible?

For two species to compete for resources, they must both use the same resources, and there is ample evidence that ungulates do consume similar resources, especially grazers of similar body size. They must also be capable of reducing the availability of these resources. Migratory species certainly consume a very large proportion of the available food. There is less direct evidence that sedentary species severely deplete their resources. Among the smaller browsers, it is unlikely that resources are depleted by consumption, since their social systems are organised around very small groups defending exclusive territories (Jarman 1974, Estes 1974). The final requirement is that depletion of resources should limit population sizes. Several lines of evidence were reviewed, providing strong support for the population limitation of ungulates by resources. The prerequisites for competition are clearly in place and a hypothesis of community structuring by resource competition is therefore reasonable.

2. Do ungulate communities appear to be structured by competition?

The idea that potentially competing ungulates tend to occupy disjunct ranges is cited frequently in the literature, but there have been few tests of the idea. One test was discussed above, for *Equus* species in the north of the Horn of Africa. The allopatric pattern was consistent with a competition hypothesis. The series of extinctions occurring in insularised portions of larger ecosystems reviewed by Prins & Olff (1998) could also be related to intensified competition between species in the same body size classes.

The most compelling evidence for competitive determination of ungulate communities comes from the resource partitioning studies reviewed. Grazing ungulates divide the apparently homogeneous grass resource finely among themselves. The division occurs along a gradient of forage quality, determined by the concentration of digestible protein and carbohydrate and indigestible fibre and secondary metabolites. The major morphological character that determines the division of resources is body size, in particular its influence on ungulate digestive systems, metabolic requirements and selective abilities (related to the size of their mouthparts).

There are therefore various observations, some of which are very fundamental and ubiquitous among ungulate communities, that are readily interpretable within a resource competition paradigm.

3. Direct tests of a competition hypothesis

The strongest test of a competition hypothesis involves the manipulation of population densities. Only one such direct test was found, between elk and cattle (Hobbs *et al.* 1996a, 1996b). Grazing by elk was found to negatively impact cattle population parameters, if food availability was relatively low.

Several other studies were reviewed where a natural or anthropogenic perturbation of the density of one species allowed competition with other species to be assessed. In these reports, culling or poaching reduced the density of large species, and some usually smaller species were released from competition for resources and their populations grew.

The arrival of the wildebeest herds to the northern Serengeti/Mara in the dry season each year provided Sinclair (1985) with the opportunity to carry out a very detailed competition study, using the migration as a natural perturbation. Although many species had diets and used habitats that overlapped with the wildebeest, only one species, impala, responded to the arrival of the wildebeest in a manner consistent with competition for shared resources. Facilitation and anti-predator strategies illustrated the complexity and diversity of inter-specific interactions in ungulate communities.

The opposite perturbation - adding a new species to a community - has been carried out several times as species have been re-introduced to various parks and reserves. The reviews of Novellie & Knight (1994) and Prins & Olff (1998) provided several examples which could be interpreted in the light of competition. However, other hypotheses could also be supported and there were few ancillary data available to throw further light on the particular conditions of each re-introduction.

The prediction that resource competition will tend to form communities that consist of species differing more than randomly in a character value that is directly related to resource capture was first made by Hutchinson (1959). It is difficult to generate a non-competitive hypothesis that also predicts such a regular distribution of character values, and as such the hypothesis of limiting similarity provides a strong, albeit indirect, test of the competition hypothesis. As discussed above, this test has yet to be carried out successfully for ungulate communities. Chapter 4 provides such a test.

FRAMEWORK AND AIMS

A major aim of this thesis is to apply the theoretical description of resource competition known as Resource Competition Theory (RCT) or Resource Ratio Theory to an important group of vertebrates whose resource use has been described in considerable detail. RCT was developed by mathematical workers using ideas taken from economics (León & Tumpson 1975, Hsu, Cheng & Hubbell 1981, Tilman 1982). The major applications of RCT have been in plant ecology generally, and algal ecology and microbiology in particular. Applications in animal ecology have been very rare, although the theory itself is generic and not obviously better suited to any particular group.

In chapter 2, RCT is introduced and ungulate foraging ecology placed within the RCT paradigm. A simple model of resource competition between wildebeest and topi is developed, and tested using published data. In chapter 3, a more detailed model of ungulate resource competition is developed, incorporating an explicit description of the digestive process, with body size as the fundamental variable describing differences in resource use among species.

Although the models of chapters 2 and 3 can predict the consequences of spatial heterogeneity in resources for community structure, they are not spatially explicit. As such, they describe competition within homogeneous patches, or within a non-spatial landscape consisting of different types of patches. The next two chapters analyse data from communities of ungulates, and are therefore concerned with a broader spatial scale. Chapter 4 tests whether there is evidence for limiting similarity in the body sizes of ungulates co-existing in a number of parks and reserves throughout Africa. Chapter 5 uses population data collected in the late 1960's and early 1970's by the Serengeti Ecological Monitoring Programme to test for interactions between ungulate species within the Serengeti ecosystem. The data has never been analysed in detail, and was in fact lost for several years.

The final analysis (chapters 6 and 7) looks at patterns in ungulate diversity at the continental scale. Satellite imagery is used to measure primary productivity and its spatial, seasonal and inter-annual variation (chapter 6). This data allows a rare test of the assumptions underlying the diversity *vs.* productivity predictions made by resource competition theory (chapter 7). Ungulate diversity is derived from range maps entered into a Geographic Information System (GIS).

2. THE USE OF RESOURCE COMPETITION THEORY IN VERTEBRATE COMMUNITIES: GENERAL REVIEW AND APPLICATION TO AFRICAN UNGULATES

CLASSICAL COMPETITION THEORY

Classical competition theory (CCT), derived from the mathematical models of Lotka and Volterra (see review in Begon, Harper & Townsend 1996), presents a descriptive model of the outcome of competitive interactions. Competition is derived in the Lotka-Volterra paradigm by coupling together expressions describing the independent growth of two populations with terms that describe the negative interactions between them. These coupling terms are the competition coefficients. They quantify competitive interactions, but do not explain them (Tilman 1982, 1987, Grover 1997).

To transform CCT into a mechanistic theory capable of generating hypotheses and predictions required the addition of a theory of competition coefficients. MacArthur & Levins (1967) provided a resource-based theory of competition coefficients when they defined resource-use distributions. Given a resource (such as seeds) that varies in some parameter (like size or hardness), the competition coefficient is proportional to the degree of overlap between the resource-use distributions of a pair of species. Nevertheless, the competition coefficient remains an essentially descriptive parameter, correlated to resource use overlap but not mechanistically derived from it. This limitation is the fundamental reason why CCT can predict the intensity of competition, but not the outcome (Tilman 1982, 1987, Grover 1997).

RESOURCE COMPETITION THEORY

Theoretical development

León and Tumpson (1975) first described a mechanistic model of exploitative competition between two consumer species for two resources. Explicitly basing their model upon a mechanism (exploitation) forced them to consider the nature of resources. Borrowing ideas from economics, they defined three resource types. Perfectly and imperfectly substitutable resources can either completely or partially replace one another in the diets of the consumers. Perfectly complementary (renamed as essential resources by Tilman, 1982) can not replace one another. León and Tumpson (1975) showed that at equilibrium, with coexistence of two consumer species on two resources, each species has to be more limited by a different resource. More precisely, the conditions for stable coexistence are

1) Two species competing for two **perfectly or imperfectly substitutable resources** will coexist in stable equilibrium if each of them removes at a higher rate that resource which contributes more to its own rate of growth.
2) Two species competing for **complementary (essential) resources** will coexist in stable equilibrium if each species consumes a greater fraction of the net rate of supply of its limiting resource than of the net rate of supply of its competitor's limiting resource.

The difference between these two situations is subtle. In the first case (substitutable resources), each species is limited simultaneously by two resources. Increasing either resource will increase the equilibrium population size of both species. Coexistence requires that each species consumes more of the resource that contributes more to its own growth than to the other species' growth. In the second case, perfectly complementary (essential) resources, at equilibrium each species is limited by only one resource, different from that limiting the other species. Coexistence requires that each species consumes more of the resource that limits its own growth.

The finding that two species can coexist on two resources was not new. Levin (1970) showed that at equilibrium, with no spatial or temporal variability, no more species can coexist than there are limiting factors. The innovation of León and Tumpson (1975) was their mechanistic description of how competitive exclusion occurs as a result of exploitative interactions. Tilman (1980, 1982, 1986) then took this two species, two resources model and generalised it to more species (and resources). He added environmental variability to the model, creating a theory of exploitative competition in multi-species communities in spatially variable environments. The incorporation of spatial variability allowed more species to coexist at equilibrium than there were resource types (figure 2.1a). This addition also provided a mechanism for predicting the relationship between resource productivity and consumer species diversity (figure 2.1a).

Grover (1997) has summarised the two main hypotheses of resource competition theory. These are the R* rule and the resource-ratio hypothesis.

The R* rule states that on a single resource, there is a single superior competitor. The superior competitor is the species that depletes the resource to the lowest level, thereby excluding all other species. R* is the minimum level of resource supply that can support a stable population of a given species, and depends upon the resource-dependent population growth function of the species, and on its loss rate (mortality). The superior competitor is the species with the lowest R*.

The resource-ratio hypothesis states that with two resources, at most two competitors can coexist at equilibrium for any given combination of the two resources. Whether co-existence is possible, and if so which particular pair of species can co-exist, and if not which single species, if any at all, can maintain stable populations on these resources, depends on the ratio of availabilities of the two resources, and on the absolute level of supply.

The R* rule, the resource-ratio hypothesis, and spatial variability together comprise the fundamental components of resource competition theory, which is also known as resource-ratio theory.

The nature of spatial variability

Tilman's theory assumes that spatial variation in resource supply rates is smaller (relative to the mean resource supply rate) in more productive habitats (figure 2.1a). Abrams (1988, 1995) pointed out the implications of this assumption, which he characterised as 'additive'. That is, Tilman's conception of habitat variability assumes that as we move from less to more productive habitats, the mean resource supply rate of the habitat increases by an added amount, but the range of resource supply rates encountered within the habitat does not increase. This is equivalent to adding a fixed amount of fertiliser to an experimental plot - mean productivity increases, but gross variability remains unchanged.

Abrams (1988, 1995) relaxed Tilman's assumptions about the nature of spatial variability in resource supply rates, therefore generalising the predictions about species richness - resource productivity relationships (figure 2.1b). Abrams (1988, 1995) suggested an alternative, 'multiplicative' model that may be more relevant to natural productivity gradients. Rather than adding a constant value to each location within the poorer habitat in order to simulate a shift to more productive habitat, Abrams multiplied the resource supply rates encountered in the poor habitat by a constant factor. This has the effect of increasing the range (as well as the mean value) of resource supply rates encountered in the richer habitat, and in fact maintains a constant coefficient of variation in resource supply rates between the two habitats.

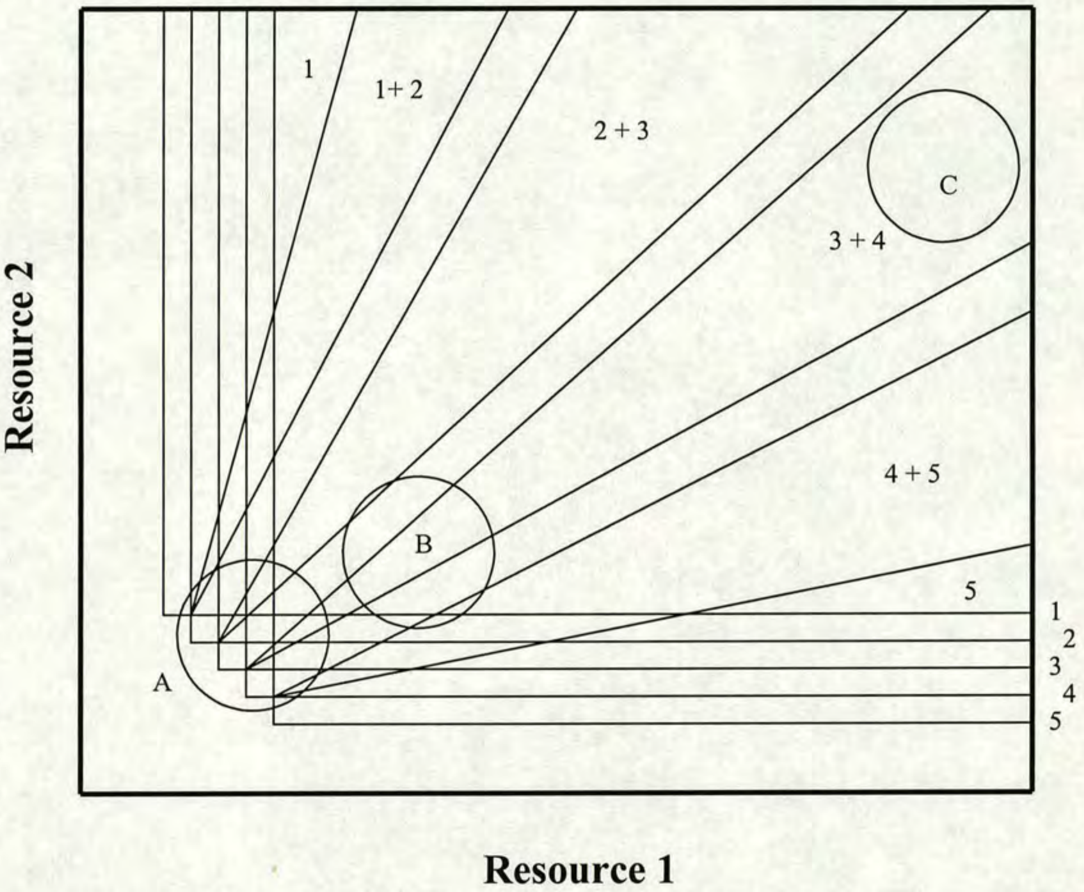


Figure 2.1a (after Tilman 1980, 1982, 1986). Spatial heterogeneity and community diversity in Resource Competition Theory: Tilman's model. This figure represents a range of habitats, varying in the supply rates of two resources. The circles (A to C) represent specific habitats. The lines (1 to 5) are the Zero Net Growth Isoclines (ZNGI's) of five species. Above and to the right of its ZNGI, a species shows positive population growth. Below and to the left, population growth is negative. Population sizes are constant on the ZNGI. The habitats have a mean supply rate for each resource (the centre of the circle), with different locations within a habitat differing to a greater or lesser degree. This variation is indicated by the diameter of the circle. Tilman's additive assumption is illustrated by habitats A, B and C. As the mean supply rate increases, variability in supply rates remains constant. Variability relative to the mean (*i.e.* the coefficient of variation) falls. Moving along a productivity gradient from the origin, to habitats A, B and C, species richness initially rises rapidly, but peaks in habitat A followed by a slower decline through habitats B and C.

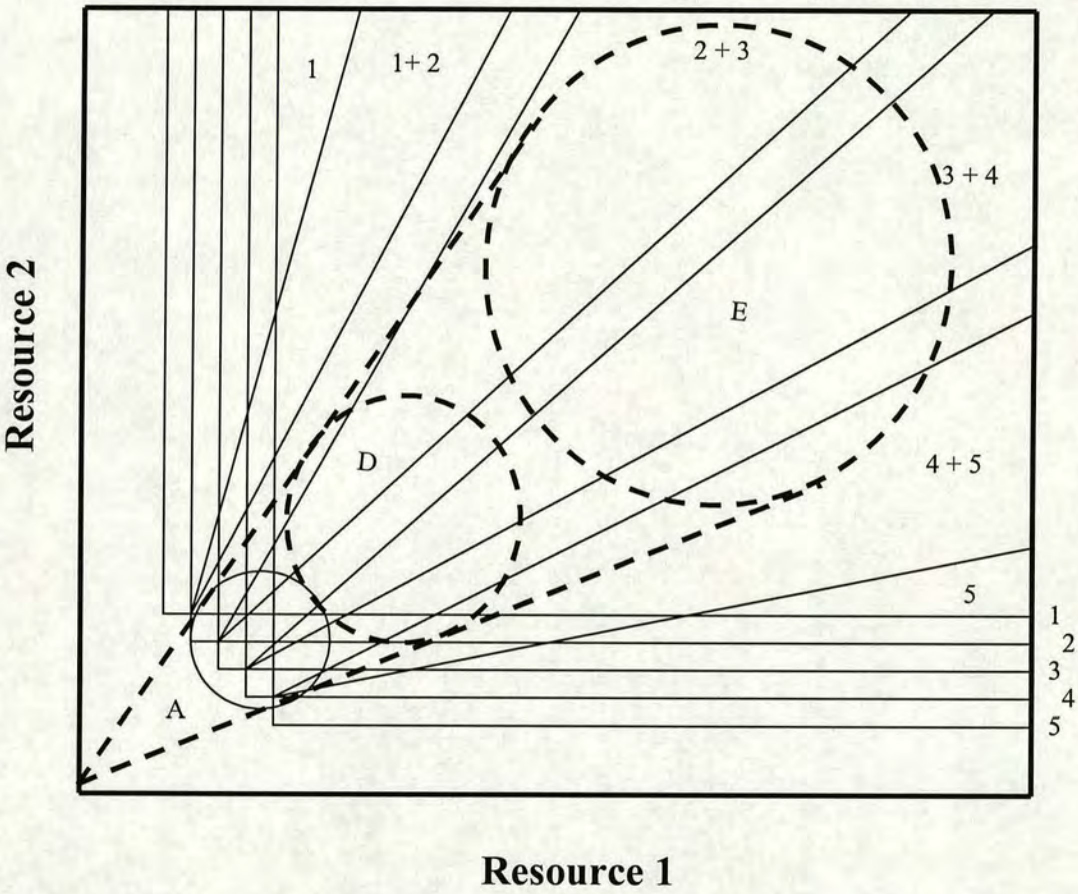


Figure 2.1b. Spatial heterogeneity and community diversity in Resource Competition Theory: Abrams' model. Abrams' (1988, 1995) alternative, multiplicative assumption, is illustrated by habitats A, D and E. The resource gradient maintains a constant CoV in resource supply rates as the mean increases, indicated by the increase in the diameter of the circles. Moving along a productivity gradient from the origin, to habitats A, D and E, species richness initially rises rapidly. However, depending on the specific details of the resource utilisation functions of the consumer species, and the nature of spatial variability in resource supply rates, diversity may continue to increase after habitat A, or may reach a maximum, or may (as in figure 2.1a) decline. Furthermore, the asymmetry predicted by Tilman's model (an early peak in diversity followed by a slow decline) may or may not be predicted under Abrams' conditions.

The species richness vs. productivity curve

The choice of model for spatial variability in supply rates is crucial. Under Tilman's assumption, species richness is predicted to first rise rapidly, reaching a peak in diversity at relatively low levels of productivity, before beginning to fall again as the relative spatial variability of productive habitats falls. Productive habitats are very simple and species poor, much like agricultural land.

Under Abrams' alternative assumption, the pattern of variation in species richness along a productivity gradient is less predictable. Diversity may rise monotonically, or rise to an asymptotic value, or may even follow the same unimodal pattern as originally predicted by Tilman. However, in this case, peak diversity may be observed at any point on the productivity gradient, not necessarily at relatively low productivity. The particular behaviour of the model depends on the resource utilisation characteristics of the group of species being modelled.

The increase phase of any diversity-productivity curve is universally accepted to be a consequence of increased population sizes of consumer species, which are therefore less susceptible to stochastic extinctions. Rare specialists can survive in productive environments (Tilman 1982, Brown 1988, Rosenzweig & Abramsky 1993, Abrams 1995, Rosenzweig 1995). The decrease phase of unimodal diversity-productivity curves has usually been attributed to decreased heterogeneity in limiting resources at high productivity, which in turn leads to more intense competition and exclusion, reducing species richness at high productivity (Huston 1979, Tilman 1982, Abramsky & Rosenzweig 1984, Rosenzweig & Abramsky 1993, Rosenzweig 1995, Begon, Harper & Townsend 1996). Rosenzweig, Tilman, Huston and co-authors all claim the unimodal pattern to be universal, and to be caused by the decreased heterogeneity hypothesis (although Rosenzweig (1995) suggests that productive regions are probably **more** heterogeneous, incorporating microhabitats with all levels of productivity).

Abrams (1988, 1995) argues that there is in fact little evidence (as opposed to opinion) in favour of the idea that productivity somehow reduces heterogeneity, and disputes both the universality and the causation of the unimodal pattern. Observations of a unimodal pattern should not be attributed to any particular theory without good supporting evidence. An important corollary is that 'productivity' should only be measured in the group of resources being competed for. Often, some measure of total energy flow through an ecosystem has been used (such as in many of the studies reviewed by Rosenzweig & Abramsky 1993). If the study measures diversity in a particular group of species, then productivity should only be measured in the resources used by those species.

The most likely explanation for the reduction phase of unimodal diversity-productivity curves is that, for some reason, competition for resources becomes more important, and competitive exclusion becomes more intense. Tilman & Pacala (1993) reviewed competition theories for mechanisms linking increases in productivity to increased intensity of competition. The best-developed idea was that high productivity is associated with reduced spatial heterogeneity. In the absence of data to back this theory, Abrams (1995) argues that monotonicity is a more likely outcome and is also the more common observation.

Despite the theoretical importance of the assumed form of spatial variability in resource supply rates, little empirical work has been undertaken to test which assumption is more often closer to the truth. This is probably due to the large amount of environmental data required to measure spatial coefficients of variation in resource supply rates. Abramsky & Rosenzweig (1984), Owen (1988, 1990) and Rosenzweig & Abramsky (1993) used Tilman's theory to explain variation in animal diversity with resource supply rates, but none of these authors had any information on the variation of spatial heterogeneity with productivity.

Conclusion

Resource competion theory (RCT) was derived from explicit statements of the resource-dependent population growth of two species. Independent measurements of the resource-based growth function of each species in isolation can then be used to predict the conditions under which coexistence is possible or impossible. Where coexistence is not possible, RCT predicts which species is excluded. Because these predictions are generated before any interactions between the species are observed, RCT is a true, testable theory, in contrast to CCT.

The development of a spatially explicit version of RCT provided a mechanistic, testable explanation for the frequently observed decrease in species richness in highly productive environments. If spatial heterogeneity falls under high productivity, then RCT predicts a unimodal diversity-productivity curve, with a relatively long tail. If spatial heterogeneity remains constant under increased productivity, then RCT predicts a monotonic diversity-productivity curve. Contrary to previous author's arguments, unimodality does not provide positive evidence in support of RCT. However, the combination of a measurement of the relationship of spatial heterogeneity to mean productivity, and of species diversity to mean productivity, would provide a good test of the theory.

RCT IN ANIMAL COMMUNITIES

RCT was first developed by León and Tumpson (1975) in a theoretical paper, and was then taken up by plant, phytoplankton and microbial ecologists (Grover 1997). Animal ecologists have been much more reluctant to embrace RCT, partly for logistical reasons and partly because of theoretical considerations.

In the CCT paradigm, a competition field experiment consists of manipulating the population density of one species and then observing changes in the density of a sympatric competitor (Connell 1983, Schoener 1983). This protocol typically involves considerable effort, particularly if generation times are long. To test the predictions of RCT requires manipulations of resources, both for isolated populations of each species and for situations of sympatry. In many animal communities the required investment of time and effort is impossibly prohibitive. In contrast, communities of microbes or phytoplankton can be set up in the lab and easily manipulated.

The main reason however that RCT is almost completely absent from discussions of animal community interactions is that the description of resources in RCT is fundamentally different from that used in CCT.

Describing resources

In this section, the major differences between the way resources are described in CCT and RCT are discussed, with reference particularly to ungulate resources.

Resources in classical competition theory

CCT focuses on a single resource, varying in some parameter, with different species specialising on different parts of the resource axis (illustrated in figure 2.2). As an aside, there is no great conceptual leap to accommodate multiple resources. Two resources are represented by a plane, with species specialising on a region of the plane, and for three resources species would specialise on a volume.

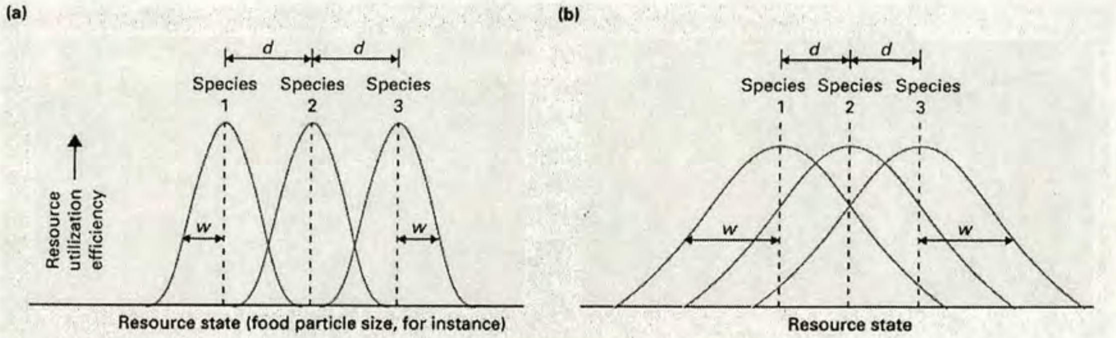


Figure 2.2. The resource axis in classical competition theory.

> "Resource-utilisation curves for 3 species coexisting along a one-dimensional resource spectrum. d is the distance between adjacent curve peaks, w is the standard deviation of the curves. (a) Narrow niches with little overlap ($d > w$), *i.e.* relatively little interspecific competition. (b) Broader niches with greater overlap ($d < w$), *i.e.* relatively intense interspecific competition."

*(**NOTE:** figure and caption reproduced from Begon, Harper & Townsend (1996), figure 7.24, with permission).*

MacArthur & Levins (1967) developed a model to predict the value of the competition coefficient from the degree of overlap between the resource use distributions of two species. Assuming that the shapes of the resource utilisation curves are the same (normal distributions, with the same amplitude and standard deviation), then the competition coefficients are equal: $\alpha_{12} = \alpha_{21} = \exp\left(-d^2/4w^2\right)$ [d and w are defined in figure 2.2].

The value of having a model of competition coefficients is that it allows observations of individual species' resource use to be used to predict whether and how strongly the two species would compete. This would allow CCT to be tested, making it a true scientific theory rather than simply a description. Unfortunately, there is no clear cut way of predicting the final outcome of competition from CCT

(Tilman 1982, 1986, 1987, Abrams 1983, Grover 1997). Even with a prediction of the (relative) strength of competition, CCT can not predict in a given case whether exclusion will occur, and if so, which species will be excluded.

Studies of competition in vertebrate groups have naturally adopted the CCT description of resources, since guilds and taxons typically consume similar food items which vary only in detail. In grazing ungulates, which consume grass, attention has focused on the fibre content of the grass as the likely parameter that determines the dietary preferences of different species. Small ungulates select low fibre components of the sward, or select patches of sward with low fibre content. Fibre is relatively difficult to digest, requiring a period of fermentation during which gut microflora can break down the cellulose and other fibres in the cell walls of plant material. The small guts of small ungulates cannot store a sufficient volume of fermenting material to supply them with sufficient energy from the fermentation products. Instead, small ungulates search out the relatively rare components of the sward that contain little fibre. This material can be rapidly digested without fermentation.

Large ungulates would also achieve higher energetic profit if they could ingest only low fibre components of the sward, but these components are too rare to support their larger energy requirements. They must accept the higher fibre material. However, they have larger guts relative to their body size than the small ungulates, allowing them to store a relatively large amount of food in their fermentation chamber.

This description of ungulate resources fits very well with the CCT definitions. A major weakness however of defining resources in this way in a model of resource-mediated competition is that there is no measure of resource availability. This aspect of resource use is addressed in RCT.

Resources in resource competition theory

RCT is derived from explicit statements about the resource-dependent population growth of consumer species (León and Tumpson 1975, Tilman 1980, 1982, 1986, Hsu, Cheng & Hubbell 1981, Grover 1997). Competition between consumer species is purely exploitative, and therefore the resource-dependent growth functions can be used to predict the conditions under which competitors can coexist, and the conditions under which one species excludes another. Exploitative competition is mediated through the depletion by one species of the resources required by another species. Both the growth of populations and the competitive interaction depend therefore on the availability of resources. This factor means that resources in RCT are described in terms of their availability in the habitat and their influence on growth when ingested. This is quite different from resources in CCT, which are used as a kind of index to estimate the competition coefficient.

The classification of resources in RCT was described originally by León and Tumpson (1975), and also by Tilman (1980, 1982, 1986) and Grover (1997), and will only be briefly summarised here. The classification was derived from microeconomics, and depends on the way consumer populations respond to varying levels in the supply of two resources. Figure 2.3 illustrates this description.

The major distinction in resource types is between *essential* and *substitutable* resources. An essential resource cannot be replaced by another resource. For example, most vertebrates cannot extract sufficient moisture from their food, and require an extra supply of drinking water. For these species, drinking water is an essential resource. Substitutable resources can at least partially replace one another. Many animal foods can be thought of as substitutable resources. An ungulate may change from grazing to browsing as seasonal change reduces the availability of grass. Grass and browse are substitutable resources if the animal is capable of digesting either type at the same time (a mixed feeder).

A class of resource that will become important in the description of ungulate foraging is *inhibitory* resources. These were described by Tilman (1982) in his detailed classification of resources. An inhibitory resource increases the minimum requirement for another resource as the inhibitory resource becomes more abundant. For herbivores, plant secondary compounds such as tannins and toxins, and indigestible residues in cell walls, behave as inhibitory resources. Tannins for example bind to digestive enzymes in the stomach, inhibiting their function. As the concentration of tannins in the plant (and therefore diet) increases, the herbivore must ingest more food to achieve the same metabolisable energy intake. This may reach the point that intake constraints prevent the animal from being able to ingest enough food for maintenance. The fibre content of cell wall can also become an inhibitory resource, since smaller animals are less capable of digesting fibre-rich diets (see below).

Another important class of resources for ungulates, and many animal species, is *switching* resources. An optimal forager choosing a diet from two switching resources will only consume one of the available types. As it moves through a habitat with variable supply rates of the two resources, it will cross thresholds of relative availabilities where it switches its diet choice from one resource to the other (see figure 2.3).

<u>Can animal resources be placed within the RCT scheme?</u>

Although it is not straightforward to place animal resources within the RCT framework, it can be very revealing to make the effort of doing so. At the very least the exercise reveals the complexity of animal resources. Part of the difficulty is that unlike plants and bacteria, animals do not absorb their food as simple, soluble chemicals surrounding them in the soil or in a growth medium.

For plants and bacteria, nutrients and resources are the same thing, but animals ingest nutrients in their food. Are animal resources the things they harvest to obtain food, or are their resources the constituents of the food from which they obtain nutrients? For ungulates, both descriptions are valid. A forager may be described as including a 'greener' component and a more fibrous component within its diet. Each of these resources provides a different set of nutrients, partly overlapping (more protein from the green component, more carbohydrate from the fibre). Alternatively, the food ingested could be described as containing two resources - cell wall (fibre) and cell contents (including most of the protein). A description of animal resources should take this nestedness into account, with nutrients derived from food, which either contains or is contained by resources, habitat patches as the container of food or resources, and landscape as the container of habitat patches. The body size of the forager can then be seen to have a fundamental influence on what components of the environment may potentially provide resources (Ritchie & Olff 1999).

Further complicating the scenario is that although the range of nutrients an animal requires is limited and fixed just as for plants and bacteria, their complex digestive systems allow them to extract these nutrients from a wide range of different

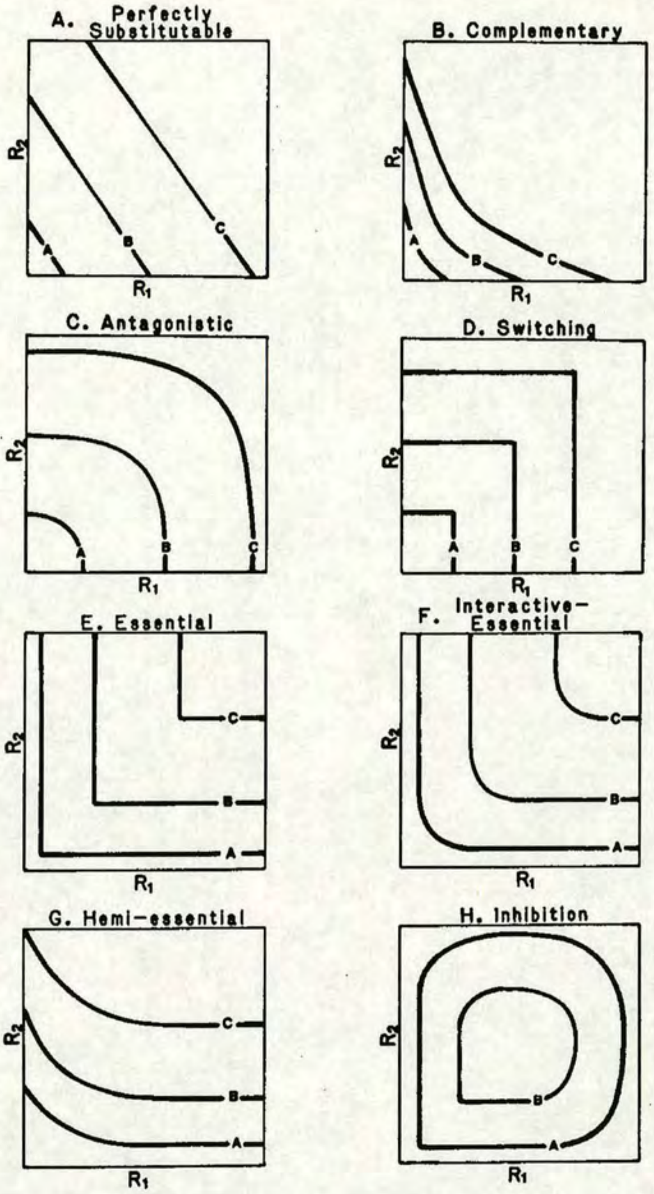


Figure 2.3. The classification of resources in Resource Competition Theory.

> "Resource-Dependent Growth (Reproduction) Isoclines. Each of the growth isoclines shown above represents the amounts of two resources which would have to exist in a habitat for an individual to have a given reproductive rate. The isoclines thus show the combinations of the concentrations of two resources which lead to a particular reproductive rate. Because reproductive rate increases with resource availability, isoclines further from the origin represent higher reproductive rates. Thus, for all cases shown above, isocline A has the lowest reproductive rate, isocline B has an intermediate rate, and isocline C has the highest reproductive rate."

*(**NOTE**: figure and caption reproduced from Tilman (1982), figure 2, with permission).*

foods that can be harvested from an even wider range of resources in their environment.

For Tilman (1982), these considerations suggested that applying RCT to animal communities would be difficult and probably unrewarding. He expected that most animal resources would turn out to be switching resources. This means that an animal would harvest a single resource until optimal foraging led it to switch to a more profitable resource, perhaps as a result of depletion of the first resource. Because most animal species seem to be capable of switching among a large variety of prey items (resources), competition between animal species would be very rare, and other processes must be explored to explain animal community structure and diversity. Tilman (1982) used this argument to explain why there are millions of animal species, but only a few hundred thousand plant species. Plants are limited by competition for a few resources, whereas animals have radiated into the extremely diverse range of habitats and niches provided by the plants.

These arguments may well hold true for many animals, such as herbivorous insects, but ecologists have long studied competition, both direct and indirect (exploitative), in vertebrates. There is abundant evidence that ungulates do compete for resources (see chapter 1), and if they do then RCT should be applicable to them. The first step is to identify, within the RCT framework, what the resources are that ungulates compete for.

Ungulate resources

The main difference between the CCT and RCT conceptions of resources is that for CCT the most important characteristic of a resource is its position along a character axis (*e.g.* seed size or hardness, or grass fibre content), whereas for RCT the most important characteristic is its availability in the environment. In some ways the two approaches may be seen to converge in the case of ungulate resources.

For CCT, grass is a single resource, varying along a quality (fibre content) axis. For RCT, grass is in fact more than one resource. Grass is composed of cell contents (CC) and cell wall (CW). CC are free from fibre, and are soluble and easily digested. CW is largely insoluble and takes time to digest - it must be fermented first. The ratio in the supply rates of these two resources determines the ability of two species to coexist or not. However, this ratio of CC / CW is in fact the 'quality' axis of CCT. Both theories predict that smaller species will have an advantage over larger species on high quality resources (see below - *Applying RCT to large herbivores*). However, as we have seen above, CCT cannot predict the outcome of competition even where it identifies that competition is intense. Resource Competition Theory not only identifies the optimal niche of each species. It can predict the outcome of competition between two species occupying overlapping niches.

The outcome of competition

The initial research undertaken in a RCT project allows the predictive competition diagram to be constructed. Several examples are contained in figures 2.4, 2.5, 2.6 and 2.7. Various regions are labelled on these diagrams. Each region represents a range of habitats varying in the abundance of the two resources. Table 2.1 lists the outcome of competition in each of these regions. These outcomes are derived from a consideration of the directions of the consumption vectors. Reference to the figures and table 2.1 will assist in the following description.

A supply point is given by the values of the supply rates of the two resources, and is defined as the equilibrium resource availability in the absence of the consumer species. Introduction of a consumer population to that habitat will result in a reduction in the available resources. This reduction follows the consumption vector of the species, and continues until the ZNGI of the species is reached. At this point the system equilibrates, with a supply vector pointing from the point on the ZNGI back towards the supply point, and an equal and opposite consumption vector pointing in the opposite direction.

If both consumer species are present, the system follows a trajectory intermediate between the consumption vectors of the two species, until the ZNGI of one species is reached. Assuming that the supply point lies outside region III (i.e. either in region I' or II'), this point will not coincide with the crossover of the two ZNGIs. The system will then move over this ZNGI and the population growth rate of the first species becomes negative. Eventually this species will be excluded, and the system now proceeds along the consumption vector of the surviving species until finally its ZNGI is reached. Because of the influence of the excluded species during the first part of this trajectory, the supply and consumption vectors will not be lined up at this point, but the system will move along the ZNGI until they do, and the system equilibrates.

If the initial supply point lies within region III, then consumption by the two populations will move the system roughly towards the point where the 2 ZNGI's cross over. However, in most cases the system will reach one of the dashed lines first (the dashed lines are extensions of each species' consumption vector at the equilibrium point). Which line depends upon the starting population sizes. At that point, the system will either move towards the cross over point and become stabilised when it reaches there, or it will cross over into region I' or II' and proceed towards the exclusion of one or other species.

The conditions for stability were described at the beginning of this chapter. Translating these conditions into the graphical model, the system will reach a stable equilibrium if the consumption vector of one species lies closer to the ZNGI of the other species. For instance, in figure 2.4C (illustrating the Bell-Jarman principle), the crossover is stable and a smaller and larger grazer can stably coexist. The system is unstable if the consumption vector of each species lies closer to its own ZNGI.

APPLIED RCT: ANIMAL ECOLOGY

Resource competition theory has seen many applications in plant ecology, especially in freshwater (Carney 1987, Leibold 1997) and laboratory algal communities (Tilman 1976, 1977, Grover 1991, Codeço & Grover 2001), as well as applications in microbial ecology (Kassen *et al.* 2000) and pathogenicity (Smith & Holt 1996). Applications of RCT in animal ecology have been very much rarer.

Zooplankton

Rothhaupt (1988) carried out very similar chemostat experiments to those originally used with freshwater algae. Instead of supplying two algae species with two soluble nutrients, Rothhaupt (*ibid.*) supplied two rotifer species with two algal species to graze or predate. The algal prey were either small or large, and the zooplankton preferred (grew more rapidly on) smaller or larger prey items, but could take either. The experiments confirmed that where enough information could be gathered to fully describe the resource-dependent growth of each population in isolation, a model could be specified which would accurately predict the outcome of competition under different resource supply scenarios. There is no fundamental reason why RCT should not be applied to animals.

Desert rodents

Abramsky & Rosenzweig (1984) appealed to RCT as an explanation of a unimodal diversity-productivity relationship they observed in rodents in the deserts of Israel. The only evidence they had that an RCT mechanism was applicable was that the decrease phase of the curve appeared to have a long tail, as predicted by Tilman (1982). However, as described above, the long tail is not necessarily characteristic of resource-based competition (Abrams 1995), and the tail depended on just one data point. Another appeal to the theory was made by Owen (1988, 1990) to explain a unimodal diversity-productivity relationship in desert rodents in the southern United States, but again no other data were presented to allow the exclusion of alternative hypotheses.

THEORETICAL RCT: UNGULATE FORAGING SCENARIOS

In this section, a number of ungulate foraging strategies and digestive capabilities are briefly described in relation to different resource types, and placed in a graphical RCT context. The sequence of scenarios begins with a highly simplified situation, and proceeds by relaxing a series of assumptions about ungulate foraging (see figures 2.4 & 2.5).

The following section constructs more detailed mathematical models of some of these scenarios.

Sward capture - figure 2.4A

In this highly simplified scenario, a large and a small grazer compete for long and short grass. Both resources are completely substitutable in the same ratio for both grazers, resulting in parallel ZNGIs. The small grazer requires fewer calories than the large grazer, and can maintain a viable population on a lower level of resources than the large grazer. In addition, because the small grazer has a smaller mouth, it is able to graze the grass to a lower level. Both circumstances mean that the small grazer can deplete both resources below the level required by the large grazer, and the large grazer is excluded.

This scenario involves the simplifying assumptions that long and short grass do not vary in quality (long grass does not have more cell wall and less cell contents), and that small grazers do not suffer lowered foraging efficiency in tall swards. In fact, this can be viewed as a model of just a single resource, grass. However, this model provides the basis for the other scenarios, where the simplifying assumptions are successively relaxed.

Selectivity - figure 2.4B

In this scenario, the body size implications for digestion are also ignored, and two ungulate species differing purely in their selective ability are considered. The two species have equal body sizes (and therefore digestive capabilities) but differing selective abilities. One species is a green leaf selector, achieving a higher proportion of green leaf in the diet than the other ungulate on the same sward. The second species is an intake maximiser, and obtains a higher proportion of stem in the diet than the other species. The two resources are perfectly substitutable, but stem provides fewer calories per *kg* per hour of digestion than green leaf. The resulting ZNGIs and consumption show that this scenario leads to stable coexistence.

This scenario may be compared to topi and wildebeest, which have similar body sizes but differ in their selectivity (Murray 1991, Murray & Brown 1993, Murray & Illius 2000). Topi have a narrower mouth and achieve a greater proportion of green leaf in their diet than wildebeest when feeding on the same sward. Topi and wildebeest do not however exactly match the pure selectivity scenario because the wider mouth of the wildebeest allows it to achieve a greater intake rate on short swards. This trade-off considerably complicates the scenario, as will be seen later when the topi vs. wildebeest scenario is formally modelled.

Bell-Jarman hypothesis - figure 2.4C

The Bell-Jarman scenario relaxes the assumption that long and short grass are equally substitutable for both species. Larger species have more efficient digestive systems because their gut volume is larger relative to body size than in smaller species (see chapter 1). Therefore a large grazer obtains more energy per kilogram of long grass than a small grazer can, because the larger grazer is able to retain its food in the fermentation chamber for longer.

The ZNGI of the large grazer has a steeper slope because a small increase in the availability of long grass can compensate for a large decrease in the availability of short grass. For the smaller grazer, long grass is a poorer resource, and reduced availability of the short grass resource can only be made up by a relatively large increase in the availability of long grass. Note that in reality, too much long grass will become a limiting factor to the smaller species. This aspect is taken up in the facilitation model.

The differing slopes mean that the ZNGIs cross, allowing potential coexistence. The stability of such coexistence depends on the directions of the consumption vectors. If at equilibrium each species consumes relatively more of the resource that most limits it, then coexistence is stable (León & Tumpson 1975). In the Bell-Jarman scenario, this condition requires that the small species is more selective of the short grass (high quality) resource than the large grazer. This is in fact the case. Smaller species have narrower mouths that are more efficient at selecting nutritious plant parts, and smaller species have lower gross energetic requirements, allowing them to devote more time to searching for high quality resources.

The model predicts that in swards with relatively little long grass, the small grazer excludes the large grazer (region I'). Where long grass is abundant and short grass scarce, the small grazer is excluded (region II'). At intermediate ratios, the species coexist (region III).

This model assumes that there are no intake constraints. The small grazer is able to substitute a large volume of poor quality stem for a smaller volume of nutritious green leaf, and is not constrained by its small gut. Intake constraints are introduced in the next scenario.

Hind-gut versus fore-gut fermentation - figure 2.4D

In this scenario an intake constraint is introduced (and the body size effects of the previous model neglected), resulting in an intriguing ZNGI diagram. Zebra, with a hind-gut fermentation, are able to achieve a higher throughput of food than the fore-gut fermenting wildebeest. On low quality, unrestricted availability swards, zebra can extract more nutrients than wildebeest. The fore-gut fermentation stage of wildebeest restricts their ability to increase intake rates on abundant swards.

However, the extra retention time allows wildebeest to extract a higher proportion of the available nutrients from the less digestible portion of their intake (the stem material), and the wildebeest ZNGI is therefore steeper. On poor quality forages, this gives them an important competitive advantage over the zebra, because wildebeest can extract sufficient resources for survival from a much shorter sward than would support zebra. On high quality swards there is much less of an advantage, because green leaf is rapidly digestible and the hind-gut fermenter is able to fully digest the material despite its shorter retention time. These considerations mean that wildebeest are able to exclude zebra from all habitats, all other things being equal.

The consumption vectors illustrate the greater selectivity of the wildebeest for green leaf. This is because with a lower intake than zebra, the wildebeest have more time available to be selective.

As well as the ZNGI of each species, the figure shows some resource-dependent net growth isoclines for each species. These are derived by considering the consumption vectors. Where green leaf is abundant, wildebeest are able to achieve a higher intake of the leaf than are the zebra. These extra resources are available for reproduction and result in a steep increase in the wildebeest population in habitats with abundant green leaf (marked 'W' on the graph). Conversely, the unrestricted intake rate of zebra when stem is abundant allow their populations to grow more rapidly than wildebeest when the sward is tall but of low quality (marked 'Z').

These differential population responses to sward conditions suggest that a relatively small amount of environmental variability, whether spatial or temporal, will allow the zebra population to persist. The basic model therefore predicts that wildebeest will exclude zebra, but it also suggests that relatively minor deviations from the habitat assumptions implicit in the model could allow zebra to thrive even in the presence of wildebeest.

Migration - figure 2.4E

Migration is a strategy used by several important species in the grazing systems of Africa. Sedentary species, which remain in the same area throughout the year, are not able to develop high population densities because they are limited by food availability for part of the year (see chapter 1). They may also be limited by predation (Sinclair 1995). Migratory species achieve their high densities by moving away in search of food when it becomes limiting in the current locality. In systems such as the Serengeti/Mara, the annual migrations are probably the most important process occurring within the ecosystem, and as such it would be very desirable to contrast the migratory and sedentary strategies in a ZNGI model. Such a model may provide insights into whether migratory and sedentary species compete for resources, and if so, under what conditions.

Unfortunately I have been unable to design such a model. Figure 2.4E is therefore blank and I invite the reader to design a suitable model and get in touch! It may be that the migratory and sedentary strategies simply do not compete, because when resources are scarce enough to limit the sedentary species, the migratory species leaves in search of greener pastures.

Facilitation - figure 2.4F

Resource competition graphical models are also capable of describing positive interactions. Facilitation of smaller grazers by larger species occurs when a large species enters habitat with a tall sward of mature, low quality grass, having a high proportion of stem and little green leaf (chapter 1). Smaller species are unable to colonise such habitat because the grass is of too low quality to support them, and also because the tall grass impedes their ability to obtain bites. The larger species can trample the grass down, and can also graze more effectively on such tall swards. The digestive advantages of larger species allow them to survive on lower quality food than the small species can tolerate.

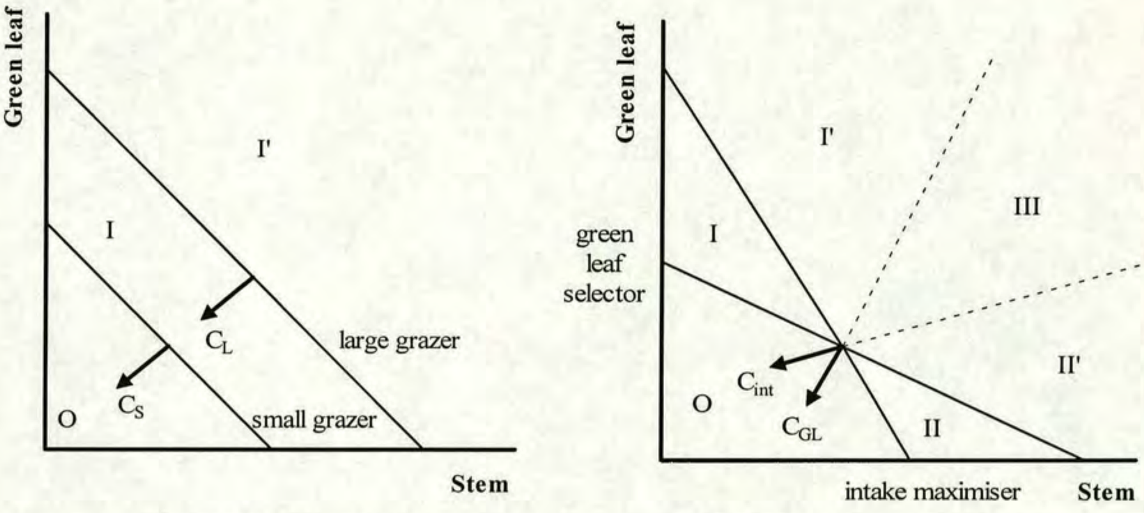
The inability of species to use swards with a high proportion of stem is indicated by the upward sloping sections of the ZNGIs. For a small species, a relatively low abundance of stem becomes intolerable. The larger species can tolerate a higher proportion of stem in the sward. This difference in the tolerance of low quality swards allows the ZNGIs to cross, even given all the other simplifying assumptions of the original sward capture model (indicated by the parallel sections of the ZNGIs, as in the sward capture scenario).

At the intersection of the ZNGIs, coexistence is possible, but examination of the diagram shows that coexistence is never stable in this system. There is no region III on the diagram, and only supply points exactly on the dashed extension to the large grazer's consumption vector can lead to the coexistence point. The new region IV indicates habitats which initially can only support one species (the larger in this case), but from which the system moves to region I' (both species supported) and finally to region I (the original species is excluded by the second, facilitated species). Region II, where the larger species can permanently exclude the smaller species, is small, and in most habitats the final outcome will be exclusion of the larger by the smaller, often after facilitation of the smaller by the larger.

Sward capture, facilitation and the Bell-Jarman principle - figures 2.4G & 2.5

In the final conceptual model (figure 2.4G), several of the assumptions are relaxed in the same diagram, by giving the ZNGIs different slopes (Bell-Jarman), by giving the consumption vectors different slopes (selectivity), and by introducing the upward sloping segments to the ZNGIs (digestive capacity constraint). Coexistence becomes stable again as in the Bell-Jarman diagram, if the ZNGIs intersect before the upward sloping segments.

Figure 2.5 further illustrates this scenario for three pairs of species, varying in the body size difference between the pairs. This model suggests that equilibrium coexistence is more likely for species that are sufficiently, but not extremely, different in body size. For species of similar body size (figure 2.5A), the consumption vectors are very similar and only a very narrow range of habitat types allow coexistence. This conclusion mirrors CCT - very similar species cannot coexist because they must compete for the same resources. For species very divergent in body size (figure 2.5C), coexistence becomes unstable. Region III (habitats allowing stable coexistence) is maximised for species with an intermediate body size difference (figure 2.5B).

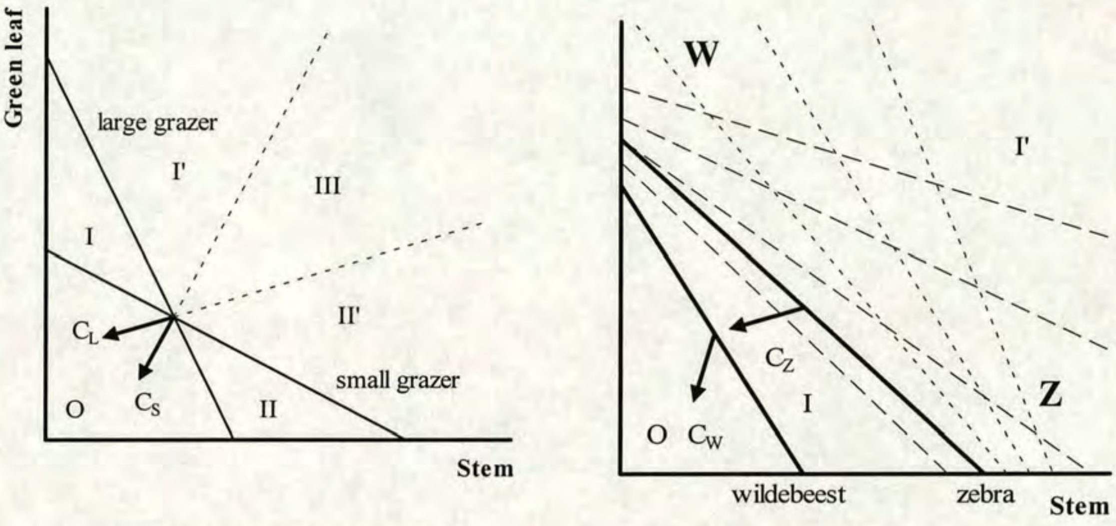


A. Sward capture

B. Selectivity *vs.* intake

Figure 2.4A, B. Simple graphical resource competition models of ungulate foraging ecology. Table 2.1 describes the dynamics associated with the labelled regions on the diagrams.

A. *Sward capture.* The only difference between the 2 species is that the smaller requires less food (can achieve maintenance intake on a lower standing biomass of forage). The smaller species can therefore continue depleting the resources when the larger species has a zero net growth rate, eventually excluding the larger species from all swards.
B. *Selectivity vs. intake.* One species is more selective for green leaf, incurring an intake rate constraint because of the extra time taken to select green leaf, or because of the smaller mouthparts adapted to being selective. The slope of the ZNGI for the green leaf selector is shallow because a small increase in the availability of green leaf can replace a relatively large decrease in the availability of stem. For the intake maximiser, the ZNGI is steep because green leaf and stem are equivalent, and the proportion of each in the diet is the same as in the habitat. The consumption vectors now diverge because of their differing selectivity. Coexistence is possible for habitats with supply points in region III, and the equilibrium is stable.



C. The Bell-Jarman principle

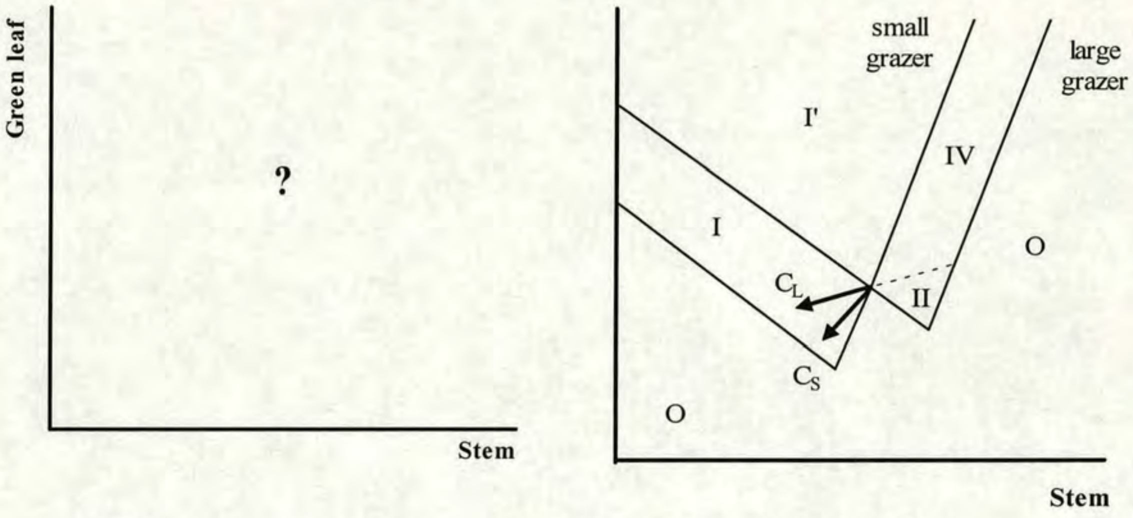
D. Hind-gut *vs.* fore-gut fermentation

-------- zebra population growth isoclines
– – – – wildebeest population growth isoclines

Figure 2.4C, D. Simple graphical resource competition models of ungulate foraging ecology. Table 2.1 describes the dynamics associated with the labelled regions on the diagrams.

C. *The Bell-Jarman principle.* This model introduces the different digestive capabilities of small and large animals. The model is in fact structurally identical to model B, but provides a physiological explanation for different levels of selectivity. Smaller animals cannot digest poor quality food efficiently, but because of their lower gross energetic requirements and smaller mouthparts, they are able to feed more selectively. Note that the model does not yet incorporate the negative effects of low quality forage on smaller species. The ZNGI of the smaller species crosses the 'stem' axis, unrealistically predicting that smaller animals can replace all the leaf in their diet with a huge amount of stem.

D. *Hind-gut vs. fore-gut fermentation*. Hind-gut fermenters achieve a greater throughput of food, carrying out a less thorough fermentation of more food than a fore-gut fermenter of similar body size. Note that *absorption* of nutrients from the gut is a relatively rapid process, and therefore the digestive efficiency of hind-gut and fore-gut fermenters for the high quality component of the diet is similar. On a diet entirely consisting of green leaf, the ZNGI's of both species cross the green leaf axis close together. On a sward consisting only of stem, the longer fermentation time of the fore-gut fermenter allows the wildebeest to survive on a much shorter sward. In a static habitat, wildebeest should be able to exclude zebra from all habitats. However, the different consumption vectors give zebra a high growth rate on abundant, poor quality swards, and wildebeest a high growth rate on abundant, rich swards, so that a minimal degree of exogenous environmental variability can allow the species to co-exist.



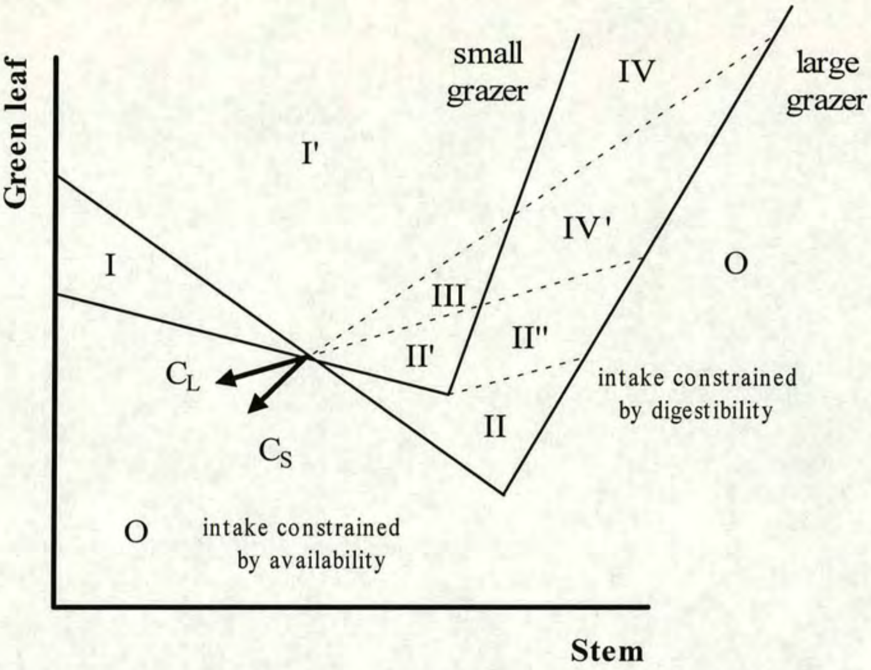
E. Migratory *vs.* sedentary

F. Facilitation

Figure 2.4E, F. Simple graphical resource competition models of ungulate foraging ecology. Table 2.1 describes the dynamics associated with the labelled regions on the diagrams.

E. *Migratory vs. sedentary.* Migration is a very important strategy of some African grazers, and as such it would be desirable to design a model to describe it. I have not been able to come up with one. Migrants by definition move around, encountering a much higher mean level of resources than if they remained in one place. Sedentary species usually encounter migrants only when resources are locally abundant. Sedentary species are likely to be limited by resources at a point in the seasonal cycle when migrants are elsewhere, and therefore migrants and sedentary species may be able to avoid competing with one another entirely.

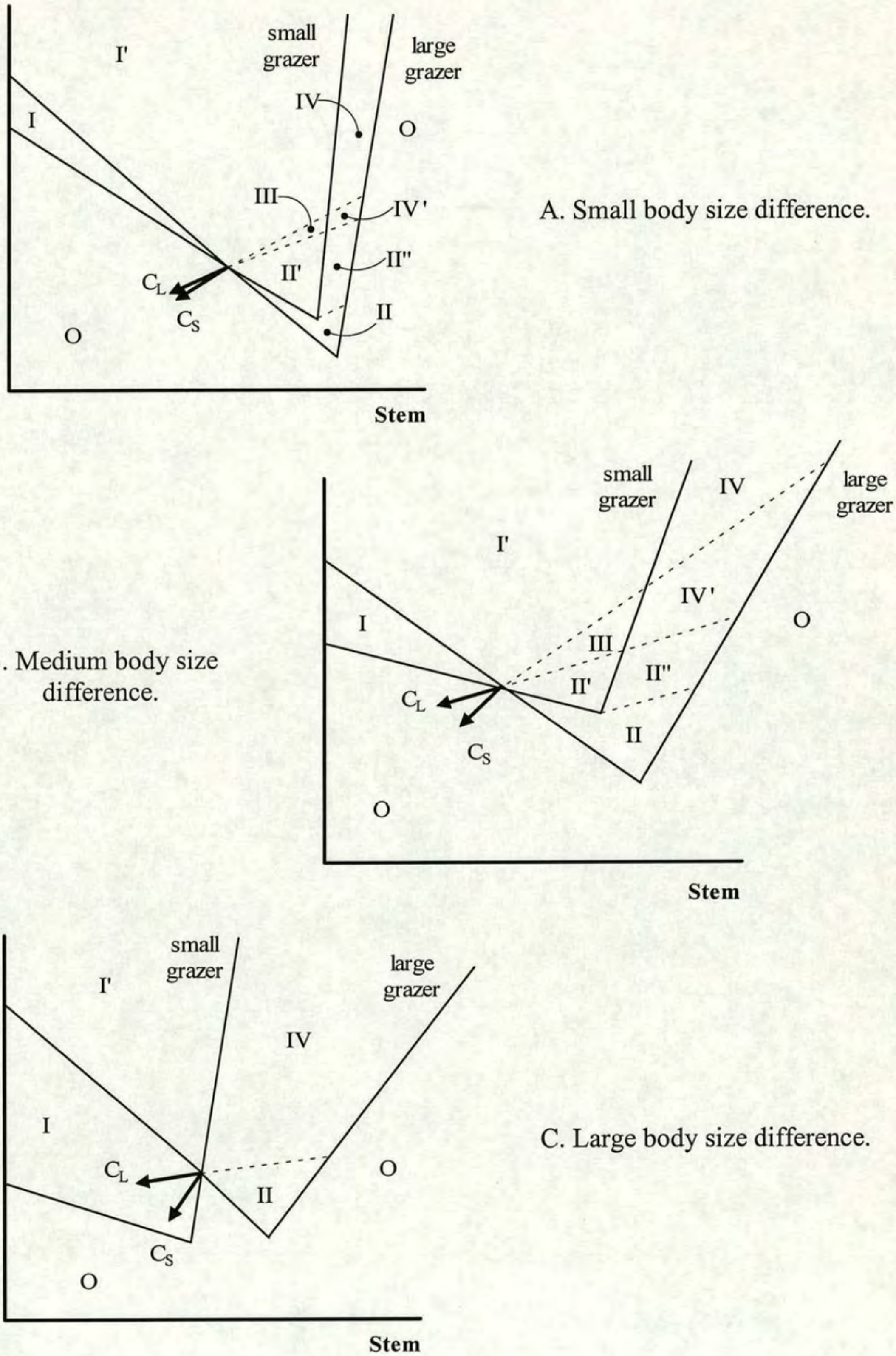
F. *Facilitation.* This model introduces the negative effects of poor quality sward. Animals are constrained by the amount of food they can ingest, with smaller herbivores constrained more strongly. Abundant stem in the sward results in a high proportion of stem in the diet, even for highly selective animals. The smaller animal digests this food less efficiently than the larger animal, so that stem becomes an resource. This effect is shown by the upward sloping portions of the ZNGI's, with the smaller species suffering first. This generates a new region, labelled 'IV', which can only support the larger species. However, consumption by the larger species eventually moves the standing biomass of resources into region I', and eventually the smaller species excludes the larger.



G. Sward capture, facilitation, and the Bell-Jarman principle

Figure 2.4G. Simple graphical resource competition models of ungulate foraging ecology. Table 2.1 describes the dynamics associated with the labelled regions on the diagrams.

G. *Sward capture, facilitation, and the Bell-Jarman principle.* The final model incorporates several factors. Sward capture occurs in regions I and II. The different slopes of the ZNGI's is caused by the differential digestive capabilities of small and large grazers (Bell-Jarman principle). The intake constraint is responsible for the inhibitory, upwards-sloping part of the ZNGI's, which in turn causes facilitation. In this model, facilitation can start in region IV, leading eventually to exclusion of the larger species by the smaller, or it can start in region IV', leading to stable coexistence.



A. Small body size difference.

B. Medium body size difference.

C. Large body size difference.

Figure 2.5. The effect of different degrees of body size divergence in the combined sward capture, facilitation, and Bell-Jarman principle model. As well as predicting a limit to body size similarity for coexistence, the models predict that there is a limit to how *divergent* the species' body sizes can be for coexistence. Table 2.1 describes the dynamics associated with the labelled regions on the diagrams.

Table 2.1. The outcome of competition in different regions of RCT diagrams

Region	Dynamics
O	Too few resources to sustain either species.
I	Too few resources to support one species (in these scenarios, the large grazer or the hind gut fermenter). Exclusive habitat of the other species (the small grazer or fore gut fermenter).
I'	Sufficient resources to support both species. However, one species (large grazer or hind gut fermenter) is competitively excluded by the other, and the system equilibrates to region I.
II	Too few resources to support one species (in these scenarios, the small species or the fore gut fermenter). Exclusive habitat of the other species (the large grazer or hind gut fermenter).
II'	Sufficient resources to support both species. However, one species (small species or fore gut fermenter) is competitively excluded by the other, and the system equilibrates to region II.
II"	The habitat is initially too adverse to support the small species because there is too much poor quality grass. The large species depletes the long grass to a point where the small species is able to invade. Coexistence however is temporary, because the two species further deplete resources until the small species is again excluded. The system therefore follows a trajectory from region II" to II' to II, with first only the large species present, then both species, and finally only the large species again.
III	Potential stable coexistence of both species, depending on the consumption vectors. If stability is impossible, the system will move into region I' or II' depending upon starting conditions (population sizes).
IV	Classic facilitation. The habitat is initially too adverse to support the small species because there is too much grass. The large species depletes the long grass to a point where the small species is able to invade. Coexistence however is temporary, because the two species further deplete resources until the large species is excluded. The system therefore follows a trajectory from region IV to I' to I, with first only the large species present, then both species, and finally only the small species.
IV'	Facilitation ending in coexistence. The habitat is initially too adverse to support the small species because there is too much grass. The large species depletes the long grass to a point where the small species is able to invade. The system equilibrates to a stable coexistence, in region III.

APPLYING RCT TO LARGE HERBIVORES

A fully specified experiment to test the predictions of RCT requires a formidable amount of information, firstly to generate the parameters used to make predictions of exclusion or coexistence, and secondly to test those predictions. The very first step is to identify the resources for which competition is taking place. The population growth rate of each species must be determined in isolation under varying resource supply rates in order to draw the ZNGIs. Consumption vectors must be measured under resource supply conditions in proximity to the equilibrium point. Finally, both populations are allowed to grow together, and observed until either exclusion of one species or stable coexistence is reached. This must be repeated under at least three different resource supply ratios (chosen to predict exclusion of one species by the other, exclusion of the other species by the first, and coexistence), with sufficient replications for statistical analysis.

Much of the empirical research on RCT has been carried out using micro-organisms growing in a chemostat in the laboratory. Micro-organisms consume simple resources. The chemostat allows resource supply rates to be measured and manipulated with ease. Population sizes are easily assayed. Consumption rates of micro-organisms can be determined easily, and populations grow rapidly so that competitive exclusion or stable coexistence is quickly reached, allowing replicated experiments to be carried out efficiently.

All of these measurements are much more difficult to make when working with vertebrates. Vertebrate populations are also difficult to maintain in laboratory conditions, so that field experiments must be relied upon with all their attendant problems of experimental control. Populations grow slowly and rarely reproduce continuously. Resources are complex, their consumption difficult or at least tedious to measure in the field, and their supply rates difficult to measure and even more difficult to manipulate. In fact the logistic difficulty of replicating the chemostat experimental design in large vertebrates means that is unlikely that a full scale field experiment of RCT in ungulates will ever be carried out.

This leaves simulation as the major tool with which we may explore the predictions of RCT for large vertebrates. Although a single experiment making all of the required measurements is unlikely, in fact much of the data required to set up the

RCT predictions already exist. Energy balances have received a great deal of attention because of the commercial importance of domesticated ungulates (see chapter 3). ZNGIs can be approximated by determining the conditions under which individual ungulates achieve zero net energy intake. Data on consumption vectors are much more sparse, but it is possible to qualitatively determine whether the consumption vector of one species is steeper or shallower than that of another species, allowing the stability conditions to be tested. In a few cases, the consumption vectors can be predicted quantitatively. With ZNGIs and consumption vectors modelled, predictions can be generated and tested against ecological observations in the wild, and ultimately, in controlled field experiments.

Using simulation to test RCT in ungulates

In this section, information from published field studies of ungulate foraging behaviour and digestive physiology is used to place ungulate foraging within a resource competition framework. Previous work on modelling ungulate foraging has used an optimal foraging approach, for instance maximising energy intake when the animal faces a trade-off between the energetic profit of a range of food items, and the energetic costs of finding, ingesting and digesting these items (see chapter 1). The RCT approach uses the same data on profit and cost to predict the outcome of competition between ungulate species for a range of resources.

The difference between these approaches is that RCT identifies the exclusive niche of a species (the range of habitats from which the species can competitively exclude other species), whereas optimisation identifies the optimal niche (the habitat from which the species can achieve the maximum energy intake net of costs). RCT can therefore predict the outcome of competition in different habitats, whereas an optimisation approach can only predict the relative intensity of competition.

Topi vs. wildebeest

The models of resource competition between topi and wildebeest presented here are based on data from Murray (1991), Murray & Brown (1993), and Murray & Illius (2000). Two models are presented, differing in the spatial arrangement of resources. The first model represents a patchy landscape and the second a homogeneous landscape. Equivalently, the second model represents resources within a single patch.

The models were programmed in Waterloo Maple V Release 5.1, a mathematical modelling environment that can be used to solve a set of equations and produce graphs of the solution. The Maple code is given in appendix 2.1.

Model 1: patchy landscape

In this model, topi and wildebeest distribute themselves between two habitat types: a short, vegetative sward and a tall, differentiated sward. Each species is an optimal forager, choosing to spend all of its foraging time in the patch type that provides the greater energetic profit. Each species is assumed to spend 10 hours per day foraging, and requires a metabolisable energy intake of 19 $MJ.day^{-1}$ to break even (Murray & Illius 2000).

On the short sward, intake is determined by the height of the sward according to equations 5 and 6 in Murray & Illius (2000). This intake is converted into metabolic energy using a conversion factor of 7.99 $MJ.kg^{-1}$ DM (1 *kg* of DM intake provides 7.99 *MJ* of metabolisable energy after digestion, M. Murray, *pers. comm.*). On the differentiated sward, intake varies according to the quality (green leaf content) of the sward. On lower quality swards, digestion takes longer and intake falls. The reduction is modelled using equation 4 in Murray (1991). This equation requires the metabolisability of the low and high quality components of the diet (stem and green leaf), and the proportion of green leaf in the diet. The metabolisabilities are $q_L = 0.336$, $q_H = 0.488$ (Murray, *pers. comm.*). The proportion of green leaf in the diet depends upon how selective the animal is, and is calculated from equations 1 and 2 in Murray & Illius (2000). Table 2.2 summarises these equations.

Model 2: homogeneous landscape

This model simulates a single sward that varies in both height and green leaf content. The same equations are used as in model 1. Merging the two sward types is achieved by separating the green leaf and stem components of the sward. Sward height is set equal to stem height, and green leaf content is varied by assigning a 'height' to the green leaf component. This 'height' is used as a substitute for biomass per m^2, and allows the proportion of green leaf to be calculated as $GL = h_{GL} / h_{stem}$. Metabolisable intake is then constrained either by the height of the sward or the proportion of green leaf in the sward, and actual ME intake is the minimum of the two constraints. If sward height is constraining, then the ME content of the sward is calculated using $ME_{GL} = 8.91\ MJ.kg^{-1}\ DM$ and $ME_{stem} = 6.14\ MJ.kg^{-1}\ DM$ (Murray 1991). This is slightly different from model 1, which assumed that $ME_{veg} = 7.99\ MJ.kg^{-1}\ DM$.

Results

Figures 2.6 and 2.7 show the ZNGIs produced by models 1 and 2 respectively. Figure 2.6 predicts stable equilibrium, with each species foraging in different patch types. Provided that patches of vegetative sward are at least tall enough to support wildebeest (1.26 *cm*), and that patches of differentiated sward have sufficient green leaf to support topi (15.4%), then the landscape will be inhabited by both species simultaneously.

Figure 2.7 makes quite different predictions, and can be interpreted as a more detailed model of competition within a single patch. In this situation, the equilibrium point is in fact unstable. Wildebeest at that point are limited by the availability of green leaf, and topi by the availability of stem (in fact, topi are being limited by the total availability of forage, which is in turn limited by the height of stem in the sward since green leaf biomass is less than or equal to stem biomass). The consumption vectors show that at this point, each species is consuming relatively more of the resource that is limiting the other species (the species are not self-limiting), and therefore the equilibrium coexistence point is unstable.

Furthermore, the range of habitat types that could lead to coexistence (region III) is very narrow. The consumption vectors show that both species are highly selective of green leaf, with topi being even more selective than wildebeest. The figure shows that wildebeest can crop a short sward down to a level that is too short to sustain topi (region I). However, if the sward is long enough to support topi, there is only a very narrow region (I') where wildebeest can capture the sward from topi. In almost all swards greater than 3 *cm* high (region II'), topi can reduce the green leaf content to the point that wildebeest are excluded. Although the difference in the quality of tall swards that each species can tolerate seems rather small (region II), the range of initial sward characteristics that will ultimately (through selective grazing) follow a trajectory into this region is large, and topi will capture virtually all tall swards.

In the very narrow region III enclosed by the consumption vectors, either species is capable of excluding the other, and the outcome of competition depends on initial conditions, in particular the initial population sizes and the population growth rates.

Table 2.2. Foraging equations for topi and wildebeest on vegetative and differentiated swards.

Equation	Source
$\text{logit}(GL_T) = -5.78 + 45.1GL_{sward}[proportion]$	Murray & Illius 2000
$\text{logit}(GL_W) = -6.83 + 45.1GL_{sward}[proportion]$	
$I_{veg,T}[g.\min^{-1}] = -77.2 + 69.6h_{veg}[cm]$	
$I_{veg,W}[g.\min^{-1}] = 37.3 + 69.6h_{veg}[cm]$	
$ME[MJ.day^{-1}] = 14.023(q_L + GL(q_H - q_L)) + 61.968(q_L + GL(q_H - q_L))^2$	Murray 1991
$q_L = 0.336$	
$q_H = 0.488$	
$GL = GL_T$ or GL_W	

GL_T, GL_W and GL_{sward} = proportion of green leaf in the diets of topi and wildebeest, and in the sward, respectively.

$I_{veg,\ T}$ and $I_{veg,\ W}$ = dry matter intake rates on a vegetative sward for topi and wildebeest.

h_{veg} = height of the vegetative sward.

ME = metabolisable energy intake

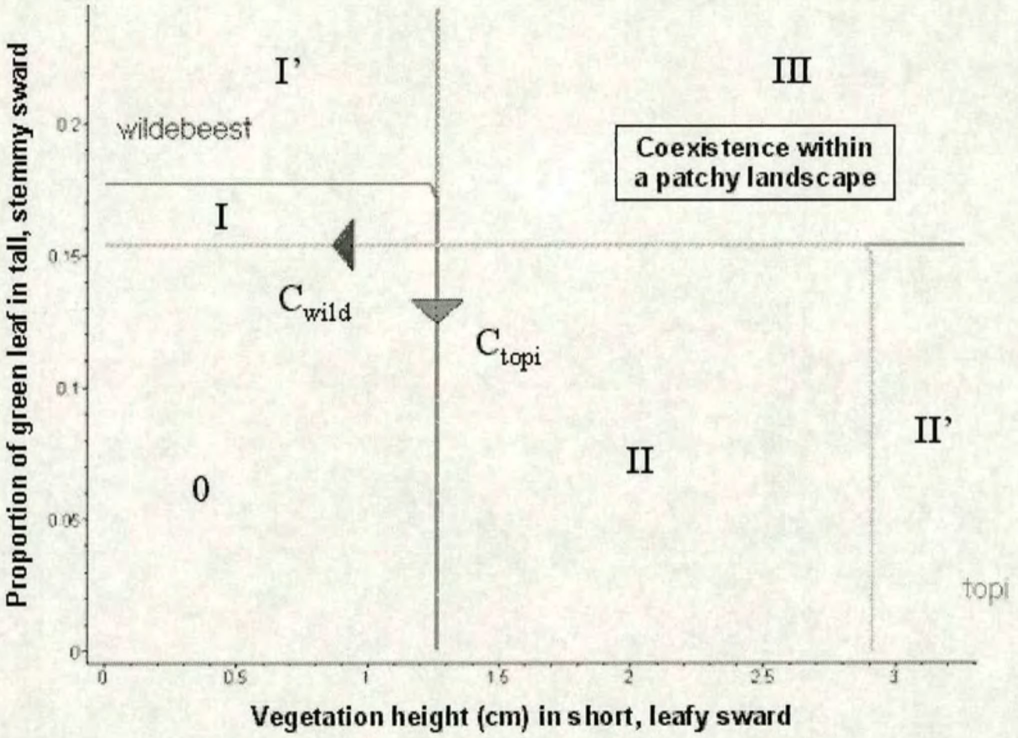


Figure 2.6. Competition between topi and wildebeest in a patchy habitat. Wildebeest have a relatively broad incisor arcade, allowing them to achieve a higher intake rate on short swards than topi, at the expense of reduced ability to select the green leaf component. Wildebeest captures short, leafy swards by grazing them down to a level below the maintenance threshold for topi (about 2.9 *cm*). Wildebeest can survive on just 1.25 *cm*. Topi captures tall, differentiated swards (consisting of both leaf and stem material) by strongly selecting green leaf and reducing the proportion of green leaf in the sward to a level below the maintenance threshold for wildebeest (about 17.5%). Topi can survive on just over 15%.

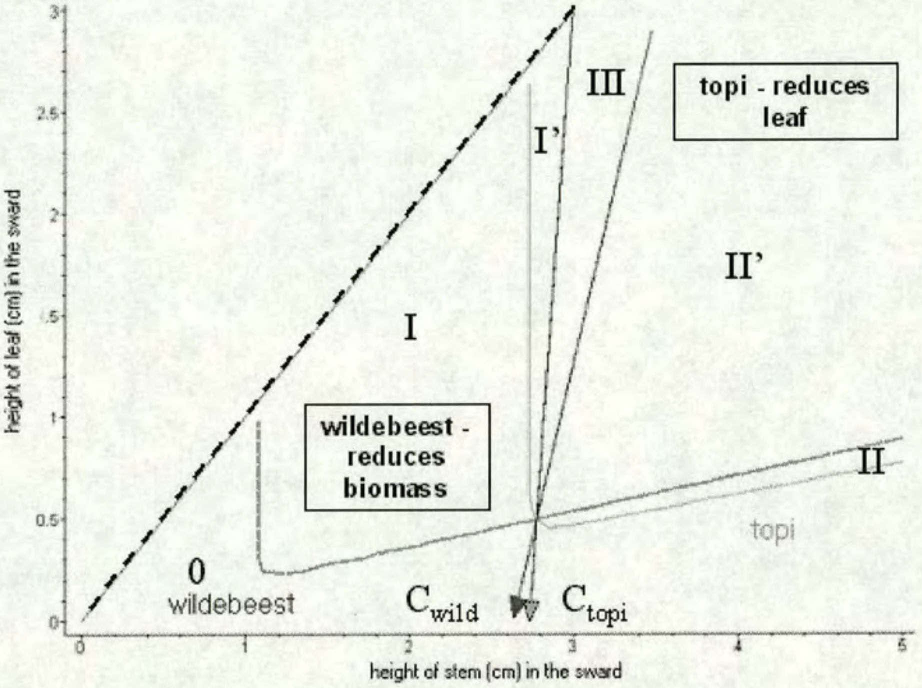


Figure 2.7. Competition between topi and wildebeest within a homogeneous patch. Leaf height is constrained to be less than or equal to stem height, indicated by the dashed line. The inhibitory nature of stem material is shown by the upward sloping ZNGI's. The consumption vectors show that both species are very strongly selective of leaf, with topi slightly more selective. Topi captures almost all tall swards (region II'). Wildebeest control the short swards (region I).

DISCUSSION

This chapter has explored the applicability of RCT to large vertebrate communities. Identifying and, particularly, describing animal resources is a considerably more complicated and subtle exercise than for plants. However, animal resources can certainly be placed within the RCT framework.

Tilman (1982) argued that such an exercise would probably not be useful, because animals are supplied with a very broad range of resources by plants (and each other), and therefore animal community structure can not be determined by resource interactions. This idea is naive. As chapter 1 has illustrated, ungulates are resource limited and different species compete for the same resources, at least under common enough circumstances. A generic theory of resource competition, such as RCT, should work in such a scenario.

The RCT models describing a set of previously described ungulate foraging strategies and constraints illustrate how ungulate foraging can be described by RCT. These graphical models provide a useful new way of thinking about ungulate communities, and can be used to develop testable hypotheses. One such idea is that coexistence of zebra and wildebeest depends upon a small amount of environmental variability, allowing each species to achieve a high population growth rate under conditions where the other species can only grow slowly. The model predicts that when resources are abundant but of low quality, zebra should thrive whereas wildebeest populations will only grow slowly. Conversely, when resources are abundant and of high quality, wildebeest populations will grow quickly whereas zebra populations will grow more slowly.

Quality is the ratio of cell contents to cell wall, with high quality forages containing relatively little cell wall material. The CCT paradigm led to the idea that quality is an axis along which species partition resources. The CCT description has larger ungulates able to subsist on poorer quality resources, despite the fact that all species would gain an advantage by consuming higher quality resources (if they were available). Generalising this idea about optimal foraging for individual species to make predictions about the type of community structure that this form of resource partitioning would lead to is not straightforward.

RCT provides a theoretical framework for how forage quality influences community composition. The ZNGI diagrams represent quality as the ratio of the two resources, which is to say as a vector from the origin pointing at the supply point. The length of the vector to the supply point represents the abundance of resources. As the characteristics of the supply point change, perhaps through seasonality or by moving from one location to another, different species will become competitively superior. Given some information describing environmental variability in an ecosystem, as well as descriptions of resource use by different species, RCT can predict the composition of the ungulate community. Chapter 3 will develop a model that describes resource use as a function of body size and which can be used to predict the outcome of competition between pairs of species in different habitats.

The model of wildebeest *vs.* topi exploitative competition is to my knowledge the first fully specified RCT model for vertebrates. The model makes few new predictions. For instance, Murray & Illius (2000) used these equations to predict the conditions under which each species would be able to exclude the other by reducing either the height of the sward (wildebeest) or its green leaf content (topi). A new prediction which the RCT model does make concerns spatial scale.

Murray & Illius (1996, 2000) have argued that the environmental heterogeneity that enhances coexistence is reduced by the grazing activity of the animals themselves. To explain coexistence, variability must be externally generated, by local rainfall events, topographic variability or whatever. In fact, this prediction depends upon the spatial scale analysed. Figure 2.7 shows that within a patch, either species may change the sward characteristics and 'capture' the sward for the exclusive use of that species. A patch may be defined as an area of habitat small enough to be modified by the grazing activity of a herd of ungulates. Figure 2.6, at a broader spatial scale, predicts that both species can coexist if coexistence is taken to mean at a broader, landscape scale. Given a homogeneous landscape, consisting of a sward initially capable of supporting both species, the different modes of grazing by the two species will result in the formation of a heterogeneous landscape of patches still capable of supporting both species. Exclusion only occurs very locally, and the model is consistent with observations of ungulate communities such as those in the

Serengeti/Mara, where wildebeest and zebra forage broadly over the same area, but maintain a degree of spatial separation (Sinclair 1985).

APPENDIX 2.1. MAPLE CODE

Homogeneous landscape model

```
> restart;
#set up
> with(plots):
> with(plottools):
> W:=100:
> q_stemdif:=0.336:      #MGM pers comm (draft of MGM & Illius 2000)
> q_GLdif:=0.488:        #MGM pers comm (draft of MGM & Illius 2000)
> ME_V_GL:=8.91:         #MGM 1991 table 1
> ME_V_stem:=6.14:       #MGM 1991 table 1
> logit:=x->ln(x/(1-x)):
> GL:=piecewise(h_GL<=h_stem,h_GL/h_stem,h_GL>h_stem,null):
> plot3d(GL,h_stem=0..40,h_GL=0..40,axes=boxed):
>
#green leaf in diet [proportion]
> GL_T:=solve(logit(g)=-5.78+45.1*GL,g):
> GL_W:=solve(logit(g)=-6.83+45.1*GL,g):
>
#Intake rates on veg  [kg.day-1]
> i_VT:=(max(0,(-77.2+69.6*h_stem)*W^0.75))*600/1000000:
> i_VW:=(max(0,(37.3+69.6*h_stem)*W^0.75))*600/1000000:
>
#ME intake rate [MJ.day-1]
#veg height constraint
> i_VT_GL:=GL_T*i_VT:
> i_VW_GL:=GL_W*i_VW:
> i_VT_stem:=(1-GL_T)*i_VT:
> i_VW_stem:=(1-GL_W)*i_VW:
>
> ME_VT:=i_VT_GL*ME_V_GL+i_VT_stem*ME_V_stem:
> ME_VW:=i_VW_GL*ME_V_GL+i_VW_stem*ME_V_stem:
>
#veg quality constraint
> ME_DT:=14.023*(q_stemdif+GL_T*(q_GLdif-q_stemdif))
      +61.968*(q_stemdif+GL_T*(q_GLdif-q_stemdif))^2:
> ME_DW:=14.023*(q_stemdif+GL_W*(q_GLdif-q_stemdif))
      +61.968*(q_stemdif+GL_W*(q_GLdif-q_stemdif))^2:
>
> ME_T:=min(ME_VT,ME_DT):
> ME_W:=min(ME_VW,ME_DW):
>
> ME_Wplot:=plot3d(ME_W,h_stem=0..40,h_GL=0..40,
      axes=boxed,color=green):
> ME_Tplot:=plot3d(ME_T,h_stem=0..40,h_GL=0..40,
      axes=boxed,color=red):
> display(ME_Wplot,ME_Tplot):
>
>
#Heat increment
> Hp_T:=19:
> Hp_W:=19:
>
#Energy retention
```

```
> Er_T:=ME_T-Hp_T:
> Er_W:=ME_W-Hp_W:
>
> zero:=plot3d(0,h_GL=0..5,h_stem=0..5,axes=boxed,color=turquoise):
> plotEr_T:=plot3d(Er_T,h_GL=0..5,h_stem=0..5,axes=boxed,color=red):
> plotEr_W:=plot3d(Er_W,h_GL=0..5,h_stem=0..5,
      axes=boxed,color=green):
> display([zero,plotEr_T,plotEr_W]);
>
>
#Plot ZNGIs
> cutoff:=implicitplot(h_stem=h_GL,h_stem=0..5,h_GL=0..3,
      axes=boxed,color=black):
> topiZNGI:=implicitplot(Er_T,h_stem=0..5,h_GL=0..3,
      axes=boxed,color=red,grid=[50,50]):
> wildZNGI:=implicitplot(Er_W,h_stem=0..5,h_GL=0..3,
      axes=boxed,color=green,grid=[50,50]):
> display(wildZNGI,topiZNGI,cutoff);
> topi10GI:=implicitplot(Er_T=2,h_stem=0..5,h_GL=0..5,
      axes=boxed,color=orange,grid=[50,50]):
> wild10GI:=implicitplot(Er_W=2,h_stem=0..5,h_GL=0..5,
      axes=boxed,color=cyan,grid=[50,50]):
> display(wildZNGI,wild10GI,topiZNGI,topi10GI,cutoff);
>
>
#Consumption vectors
#Intersection of ZNGIs:
> topiZNGI2:=implicitplot(Er_T,h_stem=1..1.6,h_GL=0.2..0.4,
      axes=boxed,color=red,grid=[50,50]):
> wildZNGI2:=implicitplot(Er_W,h_stem=1..1.6,h_GL=0.2..0.4,
      axes=boxed,color=green,grid=[50,50]):
> display(wildZNGI2,topiZNGI2);
>
>
#ZNGIs intersect at [h_stem,h_GL]=[2.7747,0.4922]
#At this point, topi intake is constrained by h_stem, and wild
intake by h_GL.
> h_stem_eq:=2.7747:
> h_GL_eq:=0.4922:
> equi:=vector(2,[h_stem_eq,h_GL_eq]):
> GL_eq:=h_GL_eq/h_stem_eq:
>
#Consumption vectors - just calculating slopes
#Topi: could get length, but don't bother
> GL_eq_T:=solve(logit(g)=-5.78+45.1*GL_eq,g):
> c_eq_T:=2:     #dummy length (could use i_VT)
> c_eq_T_GL:=GL_eq_T*c_eq_T:
> c_eq_T_stem:=(1-GL_eq_T)*c_eq_T:
>
#Wild: can get slope, not length of vector
> GL_eq_W:=solve(logit(g)=-6.83+45.1*GL_eq,g):
> c_eq_W:=2:     #dummy length
> c_eq_W_GL:=GL_eq_W*c_eq_W:
> c_eq_W_stem:=(1-GL_eq_W)*c_eq_W:
>
#conversion from biomass to veg height
> height:=biomass->-3.9334417+93.628888*biomass:  # from data in MGM
      & Brown
> c_T:=vector(2):
```

```
> c_W:=vector(2):
> c_T[1]:=-height(c_eq_T_stem):
> c_T[2]:=-height(c_eq_T_GL):
> c_W[1]:=-height(c_eq_W_stem):
> c_W[2]:=-height(c_eq_W_GL):
>
#conversion to (1/2) unit length vectors
> len_c_T:=(c_T[1]^2+c_T[2]^2)^0.5:
> len_c_W:=(c_W[1]^2+c_W[2]^2)^0.5:
> unit_c_T:=vector(2):
> unit_c_W:=vector(2):
> unit_c_T[1]:=c_T[1]/(2*len_c_T):
> unit_c_T[2]:=c_T[2]/(2*len_c_T):
> unit_c_W[1]:=c_W[1]/(2*len_c_W):
> unit_c_W[2]:=c_W[2]/(2*len_c_W):
> eval(unit_c_T);
> eval(unit_c_W);

                    [-.04350048885, -.4981041132]


                    [-.1396064526, -.4801146095]

#extrapolated consumption vectors:
> rev_c_W:=vector(2):
> rev_c_T:=vector(2):
> rev_c_W[1]:=-unit_c_W[1]*5:
> rev_c_W[2]:=-unit_c_W[2]*5:
> rev_c_T[1]:=-unit_c_T[1]*5:
> rev_c_T[2]:=-unit_c_T[2]*5:
>
> c_Warrow:=arrow(equi, unit_c_W, .001, .1, .2, color=green):
> c_Tarrow:=arrow(equi, unit_c_T, .001, .1, .2, color=red):
> c_Wrev:=arrow(equi, rev_c_W, .001, 0, .2):
> c_Trev:=arrow(equi, rev_c_T, .001, 0, .2):
> display(wildZNGI,topiZNGI,cutoff,c_Warrow,c_Tarrow,c_Wrev,c_Trev);
>
```

Patchy landscape model

```
> restart;
#set up constants
> W:=100:
> GL_veg:=0.221:
> q_stemdif:=0.336:
> q_GLdif:=0.488:
> logit:=x->ln(x/(1-x)):
> with(plots):
>
#green leaf in diet [proportion]
> GL_DT:=solve(logit(g)=-5.78+45.1*GL_dif,g):
> GL_DW:=solve(logit(g)=-6.83+45.1*GL_dif,g):
>
#Intake rates on vegetative swards [mg.min-1]
> i_VT:=max(0,(-77.2+69.6*h_veg)*W^0.75):
> i_VW:=max(0,(37.3+69.6*h_veg)*W^0.75):
>
#ME intake rate [MJ.day-1]
#on vegetative swards:
> MErate_VT:=600*7.99*i_VT/1000000:
> MErate_VW:=600*7.99*i_VW/1000000:
>
> MErate_VTplot:=plot(MErate_VT,h_veg=0..8,color=red):
> MErate_VWplot:=plot(MErate_VW,h_veg=0..8,color=green):
> display(MErate_VTplot,MErate_VWplot):
> solve(MErate_VT=19); solve(MErate_VW=19);
>
                                   2.909915998
                                   1.264801055

>
#on differentiated swards, ME intake follows equation 4 (MGM):
> MErate_DT:=14.023*(q_stemdif+GL_DT*(q_GLdif-q_stemdif))
      +61.968*(q_stemdif+GL_DT*(q_GLdif-q_stemdif))^2:
> MErate_DW:=14.023*(q_stemdif+GL_DW*(q_GLdif-q_stemdif))
      +61.968*(q_stemdif+GL_DW*(q_GLdif-q_stemdif))^2:
>
> MErate_DTplot:=plot(MErate_DT,GL_dif=0..0.3,color=red):
> MErate_DWplot:=plot(MErate_DW,GL_dif=0..0.3,color=green):
> display(MErate_DTplot,MErate_DWplot):
> solve(MErate_DT=19); solve(MErate_DW=19);

               .1250635034 + .06965837369 I, .1541184849
               .1483450999 + .06965837369 I, .1774000813

>
#daily intake of ME and DM
> ME_T:=max(MErate_VT,MErate_DT):
> ME_W:=max(MErate_VW,MErate_DW):
>
> blue19:=plot3d(19,GL_dif=0..0.4,h_veg=0..4,
      axes=boxed,color=turquoise):
> plotME_T:=plot3d(ME_T,GL_dif=0..0.4,h_veg=0..4,
      axes=boxed,color=red):
> plotME_W:=plot3d(ME_W,GL_dif=0..0.4,h_veg=0..4,
      axes=boxed,color=green):
> display(plotME_T,plotME_W,blue19):
```

```
>
#Heat increment
> Hp_T:=19:
> Hp_W:=19:
>
#Energy retention
> Er_T:=ME_T-Hp_T:
> Er_W:=ME_W-Hp_W:
> zero:=plot3d(0,GL_dif=0..0.4,h_veg=0..4,
      axes=boxed,color=turquoise):
> plotEr_T:=plot3d(Er_T,GL_dif=0..0.4,h_veg=0..4,
      axes=boxed,color=red):
> plotEr_W:=plot3d(Er_W,GL_dif=0..0.4,h_veg=0..4,
      axes=boxed,color=green):
> display([zero,plotEr_T,plotEr_W]):
>
#Plot ZNGIs
> topiZNGI:=implicitplot(Er_T,h_veg=0..3,GL_dif=0..0.2,
      axes=boxed,color=red,grid=[50,50]):
> wildZNGI:=implicitplot(Er_W,h_veg=0..3,GL_dif=0..0.2,
      axes=boxed,color=green,grid=[50,50]):
> display(topiZNGI,wildZNGI):
>
#Consumption vectors
#Intersection of ZNGIs:
> topiZNGI2:=implicitplot(Er_T,h_veg=1.26475..1.26485,
      GL_dif=0.15411..0.15412,axes=boxed,color=red):
> wildZNGI2:=implicitplot(Er_W,h_veg=1.26475..1.26485,
      GL_dif=0.15411..0.15412,axes=boxed,color=green):
> display(wildZNGI2,topiZNGI2):
#ZNGIs intersect at [h_veg,GL_dif]=[1.2648,0.1541]
#At this point, topi intake is purely GL_dif, and wild intake is
      purely h_veg.
#This is because they each choose the patch type that maximises ME
      intake.
> h_veg_eq:=1.2648:
> GL_dif_eq:=0.1541:
> equi:=vector(2,[h_veg_eq,GL_dif_eq]):
>
#Consumption vectors
#Topi: consuming GL on the differentiated sward:
> c_eq_T:=0.03:      #dummy length
> c_eq_T_GL:=c_eq_T:
> c_eq_T_stem:=0:
>
#Wild: consuming vegetative sward:
> c_eq_W:=0.4:        #dummy length
> c_eq_W_GL:=0:
> c_eq_W_stem:=c_eq_W:
>
> c_T:=vector(2):
> c_W:=vector(2):
> c_T[1]:=-c_eq_T_stem:
> c_T[2]:=-c_eq_T_GL:
> c_W[1]:=-c_eq_W_stem:
> c_W[2]:=-c_eq_W_GL:
>
#extrapolated consumption vectors:
> rev_c_W:=vector(2):
```

```
> rev_c_T:=vector(2):
> rev_c_W[1]:=-c_W[1]*5:
> rev_c_W[2]:=-c_W[2]*5:
> rev_c_T[1]:=-c_T[1]*3:
> rev_c_T[2]:=-c_T[2]*3:
> with(plottools):
> c_Warrow:=arrow(equi, c_W, .0001, .02, .2, color=green):
> c_Tarrow:=arrow(equi, c_T, .0001, .2, .3, color=red):
> c_Wrev:=arrow(equi, rev_c_W, .0001, 0, 0):
> c_Trev:=arrow(equi, rev_c_T, .0001, 0, 0):
> display(topiZNGI,wildZNGI,c_Warrow,c_Tarrow,c_Wrev,c_Trev):
>
```

3. A ZNGI MODEL OF RESOURCE COMPETITION IN COMMUNITIES OF AFRICAN UNGULATES

INTRODUCTION

CCT can be tested fairly straightforwardly by manipulating population sizes (or utilising natural or non-experimental, anthropogenic perturbations) and monitoring impacts on potential competitor populations. The information required to test RCT is much more prodigious (chapter 2). This chapter goes part of the way by providing a generic, predictive model of ungulate foraging.

The model is generic because it is dependent upon body size. Body size can be varied to produce models for a whole community of ungulates. The model is predictive because it generates ZNGI's and consumption vectors that can be used to predict coexistence, stability or instability, and competitive exclusion. Further development of some parts of the model would also allow it to predict equilibrium population sizes.

RCT applications in animal ecology have been extremely rare. Grover (1997) only knew of one such experiment, that of Rothhaupt (1988) using rotifers (see chapter 2). I have not found any other applications. Part of the difficulty is undoubtedly the lack of sufficient information to produce predictions. However, this information does exist for ungulates, mainly because of their great agricultural importance. This chapter uses the literature on ungulate foraging behaviour and digestive physiology to generate predictions within an RCT framework.

The model is designed to predict the range of conditions under which combinations of ungulates may or may not coexist. Therefore the model does not contain a description of the environment, but predicts ungulate responses over a broad range of possible (and impossible) conditions. Zero Net Growth Isoclines (ZNGI's) are plotted against resource availabilities for two classes of resource (cell wall and cell contents) for species differing in body size.

Coexistence or exclusion is predicted by examining the points where the ZNGI's of two species cross. Such crossovers are equilibrium points that may be stable or unstable, according to properties discussed by León & Tumpson (1975), Tilman (1982, 1986), and Grover (1997) (see chapter 2).

Generating predictions is the first step, but these predictions must be testable. The test requires two populations to forage together and grow or decline, preferably until equilibrium. This needs to be repeated for a number of resource supply scenarios. And resource supply should remain constant. For ungulates, with annual reproduction and long generation times, consuming a biological resource subject to its own annual cycles, the workload would be immense. An alternative to field testing would be attractive.

One option would be to use simulation modelling. The simulation model would supply vegetation to model ungulates, with vegetation growth subject to spatial variation. A large number of such models have been developed, many of which can model two ungulate species foraging simultaneously (J. Derry *pers. comm.*). These models could be used to provide a basic test of the predictions under relatively simple resource supply scenarios. More comprehensive ecosystem models, which incorporate the growth dynamics of the vegetation by modelling soil-water relations, and which use advanced physiological and behavioural models of ungulate foraging, are rarer. The SAVANNA ecosystem model (Coughenour 1993) would provide a realistic simulated environment, as would SimSAGS (Derry 1998, Illius, Derry & Gordon 1998, 2000, Illius & Gordon 1999). Both models can simulate multiple ungulate species and their impacts upon resources which are themselves subject to resource-based growth dynamics.

Until this work can be carried out, interpreting the model's predictions is limited to a consideration of the 'reasonableness' of its output. Do the predictions made by the model broadly fit in with what is known about ungulate competition?

Table 3.1. Variables and units used in the model.

variable	units	definition
V	$kg.ha^{-1}$	Vegetation standing biomass
CW_S	$kg.ha^{-1}$	Cell wall standing biomass
CC_S	$kg.ha^{-1}$	Cell contents standing biomass
W	kg	Body size
GC	$g\ DM$	Dry matter food contents in the gut
RT	hr	Mean whole gut retention time
RT_{adj}		Effect of food quality on RT
$FILL_d$	$g\ DM.day^{-1}$	Gut capacity constraint on daily food intake
R_{max}	$g.min^{-1}$	Maximum instantaneous cropping rate
b	$g.m^{-2}$	Vegetation biomass at which intake is half maximum
t_{max}	min	Maximum daily feeding time (=13*hr* = 780*min*)
$CROP_d$	$g\ DM.day^{-1}$	Feeding rate constraint on daily food intake
C_d	$g\ DM.day^{-1}$	Daily food intake
CC_i	$g\ DM.day^{-1}$	Daily CC intake
CW_i	$g\ DM.day^{-1}$	Daily CW intake
NDF	$g.kg^{-1}$	Proportion of CW in the standing biomass
DOM	$g.kg^{-1}$	Observed *in vivo* digestibility of organic matter
$INDF$	$g.kg^{-1}$	Indigestible fraction
PED	$g.kg^{-1}$	Potential extent of digestion
$PDCW_d$	$g\ DM.day^{-1}$	Potentially digestible cell wall intake
k_2	hr^{-1}	Rate of digestion of CW
CC_a	$g\ DM.day^{-1}$	Assimilated (digested) CC
CW_a	$g\ DM.day^{-1}$	Assimilated (digested) CW
ε_{CC}	$MJ.g^{-1}$	Energy content of $CC = 0.041$
ε_{CW}	$MJ.g^{-1}$	Energy content of $CW = 0.0185$
E_{CC}	$MJ.day^{-1}$	Energy intake from CC
E_{CW}	$MJ.day^{-1}$	Energy intake from CW
GE_d	$MJ.day^{-1}$	Gross energy content of digested food
FE_d	$MJ.day^{-1}$	Energy content of faeces
UE_d	$MJ.day^{-1}$	Energy content of urine
PE_d	$MJ.day^{-1}$	Energy content of methane
ME_d	$MJ.day^{-1}$	Energy intake available to metabolism
r	$MJ.kg^{-1}$	Work of rumination *per kg* ingested fibre
E_r	$MJ.day^{-1}$	Total work of rumination
E_h	$MJ.day^{-1}$	Heat production due to ferrmentation and digestion
HE_d	$MJ.day^{-1}$	Heat increment
E_{basal}	$MJ.day^{-1}$	Basal energetic requirements of a fasting, inactive animal
NE_d	$MJ.day^{-1}$	Net energy available for maintenance and growth
E_{act}	$MJ.day^{-1}$	Activity allowance
E_{maint}	$MJ.day^{-1}$	Maintenance requirement
G_d	E_{maint}	Profit, or energy available for growth, as multiples of maintenance

Appendix 3.2 provides illustrations of the shapes of many of the functions used in this model. The model was programmed in Waterloo Maple V Release 5.1. Appendix 3.3 contains the code used to specify the model. Body size data were obtained from the same sources as used in chapter 4 (see appendix 4.1). Statistical tests were carried out using Minitab 12.

INTAKE MODEL

Appendix 3.1 illustrates the structure of the intake component of the model. Vegetation standing biomass is the sum of cell wall biomass (*kg.ha*$^{-1}$) and cell contents biomass (*kg.ha*$^{-1}$). The intake model calculates daily intake as the lesser of two constraints - gut capacity and eating rate. This structure is based on the models of Fryxell (1991), Wilmshurst, Fryxell & Colucci (1999) and Wilmshurst, Fryxell & Bergman (2000), and uses their function to describe the eating rate constraint. The intake model described here differs in two main respects from the Fryxell / Wilmshurst models.

Firstly, the Fryxell / Wilmshurst models incorporate an implicit description of the environment by assuming that daily gut capacity falls with increasing vegetation standing biomass. This is because digestibility is negatively correlated to vegetation biomass, and retention times increase to cope with poorer quality food. The current model explicitly models the increase in retention times caused by poorer quality food intake, removing the direct relationship between forage abundance and gut retention time. This is necessary because the aim of the model is to predict competitive outcomes under a variety of resource supply scenarios, including variation in abundance that is independent of quality, and *vice versa*. The model does not assume that cell wall and cell content are directly correlated.

The second difference is that the Fryxell / Wilmshurst models convert dry matter intake directly into metabolisable energy intake by applying a conversion factor. The model presented here uses an explicit (though fairly simple) model of digestion, partitioning food intake into cell wall and cell contents fractions.

Model description

Gut capacity limits daily intake to the species' gut size divided by the mean retention time of food in the gut:

$$FILL_d[g\ DM.day^{-1}] = 24\,{GC}\big/{RT} \qquad \text{(eqn. 1)}$$

$FILL_d$ = maximum daily throughput of food

$GC\ [g\ DM]$ = gut capacity

$RT\ [hours]$ = mean (whole gut) passage time of food

Gut capacity is a linear function of body size:

$$GC[g\ DM] = 21W[kg] \qquad \text{(eqn. 2)}$$

($R^2_{adj} = 0.98$, n = 18, Illius & Gordon 1991).

Whole-gut retention time is modelled as a modification of:

$$RT[hrs] = 14.1W^{0.27} \qquad \text{(eqn. 3a)}$$

Illius & Gordon (1991) derived this relationship as a simplification of

$$\ln(RT[hrs]) = 2.725 + 0.251\ln(W),\ R^2_{adj} = 0.76,\ n = 26.$$

Retention time however is expected to vary with diet quality as well as body size (see above). The digestion model of Illius & Gordon (1991) could be used to derive a relationship between RT, W and diet quality. However, the maths are complex, and the current model uses an empirical adjustment to increase or decrease RT according to the proportion of indigestible food ($INDF$). Two versions of the adjustment are provided (equations 3b & c). Equation 3b is graphed in appendix 3.2. The rationale behind equation 3c is that smaller animals are less able to extend or reduce retention times in response to variation in forage quality. Results for models using both versions are presented below.

$$RT_{adj} = 0.15\tanh\left(\frac{INDF}{125} - 3\right) \qquad \text{(eqn. 3b)}$$

$$RT_{adj} = \left({W}\big/{500}\right)^{0.5} \times 0.15\tanh\left(\frac{INDF}{125} - 3\right) \qquad \text{(eqn. 3c)}$$

$$RT = \left(1 + RT_{adj}\right) \times 14.1W^{0.27} \qquad \text{(eqn. 3d)}$$

The second intake constraint models the functional response of ungulates as a function of vegetation standing biomass and body size. Fryxell (1991), Wilmshurst, Fryxell & Colucci (1999), and Wilmshurst, Fryxell & Bergman (2000) used the Michaelis-Menten equation to model the functional response:

$$CROP_d\,[g\ DM.day^{-1}] = \frac{R_{\max}.V}{b+V}.t_{\max} \qquad \text{(eqn. 4)}$$

$CROP_d$ = cropping (intake) rate

$R_{max}\,[g.min^{-1}]$ = maximum instantaneous cropping rate

$V\,[g.m^{-2}]$ = vegetation standing biomass = $0.1V\,[kg.ha^{-1}]$

$b\,[g.m^{-2}]$ = vegetation biomass at which intake is half maximum

t_{max} = maximum daily feeding time (13 *hours*, or 780 *mins*)

Although t_{max} may be expected to vary with body size, in fact there is little evidence of a systematic relationship. Data from Demment & Van Soest (1983, in Van Soest 1994 table 4.7) show only a weak correlation of time spent feeding to body size ($r = 0.31$, $n = 23$, n.s., figure 3.1), and this disappears when male and female elephant are excluded ($r = 0.024$, $n = 21$, n.s.).

The parameters b and R_{max} were derived from data in Wilmshurst, Fryxell & Bergman (2000). They collated estimates of b and R_{max} for a variety of species from the literature. Regressing their data against body size gave significant relationships which were used to predict b and R_{max} in the present model (figure 3.2):

$$R_{\max} = 1.977 + 0.162W \qquad \text{(eqn. 5)}$$

$r = 0.97$, $n = 15$, $P << 0.001$

$$b = -34.99 + 0.663W \qquad \text{(eqn. 6a)}$$

$r = 0.79$, $n = 15$, $P = 0.00045$

Equation 6a predicts negative half-maximum intake for animals smaller than 52.78kg. In fact the intercept is not significantly different from zero (P = 0.37), and the relationship was recalculated through the origin to give:

$$b = 0.577W \qquad \text{(eqn. 6b)}$$

r = 0.77, R^2_{adj} = 0.60, n = 15, P = 0.00052.

Daily intake is the minimum of the two constraints:

$$C_d[g\,DM.day^{-1}] = \min[CROP_d, FILL_d] \qquad \text{(eqn. 7a)}$$

Intake of *CC* and *CW* are modelled in two ways. In the basic model, the proportion of *CC* and *CW* in the diet are the same as in the sward. The animals are completely unselective (equations 7b & 7c). In equations 7d & 7e, selectivity is introduced by analogy to the selectivity observations of Murray & Illius (2000), with an arbitrary modification to make smaller ungulates more selective of *CC* than larger ungulates.

$$CC_i[g\,DM.day^{-1}] = C_d \frac{CC_S}{V} \qquad \text{(eqn. 7b)}$$

$$CW_i[g\,DM.day^{-1}] = C_d \frac{CW_S}{V} \qquad \text{(eqn. 7c)}$$

$$\text{logit}\left({}^{CC_i}\!/_{CW_i} \right) = {}^{5}\!/_{3} \log W - 9 + 45\, {}^{CC_S}\!/_{CW_S} \qquad \text{(eqn. 7d)}$$

$$CC_i[g\,DM.day^{-1}] = C_d \frac{CC_i}{CW_i};\;\; CW_i = C_d\left(1 - \frac{CC_i}{CW_i}\right) \qquad \text{(eqns. 7e)}$$

Results of models using both formulations are presented below.

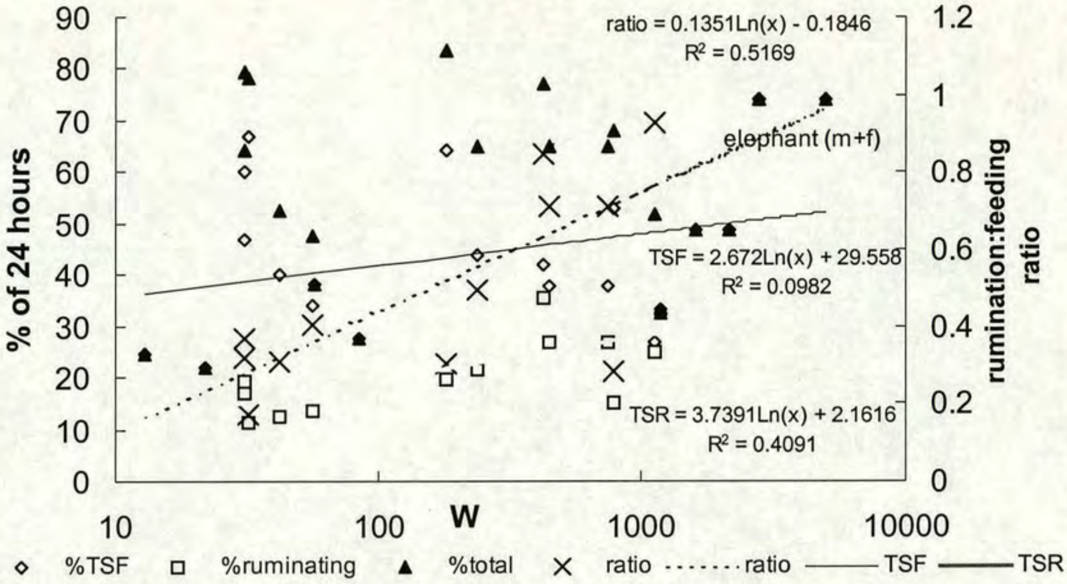


Figure 3.1. Time spent feeding by a range of ruminant and non-ruminant herbivores. Some data points represent male and female values for the same species. TSF: time spent feeding. TSR: time spent ruminating. Total: TSF + TSR. All times expressed as % of 24 hours. Regression equations are for all data in the sample. See text for regressions excluding elephant. Data from Demment & Van Soest 1983 (in: Van Soest 1994 table 4.7).

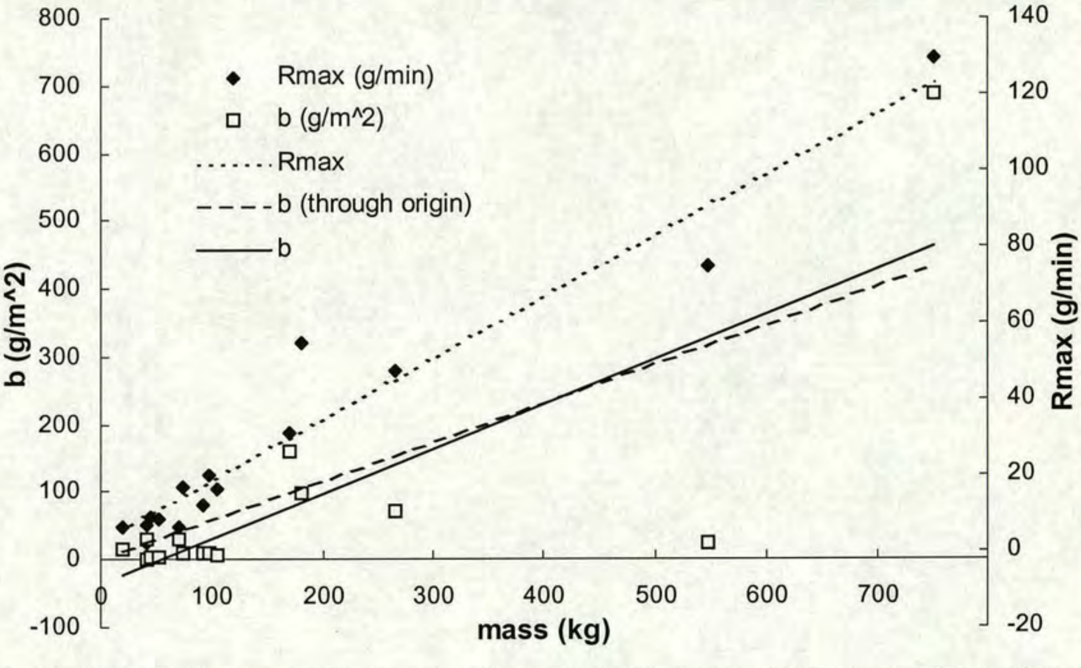


Figure 3.2. Parameters of the functional response (data from Wilmshurst, Fryxell & Bergman 2000). R_{max} is the maximum instantaneous rate of DM intake. *b* is the vegetation biomass at which intake is half maximum.

DIGESTION MODEL

Appendix 3.1 also illustrates the structure of the digestion component of the model. Most of the parameters and equations are taken from Givens, Everington & Adamson (1989, 1990a and b) and from Van Soest (1994).

Model description

Daily dry matter intake (from the intake model) is divided into cell contents and cell wall by the selectivity model if implemented, or else according to their proportions in the sward.

Cell contents

Cell contents are assumed to be completely digestible. Givens, Everington & Adamson (1990b) measured the energy content of ether extract from British commercial forages to be 41 $MJ.kg^{-1}$, and this figure is used for the energy content of cell contents:

$$E_{CC}[MJ.day^{-1}] = \mathcal{E}_{CC}.CC_a \qquad \text{(eqn. 8)}$$

E_{CC} = energy intake from cell contents

$\mathcal{E}_{CC}$ = energy content of cell contents = 0.041 $MJ.g^{-1}$

CC_a = assimilated cell contents = cell contents intake [$g.day^{-1}$]

Illius & Gordon (1991) assumed only 0.66 of the ingested cell contents were digested, and that the energy content of *CC* is only 15.6 $MJ.kg^{-1}$. Van Soest (1982, in Illius & Gordon 1992 p. 429) states that *CC* is almost completely digestible, whereas Fonnesbeck (1969, in Illius & Gordon 1992 p. 429) gives *CC* a digestibility of 2/3, and an energy content of 15.6 $MJ.kg^{-1}$. This latter seems to be an *ad hoc* modification for hind-gut fermenters, with enzymatic digestion of *CC* resulting in direct assimilation of protein from the *CC*, therefore reducing the energy value of the *CC*. The 15.6 $MJ.kg^{-1}$ figure is in sharp disagreement with that of Givens, Everington & Adamson (1990b). In the current version of the model, Van Soest is followed in that *CC* is completely digestible, and the higher energy value of 41 $MJ.kg^{-1}$ is used.

Cell wall

Cell wall digestion depends upon the composition of the cell wall, particularly its lignin content (Van Soest 1994). Cell wall is mainly composed of cellulose, hemicellulose, and lignin, with additional proteins, pectin and waxes. The latter three are relatively easily extractable, whereas the cellulose and hemicellulose are insoluble and require specialised fermentation to be reduced to soluble compounds. Lignin cannot be broken down by digestion, and in fact inhibits digestion of the other cell wall components.

The cell wall therefore cannot be completely digested. Assimilated cell wall is calculated as the product of the ingested DM of potentially digestible cell wall and the actual proportional extent of digestion. Potentially digestible cell wall intake is:

$$PDCW_d\,[g\;DM.day^{-1}] = 0.001 CW_i.PED \qquad \text{(eqn. 9)}$$

$PDCW_d$ = potentially digestible cell wall intake
CW_i = ingested CW (output of intake model)
$PED\,[g.kg^{-1}]$ = potential extent of digestion

$$PED\,[g.kg^{-1}] = 0.93 DOM + 294 \qquad \text{(eqn. 10a)}$$

$$PED\,[g.kg^{-1}] = \frac{920.48}{[1 + 6.309.\exp(-0.007173 DOM)]} \qquad \text{(eqn. 10b)}$$

$$PED\,[g.kg^{-1}] = 0.83 DOM + 350 \qquad \text{(eqn. 10c)}$$

10a: $r = 0.89$, $R^2_{adj} = 0.78$, $n = 41$, $P << 0.001$
10b: $r = 0.85$, $R^2_{adj} = 0.72$, $n = 40$, $P << 0.001$
10c: $r = 0.83$, $R^2_{adj} = 0.69$, $n = 40$, $P << 0.001$
$DOM\,[g.kg^{-1}]$ = observed *in vivo* digestibility of organic matter

Equations 10a, b and c are derived from data in Prins *et al.* (1983), from a range of ungulates fed diets of varying digestibility (figure 3.3). *PED* is the *in vitro* digestibility of the forage when digested for a long time. *DOM* is the proportion of digestible organic matter calculated from *in vivo* trials using each species. Adding body size to the linear regression (10a) did not significantly increase the variance explained (n = 14, P for *W* term = 0.16).

Inspection of figure 3.3 suggests that the relationship may in fact be curvilinear, with *PED* approaching equality to *DOM* at high digestibility. Equation 10b models this behaviour. Note that equation 10b was derived with one data point excluded. While the variance explained by equation 10b is less than that explained by 10a, if the linear regression is re-calculated with the outlier removed, the logistic model does explain a greater proportion of the variance.

DOM is calculated from:

$$DOM\,[g.kg^{-1}] = 1210 - 0.769NDF \qquad \text{(eqn. 11)}$$

$R^2_{adj} = 0.529$, n = 170 (Givens, Everington & Adamson 1990a)

NDF [g.kg^{-1}] = proportion of cell wall in the vegetation standing biomass

Using equation 11 to describe organic matter digestibility assumes that *in vivo* organic matter digestibility in sheep (the Givens data) is equivalent to the Prins *et al.* (1983) measure of *in vivo* digestibility.

The actual proportional extent of digestion is $\left\lfloor 1-(1-k_2)^{RT}\right\rfloor$, and assimilated cell wall is:

$$CW_a[g.day^{-1}] = PDCW_d\left\lfloor 1-(1-k_2)^{RT}\right\rfloor \qquad \text{(eqn. 12)}$$

RT is calculated as described in the intake model.

CW_a is affected by body size solely through *RT*. The calculation of *RT* should ideally incorporate a term relating *RT* to the proportion of indigestible cell wall in the diet. This adaptive variation in *RT* (and hence *in vivo* cell wall digestibility) would explain why *DOM* is independent of *W*, as in figure 3.4.

From data in Illius & Gordon (1991 table 2), k_2 can be related (weakly, see figure 3.5) to the indigestible fraction (*INDF* [g.kg^{-1}]) by:

$$k_2[\text{fraction } PDCW_d.hr^{-1}] = 0.0891 - 0.000106INDF \qquad \text{(eqn. 13)}$$

$r = 0.396$, $R^2_{adj} = 0.117$, $n = 23$, $P = 0.061$

$$INDF[g.kg^{-1}] = (1000 - DOM)\frac{CW_S}{V} \qquad \text{(eqn. 14)}$$

This relationship is however weak, and dependent on two data points (see figure 3.5). It is probably better to use a constant for k_2 ($k_2 = 0.06\ hr^{-1}$).

Givens, Everington & Adamson (1990b) measured the energy content of organic matter minus crude protein and ether extract from British commercial forages to be 18.5 $MJ.kg^{-1}$, and this figure is used for the energy content of cell wall:

$$E_{CW}[MJ.day^{-1}] = \mathcal{E}_{CW}.CW_a \qquad \text{(eqn. 15)}$$

E_{CW} = energy intake from cell wall

$\mathcal{E}_{CW}$ = energy content of cell wall = 0.0185 MJ.g^{-1}

CW_a = assimilated cell wall

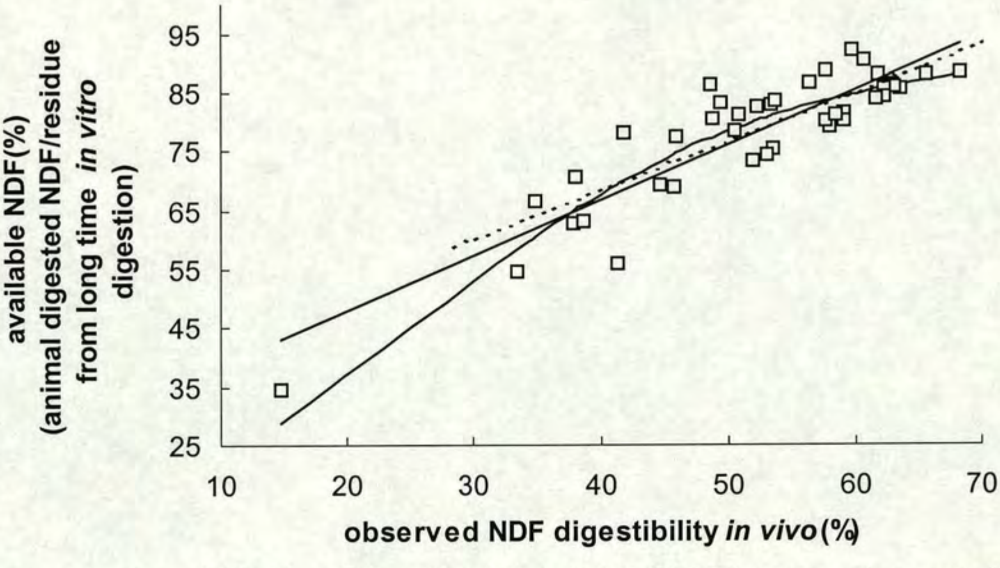


Figure 3.3. Potentially digestible cell wall (available NDF) is greater than actual (*in vivo*) cell wall digestibility. There is some evidence that the relationship is curvilinear, with *PDCW* approaching actual digestibility at high digestibilities. The curvilinear fit is a logistic model, and excludes the outlying data point at very low digestibility. The dashed fit is a linear regression excluding the outlier. Data from Prins *et al.* (1983).

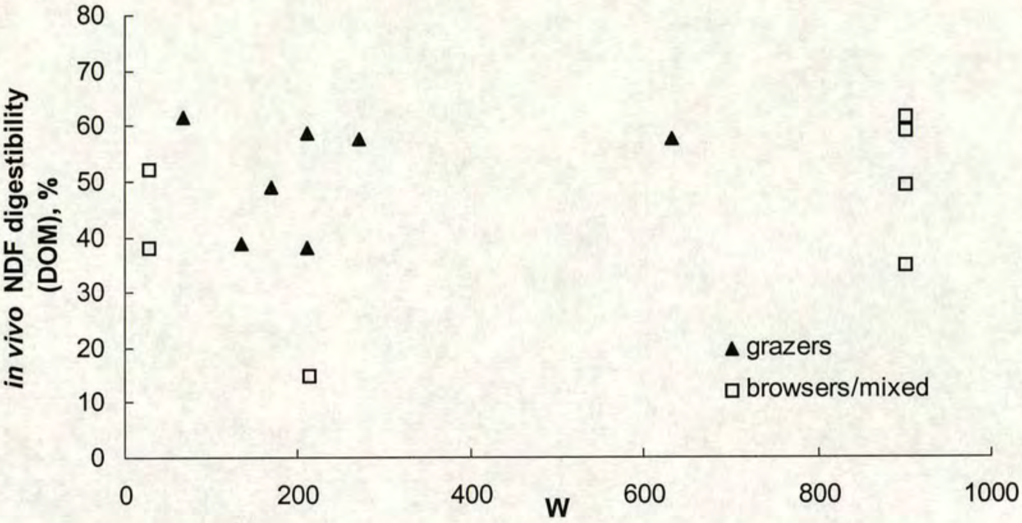


Figure 3.4. Observed digestibility is not a function of body size. This is probably partly due to selectivity (smaller species consume proportionately less cell wall, which therefore can be digested more completely), and partly due to adaptive variation in retention time (when *CW* in the diet increases, retention time increases and *CW* fermentation goes on for longer). *NDF* digestibility data from Prins *et al.* (1983). Note reduced data set (no *W* values for non-African species).

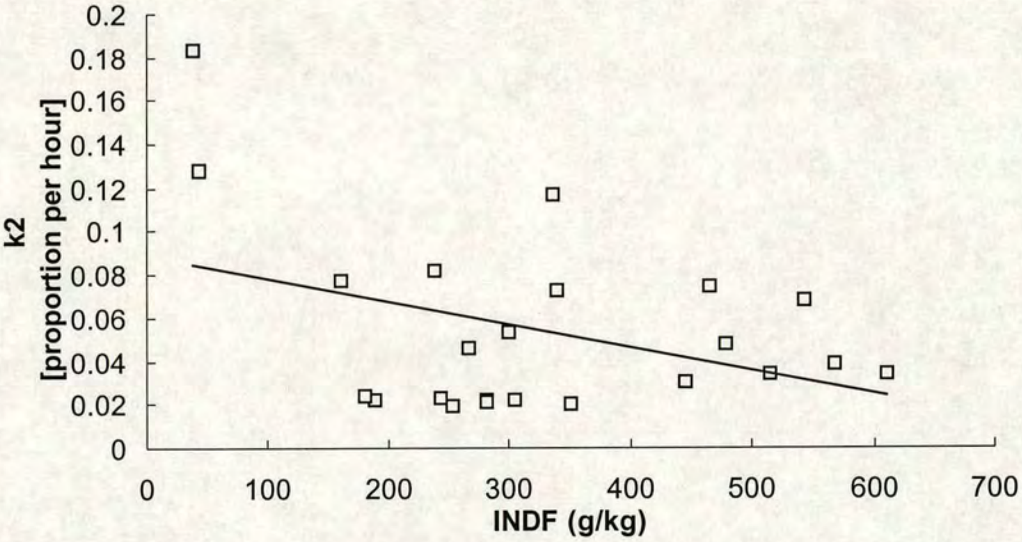


Figure 3.5. Rate of cell wall digestion (k_2) falls with increasing concentration of indigestible cell wall (*INDF*). Note that the relationship (which is just non-significant), relies on two points. In the model, a constant value is used for k_2. Data from Illius & Gordon (1991 table 2).

ENERGY BALANCE

The structure of the energy balance model is shown in appendix 3.1, and is modified from Van Soest (1994, chapter 2). Energy available for growth is the gross energy intake from food, minus allowances for various metabolic and digestion-related functions, maintenance requirements, and activity. The complete model is solved by setting the growth term to zero to calculate the ZNGI.

Model description

Gross energy intake (GE_d) is the sum of the energy contents of assimilated *CW* and *CC*, calculated by the digestion model. Not all of this energy is available to metabolism. Faeces contain undigested food, microbial matter and endogenous material that have a total energy content (FE_d) that is lost to metabolism (Van Soest 1994). Illius & Gordon (1991) estimated faecal energy as 10% of energy intake (GE_d), whereas Givens, Everington & Adamson (1990a) reported a figure of 26% of GE_d for sheep.

As well as energy lost in faeces, there is a small amount of energy lost in the urine (UE_d) and methane (PE_d). Urinary energy is positively related to the protein content of the food:

$$UE_d = 0.0121 + 0.000259CP \qquad \text{(eqn. 16)}$$

mean $UE_d = 0.055GE_d$

$R^2_{adj} = 0.541$, $P < 0.001$ (Givens, Everington & Adamson 1990a)

Energy lost as methane is a negative function of digestibility and of GE_d (Blaxter 1969). Givens, Everington & Adamson (1989) used an equation from Blaxter & Clapperton (1965) to predict methane losses (in sheep), with:

$$\text{mean } PE_d = 0.083GE_d \qquad \text{(eqn. 17)}$$

Van Soest (1994) gives ranges for PEd = 5-12% GE_d, UE_d = 3-5% GE_d, and the heat increment (see below) = 20-30% GE_d at maintenance, 30% GE_d when lactating, and

42% GE_d when fattening. For the current model, the mean values reported in Givens, Everington & Adamson (1989) were used.

With these losses, metabolizable energy intake is:

$$\begin{aligned} ME_d[MJ.day^{-1}] &= GE_d - (FE_d + UE_d + PE_d) \\ &= [1-(0.26+0.055+0.083)]GE_d \\ &= 0.602GE_d \end{aligned} \quad \text{(eqn. 18)}$$

Fermentation and digestion of the food are important energetic processes. The total energy cost of digesting the food is termed the heat increment. It is made up of the heat of fermentation, the heat of digestion, the work of rumination, and a term for radiative losses. The heat increment is particularly high in ruminants, and is strongly influenced by the fibre content of the diet (Van Soest 1994).

The work of rumination is proportional to fibre content (Van Soest 1994). Heat production of sheep increases 40-80% during and for up to two hours after feeding, and is a function of time spent feeding rather than intake (Webster 1978, in Van Soest 1994). These observations suggest a structure to account for the heat increment:

$$E_r[MJ.day^{-1}] = r.CW_i \quad \text{(eqn. 19)}$$

$$E_h[MJ.day^{-1}] = 0.5E_{basal}\frac{(t_{\max}+2)}{24} \quad \text{(eqn. 20)}$$

$$HE_d[MJ.day^{-1}] = E_r + E_h \quad \text{(eqn. 21)}$$

HE_d $[MJ.day^{-1}]$ = heat increment

t_{max} $[hours]$ = time spent feeding (as in the intake model)

r $[MJ.kg^{-1}]$ = work of rumination per kg of ingested fibre

C_d = daily DM intake [*g*], from intake model

E_{basal} $[MJ.day^{-1}]$ = daily basal requirement is calculated below

Webster (1978, in Van Soest 1994) estimated that cattle (400 *kg*) expend about 21.15 *MJ* per day ruminating. From equation 1, and using the body size regression (eqn. 3a) to calculate *RT*, daily fill for a 400kg animal is 2836 $g.day^{-1}$. Assuming a

50% fibre content ($NDF = 500\ g.kg^{-1}$) and non-selective feeding, $CW_i = 1418\ g.day^{-1}$ and equation 19 gives:

$$r = 14.92\ MJ.kg^{-1}$$

Subtracting the heat increment from the metabolisable energy intake gives the net energy available for maintenance and growth: $NE_d\,[MJ.day^{-1}] = ME_d - HE_d$.

Maintenance energy is the sum of basal heat production at maintenance levels of energy intake, plus an allowance for activity. The activity allowance ranges from one to two times the basal heat production (Peters 1983). Wilmshurst, Fryxell & Bergman (2000) set basal requirements to

$$E_{basal}\,[MJ.day^{-1}] = 0.45W^{0.73}$$

following Konoplev, Sokolov & Zotin (1978). Illius & Gordon (1991, using a relation from Brody 1945) estimated basal heat production plus the activity allowance as

$$(E_{basal} + E_{act})[MJ.day^{-1}] = 0.4W^{0.73}$$

Demment & Van Soest (1985, quoting Kleiber 1975) estimated basal requirements as

$$E_{maint}[MJ.day^{-1}] = 0.2975W^{0.75}$$

In the current model, the Wilmshurst, Fryxell & Bergman (2000) figures are used:

$$E_{maint}[MJ.day^{-1}] = E_{basal} + E_{act} = 2 \times 0.45W^{0.73} = 0.9W^{0.73} \qquad \text{(eqn. 22)}$$

The resulting profit or loss is called G_d, the energy available for growth, and is expressed as multiples of maintenance requirements:

$$G_d = \frac{NE_d - E_{maint}}{E_{maint}} \qquad \text{(eqn. 23)}$$

To generate the ZNGI, the model is solved for $G_d = 0$. In practice, the model is too complex to solve analytically, but the numerical estimation graphing capabilities of Maple were used to plot the ZNGIs.

RESULTS

The shapes of many of the functions used in the model are illustrated in appendix 3.2. The model as described failed to supply enough energy to any body size of grazer to achieve maintenance energy intake. The results described were obtained by neglecting to subtract the metabolisable energy losses from faeces, urine, and methane production (equation 18 was replaced with $ME_d = GE_d$; see discussion).

Four versions of the model were run, depending on whether selective foraging and body-size dependent adjustment of retention time to forage quality were implemented (table 3.2). The ZNGI diagram output from each version is shown in figure 3.6.

Consumption vectors are not illustrated. In models *b* and *d*, the consumption vectors at equilibria (ZNGI intersections) have the same direction (but different magnitudes), because selective foraging was not modelled. The directions of the consumption vectors at any point are given by the relative availabilities of *CW* and *CC*. In models *a* and *c*, with a basic model of selective foraging, the consumption vectors of all species are strongly skewed towards more *CC* in the diet than in the sward, with an even stronger skew for smaller species.

Table 3.2. Components implemented in the 4 versions of the model.

	RT_{adj} depends on body size	selective foraging
model *a*)	YES	YES
model *b*)	YES	NO
model *c*)	NO	YES
model *d*)	NO	NO

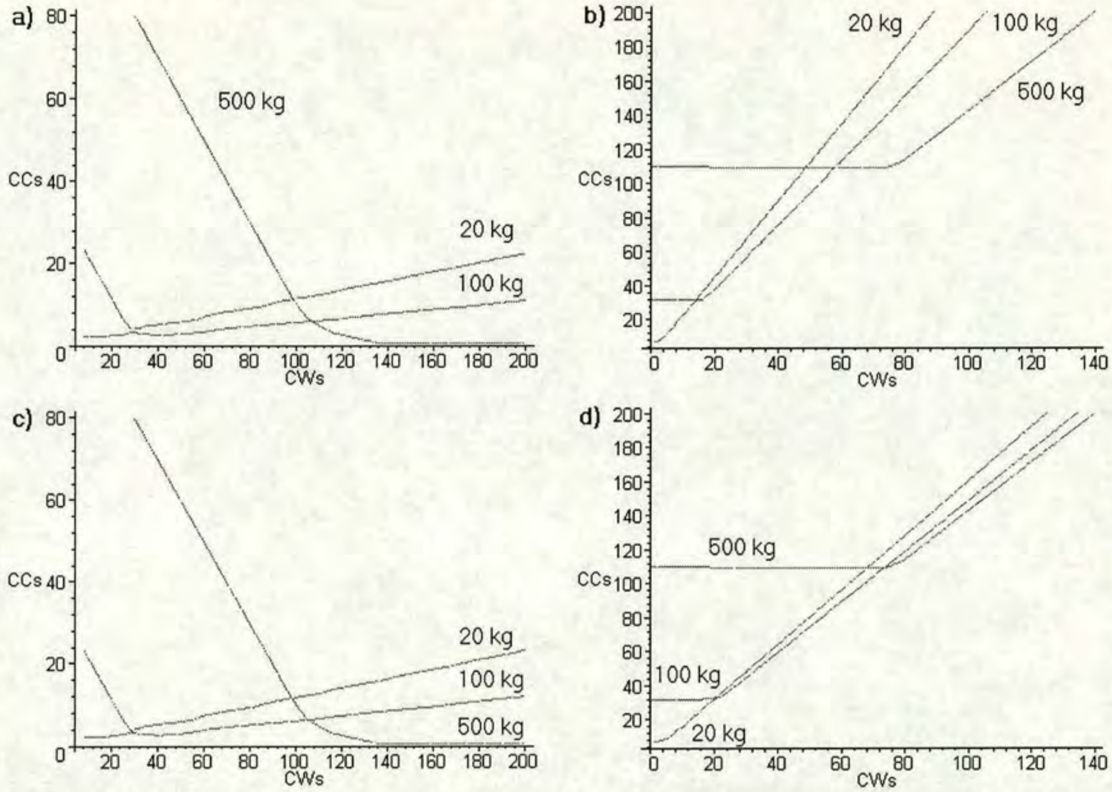


Figure 3.6. Zero Net Growth Isoclines predicted by the model for 3 ungulates of different body sizes. a) full model; b) non-selective foragers; c) *RT* adjustment independent of *W*; d) basic model. CC_S and CW_S are the supply rates of cell contents and cell wall respectively, in $kg.ha^{-1}$.

In all four versions, the right-hand section of the ZNGI has an upward slope, indicating an inhibitory effect of *CW*. As the proportion of *CW* in the diet increases, the rate of energy intake falls because *CW* takes time to ferment, therefore reducing the rate of energy intake. This inhibitory effect is reduced in the selective foraging models (*a* and *c*), because the animals are able to ingest a higher proportion of *CC* than is present in the sward. Nevertheless, even for selective foragers, increasing the supply rate of *CW* increases its intake, and beyond a threshold supply rate *CW* becomes inhibitory. The minimum quality of forage that each species can tolerate is given by the slope of the upward segment of its ZNGI. In all four models, larger animals are able to tolerate lower quality diets, indicated by the shallower slopes. The inhibitory effect of *CW* also starts at higher *CW* supply rates for the larger animals.

Retention time is dependent on body size in all four models, but in models *a* and *b*, the adjustment to retention time in response to forage quality is also dependent on body size. Larger animals apply a greater modification to their retention times than smaller animals. This has very little effect on selective foragers (compare figures 3a and 3c). Selective foragers have a relatively high proportion of *CC* in their diets even on poor quality swards, and therefore retention time is not subject to large modifications in response to forage quality.

For unselective foragers (figures 3b and 3d), the ability to modify retention time in response to forage quality is more important. In figure 3b, smaller animals are less able to increase retention time in response to low quality forage . As a result, they are even more sensitive to the inhibitory effect of *CW*, and the slope of that segment of the ZNGI is steeper for smaller animals in figure 3b than in figure 3d.

In all four models, ZNGI's cross the *CC* axis closer to the origin for smaller animals than for larger animals. Smaller species can therefore exclude larger species from high quality swards. ZNGI's do not cross the *CW* axis, and therefore none of the species modelled can survive purely on *CW*. Larger animals however can tolerate a higher abundance of *CW*. In fact, for models *a* and *c*, very large animals (1000 *kg*) *can* survive entirely on *CW*, and the right-hand segment of their ZNGI never slopes upwards (figure 3.7).

Figure 3.7. ZNGI for a very large animal (1000 *kg*) predicted by the full model. Cell wall never becomes inhibiting, and the animal can survive on a diet consisting entirely of cell wall. However, a small amount of cell content in the sward can replace a large amount of cell wall, partly because of its high energy content, and partly because the animal forages selectively, obtaining a large *CC* intake even when *CC* is rare. This shape of ZNGI classifies cell wall and cell content as *complementary resources* (see figure 2.3), for very large animals.

Although consumption vectors are not shown, the stability of equilibria (ZNGI intersections) can be assessed by assuming that smaller species are more selective of *CC* (as actually modelled in figures 3a and 3c).

For non-selective foragers (models *b* and *d*), at equilibrium the larger species is limited by *CC*, whereas the smaller species can tolerate a reduction in *CC* if there is a small reduction in *CW*. The smaller species would benefit from any consumption by the larger (since the larger species disproportionately depletes *CW*). The larger species however would be shifted below its ZNGI by the smaller species depleting *CC*. The crossover is therefore not stable and the larger species would be excluded. In habitats above and to the right of the crossover in figures 3.6b and d, consumption by the larger species will eventually reduce *CW* until the system either reaches the crossover point, or crosses the ZNGI of the smaller species. In either case, the smaller species will eventually exclude the larger.

For selective foragers (models *a* and *c*), stable coexistence is possible. At equilibrium, the smaller is limited by *CC*, which it consumes relatively more of than does the larger species. The larger species is more strongly limited by *CW*, which it consumes relatively more of than does the smaller species. This satisfies the León & Tumpson (1975) conditions for stable coexistence (see chapter 2).

Facilitation is possible in these models, depending on the directions of the consumption vectors and the body size difference of the species. Figure 3.8 shows a close-up of the crossover for a 20 *kg* and a 100 *kg* species predicted by the full model. The arrangement of ZNGI's and consumption vectors is similar to that of figure 2.5c, generating habitats from which each species excludes the other, and habitat that the larger species will modify by consumption until the smaller species is facilitated. Depending upon the precise orientation of the consumption vectors, there may or may not be habitat within which stable coexistence is possible. In figure 2.5c, the consumption vectors were drawn to exclude this possibility.

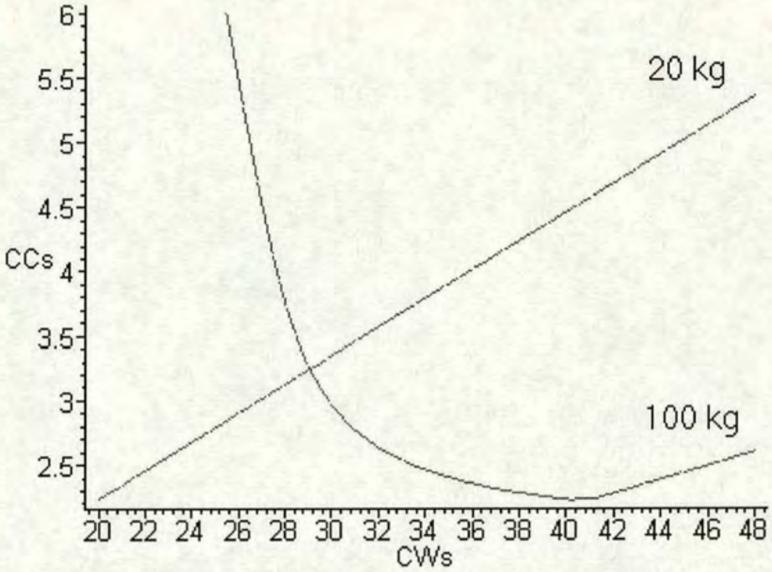


Figure 3.8. Close-up of the ZNGI's for 2 species from figure 3.6a

DISCUSSION

Shortcomings of the model

Energetic shortfall

The model suffers from several important defects. The most obvious upon running the model as specified above is that it fails to supply enough energy for maintenance requirements to any body size of forager. There could be four reasons for this:

1. The animals are not ingesting enough food.
2. The food they ingest does not contain enough digestible energy.
3. The animals are not extracting enough of the potentially available energy from their food.
4. The animals are expending too much energy.

Ingestion is modelled as the minimum of two constraints: eating rate and gut capacity. The gut capacity constraint is straightforward and based on strong data (equations 1, 2 & 3). The retention time adjustment is limited to ± 15% and should not severely restrict energy intake. The cropping constraint only becomes limiting at very low standing biomasses of *CC* and *CW*. The ingestion constraints do not appear to unrealistically restrain intake.

The second part of the ingestion model describes selectivity. All ungulates forage selectively, achieving a higher proportion of *CC* in their diet than is present in the sward. No data were available in the literature to quantitatively predict selectivity from body size and forage characteristics. Murray & Illius (2000) fitted a logistic model to data for wildebeest and topi selectively foraging on differentiated and undifferentiated swards. This model was used here, with an *ad hoc* adjustment for body size. Although the CC_i and CW_i figures in appendix 3.2 indicate a high degree of selectivity for *CC*, it may be that real ungulates are even more selective.

The second possibility - that the food contains too little energy - is unlikely to be true. Energy content of *CC* and *CW* comes from Givens, Everington & Adamson (1989, 1990a, 1990b). These authors analysed UK commercial forages, which are likely to be more digestible and contain more extractable calories than tropical grasses. Their data were used because such detailed information on tropical forages were not available. Murray (1991) used these data to estimate parameters in a model of tropical ruminant digestion and energy balance. They represent energy supply at the highest end of the sample range in tropical forage.

The third potential error is that the digestion model fails to extract sufficient energy from the food. However, the digestion model only applies to the *CW* component of the diet. Cell contents are 100% digestible, and are given the highest energy content found in the literature. If the digestion model was overly restrictive, it should be possible to feed the ungulates pure *CC* and achieve a positive energy balance. It is not.

Finally, the energy balance model may be overestimating losses. This seems to be the most likely explanation, partly because the first three seem unlikely. Also, the energy balance model incorporates many energetic costs, some of which are substantial.

To generate positive energy balances, the model was run with a modified energy balance model. Metabolisable energy losses - energy lost in faeces, urine and methane - were removed from the model (see appendix 3.3). These losses are all proportional to the energy extracted from the food. They do not vary with body size, and therefore should not affect the model in a non-linear, complex fashion. The effect is equivalent to increasing the energy content of both *CC* and *CW* by a constant factor, for all body sizes. All results presented and discussed are from models incorporating this quick fix.

Unjustified assumptions

Two features of the model were derived from minimal data. These are the description of selective foraging, and the adjustment of retention time in response to variations in forage quality. The model was therefore run in four versions (see table 3.2) to study the implications of these estimated relationships.

All ungulates forage selectively. Data in Murray & Illius (2000) show that topi and wildebeest diets contain very much more green leaf than is available in all but the poorest swards. They fitted a logistic model to their data, and this fit was applied to the current model (equation 7d). However, their data describe the proportion of green leaf in the diet, whereas the present model is parameterised in terms of cell contents and cell wall. The selectivity component would be improved if a relationship between the proportion of green leaf in the sward and the proportion of cell contents could be developed.

A further modification to the selectivity component was to increase or decrease selectivity according to body size. This modification was limited to a relatively small range. There are no data available to estimate a true relationship. Equations 7b and 7c describe unselective intake, and equations 7d and 7e describe selectivity.

The lack of supporting data to estimate selectivity mean that consumption vectors cannot be drawn accurately. In the unselective models, consumption vectors coincide. However, it is reasonable to assume that smaller animals are more selective than larger animals, which allows the conditions for stability to be assessed for each model.

The second guestimated model component concerns the adjustment of retention time according to body size. There are good data to estimate the inter-specific variation of mean retention time with body size (see equation 3a). However, retention time also responds to forage quality, and this response is itself related to body size. Larger animals are able to modify retention times more than smaller animals (Van Soest 1994). The digestion model of Illius & Gordon (1991, 1992) is sufficiently detailed to provide a description of this relationship, but the mathematical derivation is complex and has not been attempted. Instead, an empirical adjustment is used (equation 3b) which increases retention time by up to 15% for the poorest forages, and decreases it by up to 15% for the best forages. This adjustment is further modulated by body size (equation 3c), with 500 *kg* animals receiving the full adjustment and smaller animals less. All the model versions reported here incorporate the forage quality adjustment to *RT*, but the body size modulation may or may not be applied (see table 3.2).

Interpretations and predictions

The basic interpretation of the models was carried out in the results section, where exclusion, facilitation, the inhibitory effect of cell wall, and the stability of equilibria were identified. These predictions fit well with what is known about ungulate foraging (chapters 1 and 2). The inclusion of selective foraging (figures 3.6a and c) results in a more realistic model, which is similar in many respects to that describing wildebeest and topi foraging in chapter 2 (chapter 2.7).

Complementary resources

On rich swards, *CW* and *CC* are complementary resources. Beyond a threshold supply rate of *CW*, higher for larger animals, *CW* becomes inhibitory, and maintenance can only be achieved if the supply of *CC* also increases. The rate at which *CC* supply must increase to compensate for the inhibitory effect of *CW* is lower for larger animals.

Bell-Jarman effect

It is surprising that the left-hand sections of the ZNGI's are parallel for species of different body sizes. The slopes of this part of the ZNGI's show that *CW* and *CC* are complementary. The conceptual model of Bell-Jarman foraging presented in chapter 2 (figure 2.4C) predicts that the slope should be steeper downwards for larger grazers. The difference in slope was predicted because larger grazers should be able to extract more energy from the *CW* component, so that as the supply of *CW* increases, their requirement for *CC* falls more rapidly than happens for a smaller animal. The current model suggests that this differential digestive capability only becomes important when *CW* becomes inhibitory. I am not clear as to why the initial section of the ZNGI's should be parallel, since a Bell-Jarman effect is clearly indicated by the right-hand sections.

Spatial heterogeneity

Typical productivity ranges (standing biomasses) for African grazing systems are from 0 to about 150 $g.m^{-2}$ (data in McNaughton 1985; equivalent to1500 $kg.ha^{-1}$). This provides a range for $V = CC_S + CW_S$. In real systems, quality is negatively correlated to standing biomass (see chapter 1), so that CC_S / CW_S falls as V increases.

Figures 3.6a and c predict that if productivity is high, and mean quality too low to support some smaller species, then a relatively small amount of variability in forage quality could provide microhabitats suitable for the smaller species. In figures 2.1a and 2.1b, circles were used to describe a habitat and its range of resource supply rates. Figures 3.6a and c show that such a habitat would support the maximum number of species at quite low productivities of around 100 $kg.ha^{-1}$ CW_S and just 10 $kg.m^{-2}$ CC_S. This matches the original prediction of Tilman (1982, 1986), that diversity should at first rise rapidly with productivity, reaching a peak at quite low productivity before tailing off more slowly.

Community composition

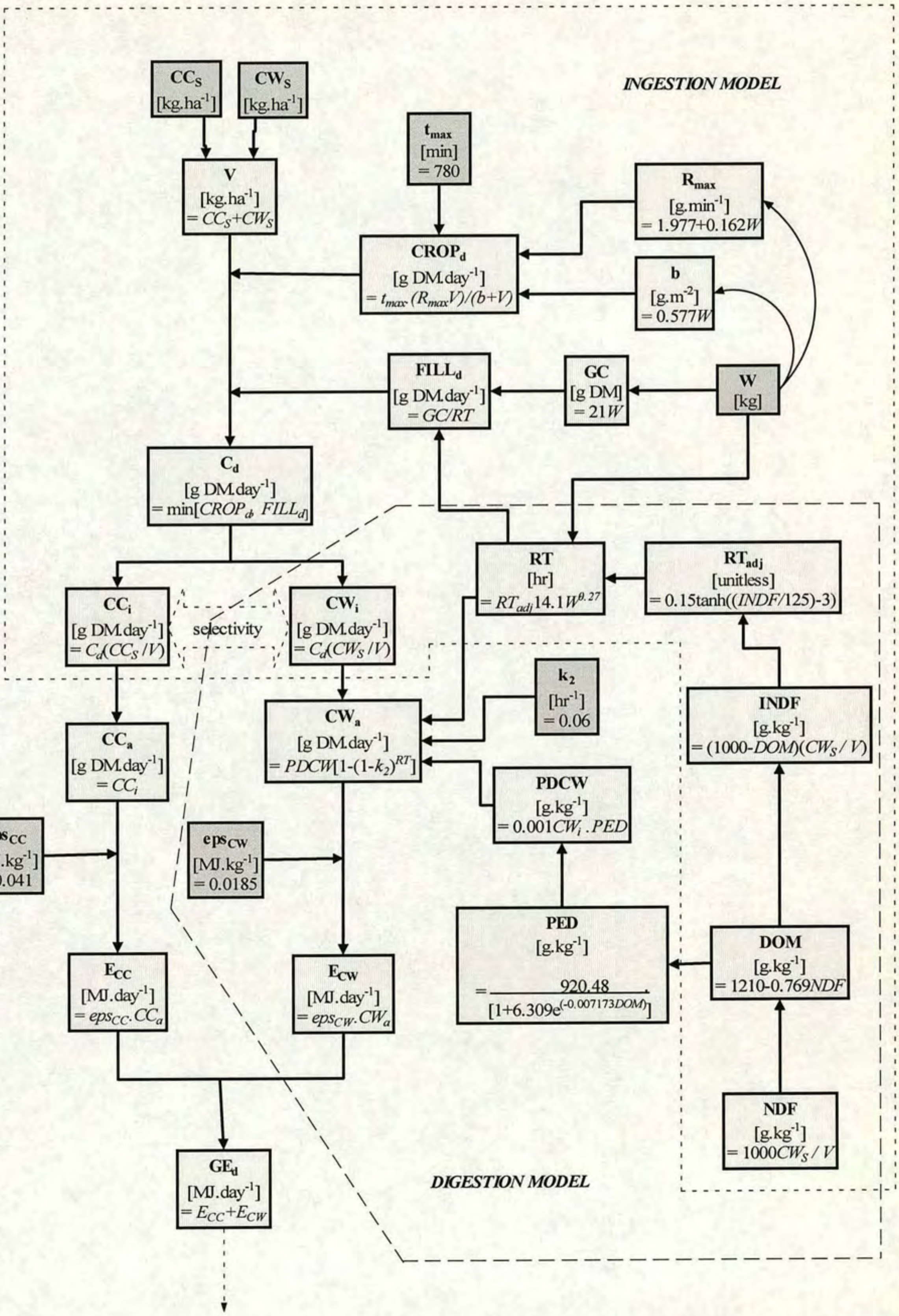
Figure 3.6a also predicts a change in the composition of ungulate communities along a productivity gradient. Low productivity habitats can only support small species. High productivity habitats can only support larger species, because forage quality is low. This matches the predictions of Bell (1982, 1984) and East (1984). They provided data in support of the hypothesis that in high rainfall areas of Africa, soil nutrients would be leached out, and the resulting vegetation would be highly productive but of low quality and would support a community of large-bodied herbivores. Where rainfall was lower, the vegetation standing biomass is lower but of higher quality, and small-bodied herbivores dominate the fauna.

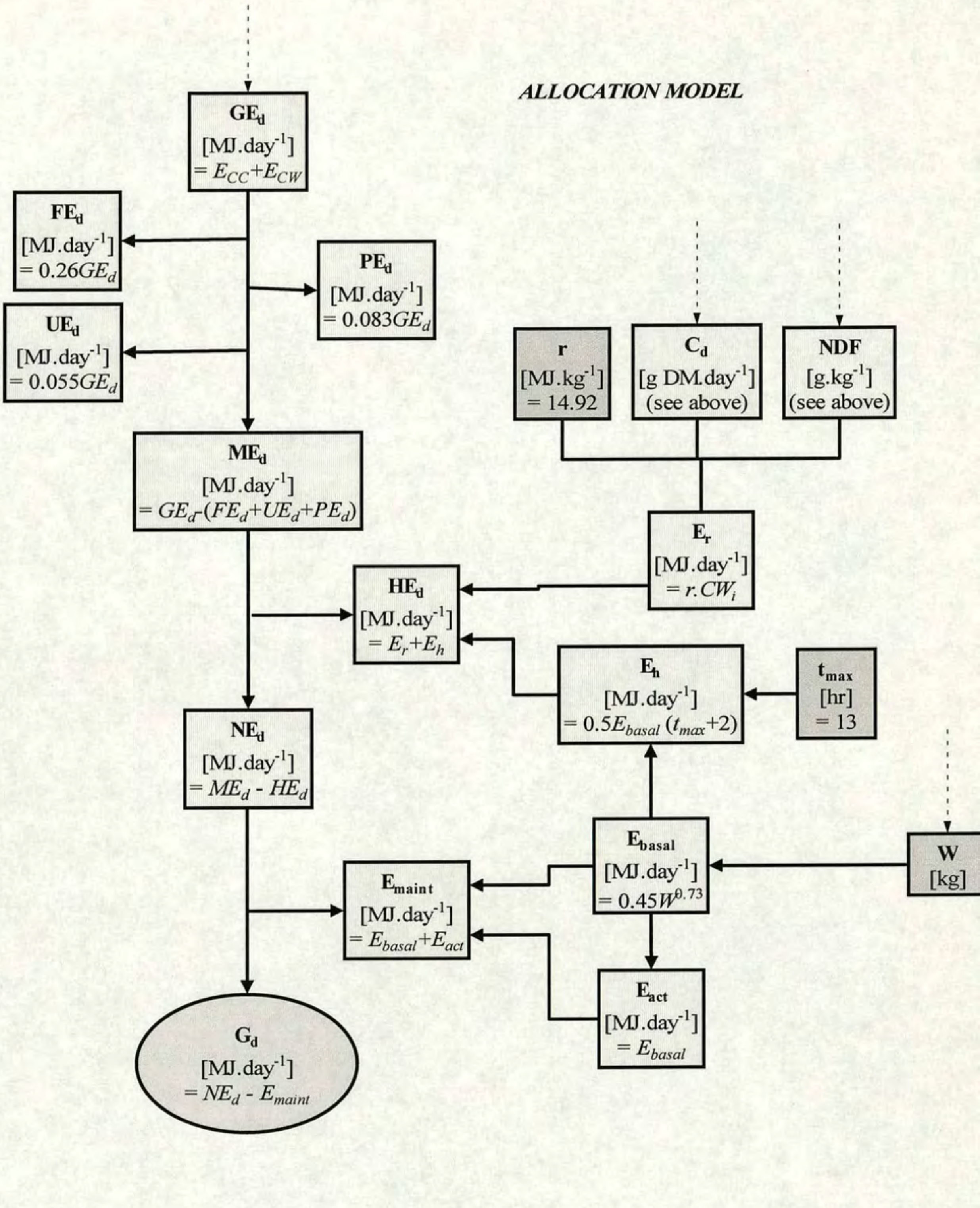
Conclusions

The model would benefit from a more realistic model of changes to retention time in response to forage quality, and from a better description of selective foraging. The former could be obtained from the literature, but data relating body size to selectivity are lacking. The energy balance component of the model appears to overestimate energetic losses.

The model predictions agree with many well described aspects of ungulate foraging and community ecology. Its hypotheses are reasonable and should therefore be tested in detail, using simulation modelling as mentioned previously. It is capable of making both detailed predictions about the outcome of competition between different species in different habitats, and more general predictions about the way ungulate diversity and community structure will change along productivity gradients. Some of these predictions will be tested in chapters 5 and 6.

APPENDIX 3.1. FLOW DIAGRAMS OF MODEL COMPONENTS

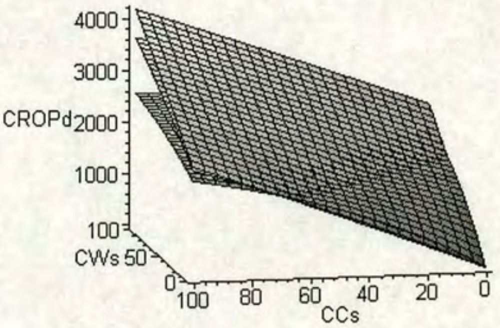



ALLOCATION MODEL
GE_d [MJ.day^-1] = E_CC+E_CW
FE_d [MJ.day^-1] = 0.26GE_d
PE_d [MJ.day^-1] = 0.083GE_d
UE_d [MJ.day^-1] = 0.055GE_d
ME_d [MJ.day^-1] = GE_d-(FE_d+UE_d+PE_d)
r [MJ.kg^-1] = 14.92
C_d [g DM.day^-1] (see above)
NDF [g.kg^-1] (see above)
E_r [MJ.day^-1] = r.CW_i
HE_d [MJ.day^-1] = E_r+E_h
E_h [MJ.day^-1] = 0.5E_basal (t_max+2)
t_max [hr] = 13
NE_d [MJ.day^-1] = ME_d - HE_d
E_basal [MJ.day^-1] = 0.45W^0.73
W [kg]
E_maint [MJ.day^-1] = E_basal+E_act
E_act [MJ.day^-1] = E_basal
G_d [MJ.day^-1] = NE_d - E_maint

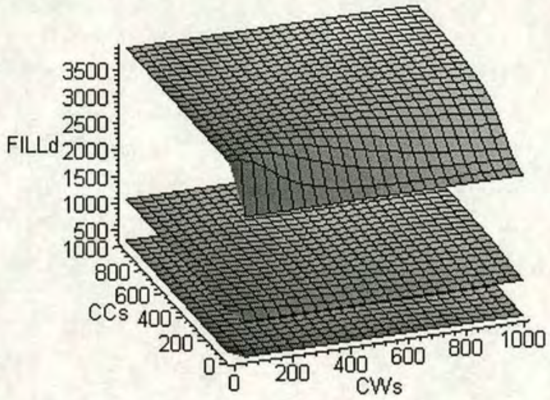
APPENDIX 3.2. SHAPES OF FUNCTIONS IN THE INTAKE AND DIGESTION COMPONENTS

Functions are plotted for body sizes of 20, 100 and 500 *kg*.

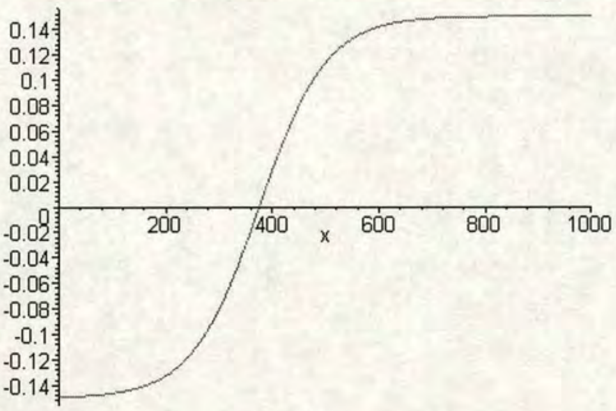
Intake component



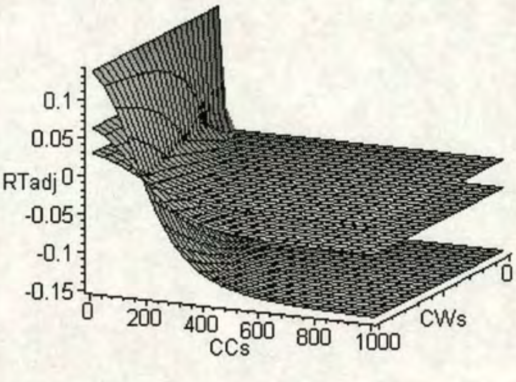
$CROP_d$ - the daily cropping constraint



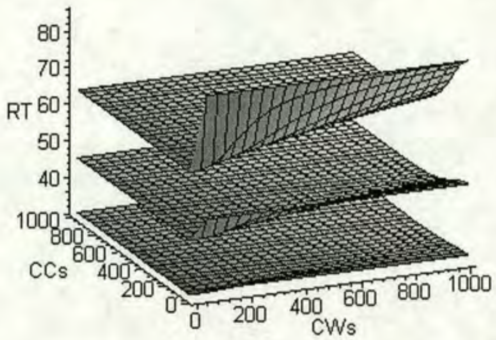
$FILL_d$ - the daily gut fill constraint



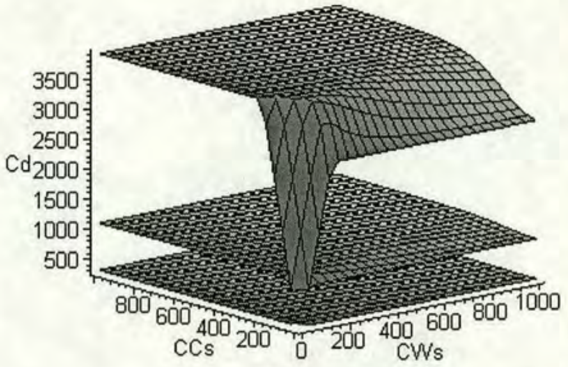
RT_{adj} - the adjustment to retention time due to food quality. $x = INDF$ (indigestible fraction).



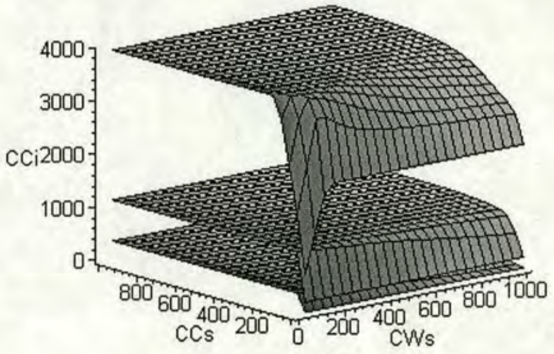
RT_{adj} - as a function of CW_S and CC_S



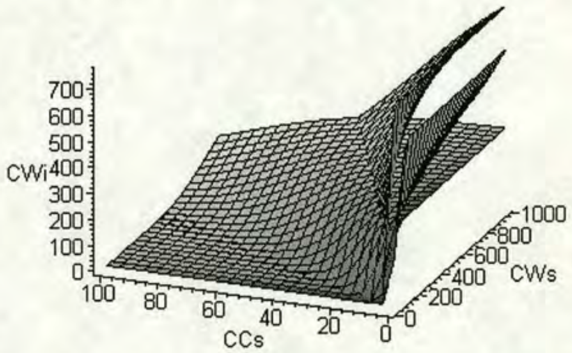
RT - retention time of food in the gut



C_d - daily intake

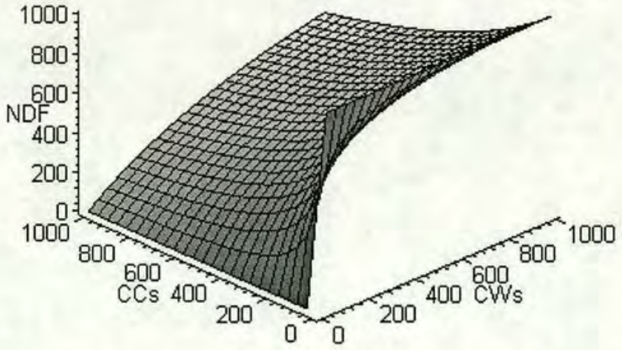


CC_i - daily intake of *CC*

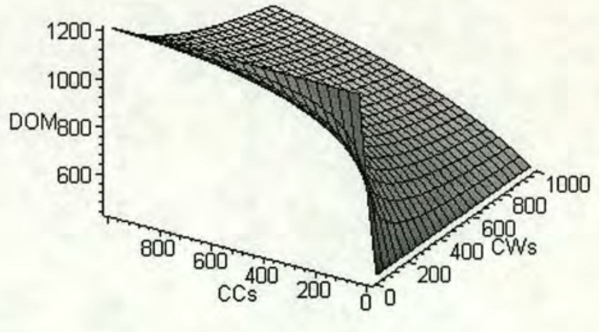


CW_i - daily intake of *CW*

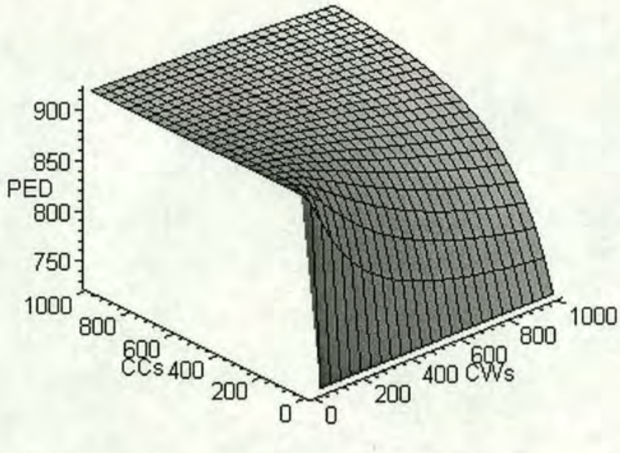
Digestion component



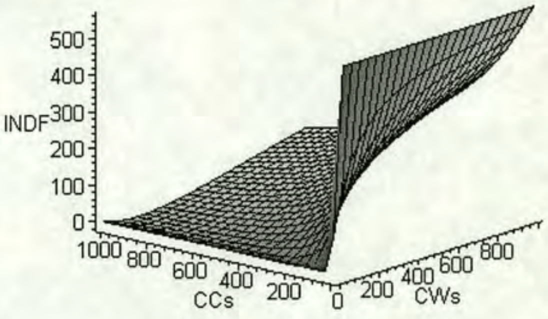
NDF - proportion of cell wall in the sward



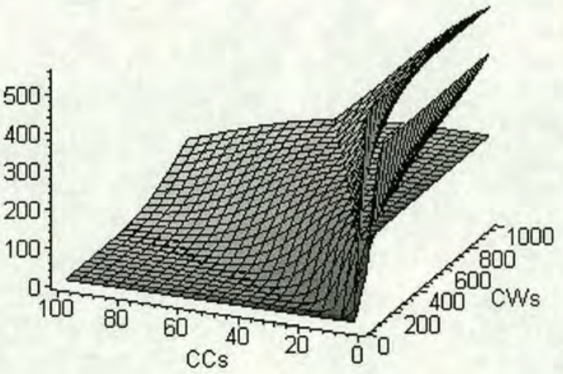
DOM - observed digestibility of organic matter content



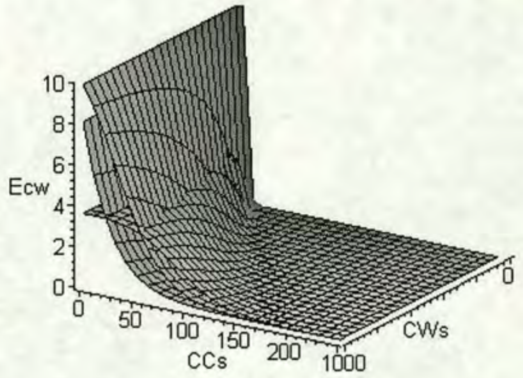
PED - potential extent of digestion



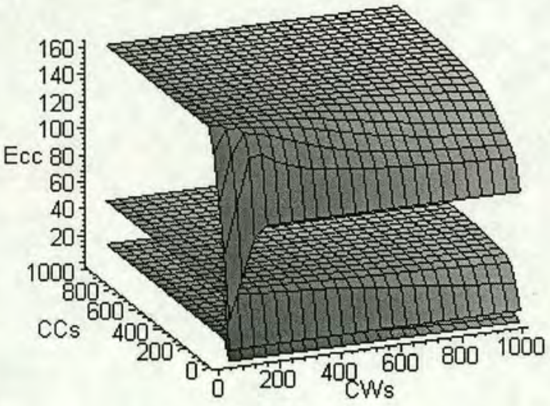
INDF - indigestible fraction



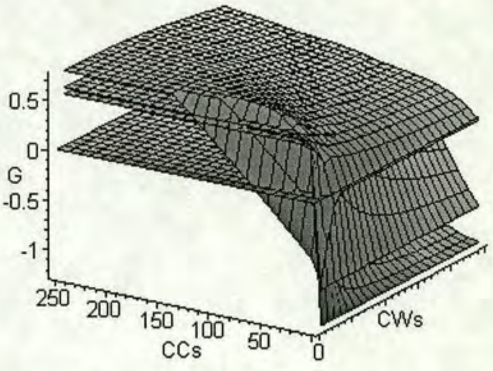
PDCW$_d$ - potentially digestible cell wall intake



E$_{CW}$ - gross energy value of digestible cell wall intake



E$_{CC}$ - gross energy value of cell content intake



G$_d$ - daily energy profit or loss, as multiples of maintenance

APPENDIX 3.3. MAPLE CODE

```
> restart;
#Vegetation
> V := CCs+CWs:
> NDF := 1000*CWs/V:
> DOM := 1210-.769*NDF:
> PED := 920.48/(1+6.309*exp(-.7173e-2*DOM)):
> INDF := (1000-DOM)*CWs/V:

#Intake model
> Rmax := .1617*W+1.9771:
> b := .5768*W:
> tmax := 13*60:
> CROPd := tmax*Rmax*.1*V/(b+.1*V):
> GC := 21*W:

      #retention time not dependent on W
      > RTadj := .15*tanh((INDF)/125-3):
      #retention time dependent on W
      > RTadj := ((W/500)^0.5)*.15*tanh((INDF)/125-3):

> RT := (1+RTadj)*14.1*W^.27:

> FILLd := 24*GC/RT:
> Cd := min(CROPd,FILLd):

      #selectivity
      > param_a:=(5/3)*log(W)-9: #-6:
      > param_b:=45:
      > P_CCs:=CCs/CWs:
      > logit:=x->ln(x/(1-x)):
      > P_CCi:=solve(logit(PCCi)=param_a+param_b*P_CCs,PCCi):
      > CCi:=P_CCi*Cd:
      > CWi:=(1-P_CCi)*Cd:

      #no selectivity
      > CCi := CCs*Cd/V:
      > CWi := CWs*Cd/V:

#Digestion model
> PDCW := 0.001*CWi*PED:
> k2 := .06:
> CWa := PDCW*(1-(1-k2)^RT):
> epscw := .185e-1:
> Ecw := epscw*CWa:
> CCa := CCi:
> epscc := .41e-1:
> Ecc := epscc*CCa:

#Energy balance
> GEd := Ecc+Ecw:
> FEd := .26*GEd:
> UEd := .55e-1*GEd:
> PEd := .83e-1*GEd:
> MEd := GEd: #-(FEd+UEd+PEd):  #subtraction not implemented
> Ebasal := .45*W^.73:
> Eh := .5*Ebasal*((tmax/60)+2)/24:
```

```
> r := 14.92:
> Er := r*CWi/1000:
> HEd := Er+Eh:
> NEd := MEd-HEd:
> Eact := Ebasal:
> Emaint := Eact+Ebasal:
> GROWTHd := (NEd-Emaint)/Emaint:
```

4. TESTING THE EVIDENCE FOR LIMITING SIMILARITY IN COMMUNITIES OF AFRICAN UNGULATES

INTRODUCTION

Limiting similarity

The idea that there is a limit to the similarity in resource use that two species can exhibit and stably coexist is one of the fundamental organising principles of theoretical community ecology (Hutchinson 1959, MacArthur & Levins 1967, Abrams 1983, Lewin 1983, Grant & Schluter 1984). Although the theory explicitly depends upon resource use similarity, field tests of experimental predictions have instead focused on studies of the similarities in morphology of supposed competing species, in particular the morphology of structures associated with resource capture. Thus Lack and others (Lack 1983, Schluter, Price & Grant 1985) studied the bill morphology of Darwin's finches, Hutchinson (1959) mused upon the skull length of mammals and the culmen length of birds, and a number of authors have studied the teeth and mouths of carnivores (Kiltie 1984, 1988, Dayan *et al.* 1989, 1990, Dayan & Simberloff 1994, Van Valkenburgh & Wayne 1994; see review by Dayan & Simberloff 1998).

Dayan & Simberloff (1998) argued that oral and skull morphology can be subject to complex selection pressures, and may provide ambiguous indices of resource-based coevolution. Body size has been used as a more general index of resource use in some studies (Schoener 1984 for bird-eating hawks; Prins & Olff 1998 with ungulates). For those groups, body size can be directly related to resource use (see chapters 1 and 2 for ungulates).

Abrams (1983) points out that in nature, the observed difference in species characteristics should be greater than the expected limiting similarity. The optimal difference is larger than the minimum difference, because as two species approach the minimum difference, the population size of at least one of the species should fall. This observation is a happy one, since it makes it potentially easier to detect such differences. However, when unexpectedly large differences are observed, they should be interpreted as placing an upper bound on the limiting similarity for coexistence, which is likely to be somewhat smaller than the observed difference.

Character displacement

A distinction must be made between limiting similarity, which is an evolutionary phenomenon, and character displacement, which is evolutionary process or mechanism. In both cases, competition for resources is more intense among species that use more similar resources. If resource use is related to morphology, then evolutionary theory would predict that individuals possessing more divergent morphologies will benefit from reduced intensity of competition because they are using slightly different resources. Over time, this divergent evolution will result in the formation of a community of resource exploiters whose morphologies are more different from one another than may be expected in the absence of competition.

This evolutionary process can operate over short time scales, and within geographically distinct populations of the same species, to generate ecological character displacement. Depending upon the identity of sympatric competitors, the morphology of a given population can shift in response to competitive pressures. The morphology of a given species may therefore become distinct in different populations. This scenario is easier to test, because populations of the same species can be compared, and then differences in morphology must be explained, perhaps by the character displacement hypothesis.

The classic example of character displacement was described by Lack (1983, see also Grant & Schluter 1984), where beak characters of Darwin's finches were dissimilar in sympatric populations but similar in allopatric populations. Schluter, Price & Grant (1985) controlled for variations in food supply, which could potentially explain geographic variation in bill morphology, but found strong corroboration for the character displacement hypothesis. Schluter (1994) has also experimentally tested character displacement by growing populations of 2 species of stickleback either in isolation or mixed together. When mixed, individuals of either species that were morphologically more similar to the other species suffered a reduced growth rate. The reduction was correlated to the degree of similarity to the competitor species.

Testing limiting similarity

Character displacement therefore provides one mechanism by which patterns of limiting similarity may become established in a community. There are others. Species with similar morphologies may be more prone to extinction if they suffer higher levels of competition for resources. Alternatively, immigration rates of morphologically similar species may be reduced because of more intense competition. Any or all of these processes could lead to the formation of a community of species whose characters differ systematically from one another.

Reliably detecting regular character values is much more difficult than detecting differences in mean character values among populations. The search for such a test led to one of the major debates in evolutionary ecology of the early 1980's. Simberloff & Boecklen (1981) complained that many (perhaps all) claims in support of limiting similarity were not backed up by proper statistical tests. They proposed a test described by Barton & David (1956) and re-analysed a large number of claims from the literature. Simberloff & Boecklen (*ibid.*) introduced the null hypothesis for testing claims of non-random body size distributions. It was

> *"...that the logarithms of species sizes did not differ from an independent set of points uniform-randomly distributed on a line segment between the logs of the largest and smallest observed sizes."*

They found that few published data sets rejected this null hypothesis at P = 0.05, and only about half of the claims were supported at P = 0.30.

The debate about using null hypotheses in community ecology plumbed the depths of the philosophy of science (Roughgarden 1983, Quinn & Dunham 1983, Simberloff 1983). The disagreements focussed on two substantive issues: a methodological and philosophical argument about the use and design of null hypotheses and null models, and a theoretical argument about the prevalence and importance of competition as a structuring force in ecological communities.

The disagreement about whether it was even appropriate to use null models focussed on studies of the co-occurrence patterns of species on islands (Connor & Simberloff 1983, 1984, Gilpin & Diamond 1984). The discussion was overdue, and null hypotheses now form the basis of scientific testing in community ecology, as they must (Harvey *et al.* 1983, Colwell & Winkler 1984).

Those who argued for stronger statistical testing of community ecological hypotheses were unfairly identified as arguing against the possibility of competition being important in structuring ecological communities. They were in fact simply reserving judgement until claims were substantiated by rigorous tests, and indeed went on themselves to provide many well tested examples of competitive structure (*e.g.* Dayan *et al.* 1989, 1990, Dayan & Simberloff 1994, 1998).

Previous work on structure in African ungulate communities

Limiting similarity among African browsing ungulates has been claimed (Owen-Smith 1985) but not tested. Conversely, unexpected coexistence of animals with similar body sizes has been claimed for African grazing ungulates, but again the claim was not subjected to statistical testing (Owen-Smith 1985, Demment & Van Soest 1985).

Only one test of a hypothesis of limiting similarity in African grazers (mammals larger than 2 *kg* and ostrich) has been carried out. Prins & Olff (1998) compared communities of grazers in several reserves to a null model, and found strong support for the limiting similarity hypothesis, with unexpectedly constant size ratios among sympatric species. Unfortunately, their null model was flawed.

The null model used by Prins & Olff (*ibid.*) was a random uniform distribution of body weights. Body weights were *not* log transformed before sampling from the random distribution. By using untransformed body weights, the absolute difference in body size between two species is equivalent, whether the pair of species is large or small. The difference between a 10 *kg* and 20 *kg* animal is equivalent to that between 100 *kg* and 110 *kg*. This model is inappropriate - body sizes should have been log transformed for the null model. In fact Prins & Olff (*ibid.*) report all data in terms of weight ratios (not differences), and construct all their plots using log transformed body weights.

Prins & Olff (*ibid.*) themselves supply the appropriate null model in their equation (7): $\ln(W_i) = ai + b$, where i is the body size rank order ($i = 0$ being the smallest species). Figure 4.1 illustrates this model, which is indistinguishable from their observed data, being a straight line joining the smallest species to the largest. The null model actually used by Prins & Olff (*ibid.*) is $W_i = ai + b$. When plotted on a graph of rank *vs.* $\ln(W_i)$ (such as figure 4.1), the null model produces a power curve that rises steeply over the first few ranks, before becoming much shallower and asymptotic (see Prins & Olff (*ibid.*) figure 17.7).

Prins & Olff (*ibid.*) carried out their test by plotting log transformed body weights against their rank, and comparing the curve with that defined by a null model. In all cases, the actual body weights lay on a straight line, whereas the null model followed a power curve. Linearity of the plot was taken to indicate regularity in the difference in log body weights, with the average weight ratio in the community given by the slope of the plot (see their figure 17.7).

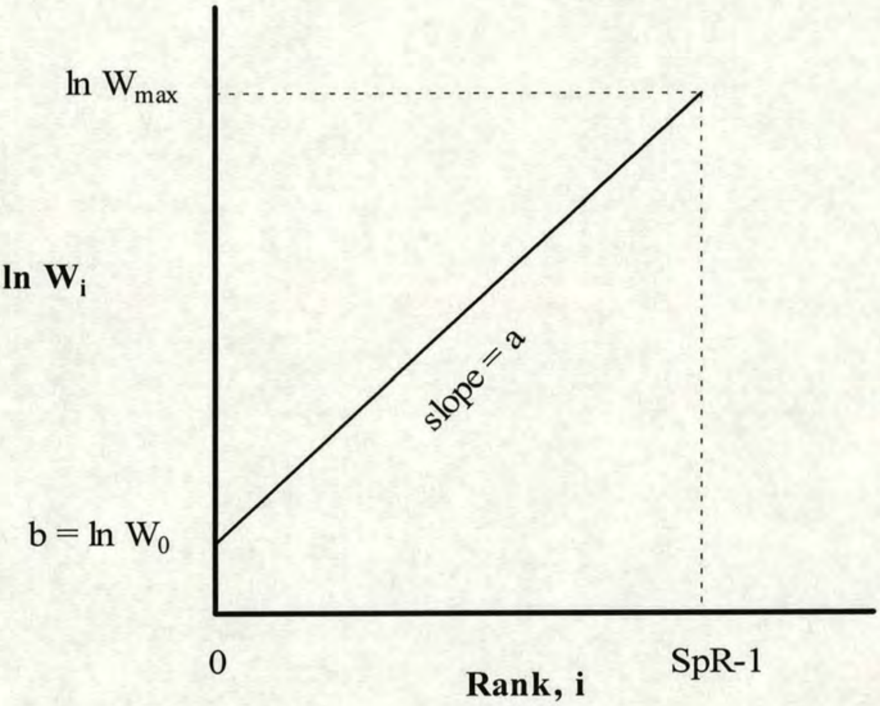


Figure 4.1. A null model for expected body weights drawn from a uniform distribution of log-transformed body weights. The expected slope is given by

$$a = \frac{SpR-1}{\ln(W_{\max}) - \ln(W_0)} = \frac{SpR-1}{\ln\left(W_{\max}/W_0\right)}$$

The uniform random distribution of log body weights is supported as a null expectation by figure 17.9 in Prins & Olff (*ibid.*), which shows that the body sizes of their continental list of grazers are approximately distributed in this manner. Bakker & Kelt (2000) found that body size distributions of Neotropical mammal communities were log uniform distributed if communities were stratified by foraging stratum. A log uniform distribution was also described in mammal communities from temperate regions of North and South America (Brown & Nicoletto 1991), and for the non-volant mammals of Mexico (Arita & Figueroa 1999).

Hypotheses

The limiting similarity hypothesis, strictly interpreted, refers only to the smallest difference in character values found in a community, and therefore depends upon data from just two species. A corollary of the hypothesis (see *Methods*) is that all ratios of the character values between sets of three species adjacent on the character axis will be closer to a constant value than expected.

The statistical null hypotheses against which these hypotheses will be tested are random distributions. These distributions can either be generated from infinite populations, or from a given population. Infinite distributions (such as the normal, log normal, and log uniform) test an evolutionary null hypothesis, in which all character values can potentially evolve, with the probability predicted by the null distribution in use. Finite distributions are generated from a pool of species. The test community is compared to the distribution of character values in the pool, and the null hypothesis is therefore ecological in nature. The observed community is a subset of a larger, regional pool. These hypotheses are discussed further in the *Methods* section.

H1: limiting similarity in ecological assemblages

The smallest observed difference in body size between two species in a community is larger than expected from a random sample of communities with the same number of species taken from the regional pool.

H2: limiting similarity in evolutionary assemblages

The smallest observed difference in body size between two species in a community is larger than expected from a random sample of communities with the same number of species from a log uniform distribution of body sizes with the smallest and largest body sizes equal to those in the observed community.

H3: regularity of ratios in ecological assemblages

The ratio of body size differences between species p and species q, and between species q and species r, where species p, q and r are adjacent on the body size axis, is closer to unity than expected from a random sample of communities with the same number of species taken from the regional pool.

H4: regularity of ratios in evolutionary assemblages

The ratio of body size differences between species p and species q, and between species q and species r, where species p, q and r are adjacent on the body size axis, is closer to unity than expected from a log uniform distribution of body sizes with the smallest and largest body sizes equal to those in the observed community.

METHODS

The two predictions that a hypothesis of limiting similarity generates which are tested here are 1) an unexpectedly large minimum ratio (or difference) in the characteristics of pairs of species in a community, and 2) the ratio of adjacent pairs of species on the character axis is unexpectedly regular.

If a community of $n + 1$ species is arranged along a character axis, then there will be n differences in the character values of each smaller species to the next largest species. These differences are usually designated g_i. If the character of interest is body size, as in this paper, then differences of log body weights should be used. Ratios of these differences are commonly used in statistical tests, and are designated as $G_{rs} = g_r / g_s$, where $g_r < g_s$. If the g_i are unusually regular, then the G_{rs} will be unexpectedly large (closer to 1).

Simberloff & Boecklen (1981) introduced the use of a test by Irwin (1955) to establish the probability of observing a particular minimum ratio. For $n + 1$ body weights uniform-randomly distributed on a log scaled axis, the probability of generating a minimum difference in log body sizes (g_1) that is smaller than an observed minimum a is given by:

$$\begin{aligned} P[g_1 < a] &= 1 - (1 - na)^{n-1} && \text{for } a \leq 1/n \\ &= 1 && \text{for } a > 1/n. \end{aligned}$$

Poole & Rathcke (1979) suggested using the variance of the g_i as a test for regularity of these ratios. Simberloff & Boecklen (1981) found the variance to be inferior to a test described by Barton & David (1956). The Barton & David test calculates the probability of any observed G_{rs}. Simberloff & Boecklen (*ibid.*) used a subset of all the possible G_{rs} values: G_{1n}, G_{2n} and $G_{1(n-1)}$. These values were chosen because they are defined for any community of four or more species, but any (or all) of the G_{rs} statistics could potentially be used.

The Barton & David regularity test

Barton & David (*ibid.*) derived the probability distribution of random intervals on a line, and developed several statistics from it. A number of points are located at random along a line. Every location on the line is equally likely to be chosen for any point. The result is a random, uniform distribution of points along the line. The length of each interval between pairs of adjacent points is then recorded. These intervals are then ordered from g_1, the shortest, to g_n, the longest. The ratio between any two of these intervals is then denoted by

$$G_{rs} = \frac{g_r}{g_s}, \qquad r < s.$$

Therefore $G_{rs} \leq 1$. The probability of observing a value of G_{rs} less than a given value $a \leq 1$ is given by

$$P[G_{rs} < a] = a\,{}^{n}C_{s}\,{}^{s}C_{r+1}\,r(r+1)\sum_{i=0}^{r-1}\sum_{j=0}^{s-r-1}(-1)^{i+j}\frac{{}^{r-1}C_{i}\,{}^{s-r-1}C_{j}}{(n-s+j+1)[(s-r+i-j)a+(n-s+j+1)]}$$

(Barton & David 1956).

For ecological applications, we are normally interested in the probability of observing a larger G_{rs}. This is simply $P[G_{rs} > a] = 1 - P[G_{rs} < a]$. Although the above equation is not structurally complex (in terms of programming a computer), it is unfortunately extremely sensitive to rounding error, because of the very large numbers involved and the large number of addition and subtraction operations. This error renders it impossible to use for species-rich communities such as those analysed here (up to 20 species). A Monte Carlo procedure was therefore used which replicates the Barton & David test.

Monte Carlo tests: evolutionary and ecological null hypotheses

In a Monte Carlo test, repeated samples are taken from an appropriate distribution, and a statistic calculated (such as a G_{rs} score). This is compared to the statistic observed in the real data. The frequency with which a more extreme statistic is derived from the simulated data than was observed in the real data provides the probability for hypothesis testing. If a more extreme statistic is rarely generated, then the observed statistic must be unusual (Crowley 1992).

In this chapter, two different Monte Carlo tests were carried out for each community. These correspond to the evolutionary null hypothesis and the ecological null hypothesis. The evolutionary null hypothesis uses a uniform random distribution to generate samples of log weights. The ecological null hypothesis uses a regional species pool as the sample distribution.

The evolutionary test was designed to directly replace the Barton & David (1956) test where rounding errors make it impracticable. In species-rich communities, the repeated addition and subtraction of very large numbers carried out during the probability calculation results in the accumulation of large rounding errors. The evolutionary Monte Carlo procedure is exactly equivalent to the Barton & David (1956) test. For each G_{rs} statistic calculated for an observed community of $n + 1$ species, 1000 random communities were constructed by drawing $n + 1$ log body weights from a log uniform distribution having minimum and maximum equal to the observed community. The number of these random communities having a G_{rs} value greater than the observed G_{rs} was counted. This test may be termed 'evolutionary' because all character values are possible.

The second Monte Carlo procedure drew the character values at random from a pool of character values. The pool contains the observed character values as a subset. Two pools were constructed for each community. The local pool contains all species whose extent of occurrence (EO, Gaston 1991) approaches to within 150 *km* of the borders of the protected area. The regional pool is constructed from species whose EO approaches to within 600 *km* of the protected area. This test is ecological in that only currently existing character values may be selected. The local community is a subset of the regional community. This test also solves the problem of the null distribution (see *Discussion*), since the real distribution of all existing character values is used.

Combining tests

A more careful analysis of the constant ratio hypothesis makes it apparent that not all G_{rs} ratios are of equal interest. In fact, the hypothesis states that the size ratios of *adjacent species on the character axis* are unexpectedly constant. This is tested by examining whether G_{rs} values, generated by triplets of adjacent species on the character axis, are unexpectedly large (close to 1). These tests are not entirely independent because they re-use data from (species richness - 4) species three times, from two species twice (second largest and second smallest), and from two species just once (largest and smallest).

Fisher's log sum statistic (Sokal & Rohlf 1995) can be used to combine the results of independent tests of the same hypothesis to provide a single, more powerful test of the hypothesis. It is argued here that this set of G_{rs} scores can be combined into a single community-wide test using the Fisher log sum of probabilities because: 1) the test uses data from the whole community to test a community wide hypothesis; 2) the set of G_{rs} scores used relates directly to the hypothesis; and 3) the re-use of data (which compromises independence) is limited and much less than if all possible G_{rs} scores were used.

In both cases (evolutionary and ecological), the set of G_{rs} values generated by adjacent triplets of species on the log body size axis was combined in a community-wide Fisher test. For comparison to this test, a Fisher test was also carried out on the entire set of G_{rs} values (a procedure that is likely to result in extreme non-independence of the individual $P[G_{rs}]$ scores). The Simberloff & Boecklen (1981) G_{rs} probabilities ($G_{1,n}$, $G_{2,n}$ and $G_{1,n-1}$) were also calculated and a Fisher test carried out. Simberloff & Boecklen (*ibid.*) scored a community as showing significant structure if 2 of these 3 G_{rs} values were significantly large. They used P values of 0.05 and 0.3 . The results of testing under the Simberloff & Boecklen criteria are also presented.

LimSim

A computer program (LimSim) was written in Microsoft Visual Basic to carry out the Irwin tests and Monte Carlo simulations and to combine the various sets of G_{rs} tests and calculate Fisher log sums of probabilities. The number of iterations can be varied from the program interface, but all tests reported here used 1000 runs. The program can also be used to carry out the analytical Barton & David calculations of probabilities, using extended decimal place numbers to try to minimise rounding error, although this procedure was not used in the results reported here.

The program reads a text file containing the body weights of a community of grazers. It will optionally also read a file containing the body weights of a regional pool. If the option to test the evolutionary hypothesis is selected, then the Monte Carlo procedure uses a log uniform distribution to generate simulated communities. If the option to test the ecological hypothesis is selected, then the program generates simulated communities by sampling from the regional pool file of body weights. Both options may be selected simultaneously. An example of the output generated by the program is provided in appendix 4.2. The program code is provided in appendix 4.3.

Species lists and body size data

Lists of grazers occurring in 17 protected areas throughout Africa were assembled from the literature (table 4.1 and appendix 4.1). The number of protected areas for which accurate ungulate inventories exist is limited (Murray, Green & Walter 1992), and only a subset of these publications were available (the World Conservation Monitoring Centre library would be a good source for further inventories). From these lists, species whose diet includes an appreciable proportion of grass were selected, and their body sizes recorded.

A map of each ungulate species' Extent of Occurrence (EO) was obtained from the African Mammals Databank (AMD - Boitani *et al.* 1998). The Extent of Occurrence of a species is a map of the region within which the species occurs in suitable habitat patches (Gaston 1991). It is not a highly detailed map of those habitat patches - such a map is termed the Area of Occupancy (AO), and clearly requires much more data. The African Mammals Databank is a print and digital collection of

EO maps for every medium and large sized non-volant mammal in Africa, together with a model predicting its AO from environmental and climatic data (including the satellite-derived seasonality index described in chapter 6). The EO maps in the AMD were derived from the literature and from expert consultation.

For each protected area, two regional species pools for statistical comparisons were constructed by creating buffers at 150 and 600 *km* outside the borders of the park (figure 4.2). Each EO map was overlaid each buffer map and the species was included within a pool if its EO entered the respective buffer zones.

Appendix 4.1 lists the presence/absence data, body sizes, diets and authorities for these data. Each species whose EO impinged upon a buffer zone was added to the relevant pool. Maps of the protected areas were obtained from the WCMC Protected Areas Database (WCMC 2000) and imported into ArcView GIS software, where the buffer zones were generated.

Sources of error

Occasionally a species is listed in the literature source as being present at a locality, but its EO does not extend to within one or more of the buffers for that locality. In these cases, the species was added to any pools that it was absent from. In the worst case, the following species were reported as being present in Upemba NP, DR Congo, but their EO does not approach within 150 *km* of the park boundaries*: Peter's duiker, bay duiker, black-fronted duiker, topi, water chevrotain, giant forest hog, dwarf antelope, forest bushpig, bongo*. Of these species, three figure in grazer analyses: giant forest hog and forest bushpig are mixed feeders, and topi are grazers. Topi very closely approaches the 150 *km* limit. Forest bushpig approaches to just under 100 *km* of the buffer, and giant forest hog is 280 *km* outside the buffer. All three species were added to the 150 *km* pool.

Black and white rhino were added to the pool only if they were already present in the locality list. Elephant were added to all pools. Body sizes for elephant and buffalo depend on the main habitat type - forest or non-forest. In forest ecosystems, elephant were assumed to be *Loxodonta africana cyclotis*; in savanna and mixed ecosystems, they were assumed to be *L. a. africana*. Buffalo were assumed to be *Syncerus caffer caffer* in savanna and mixed ecosystems, and *S. c. nanus* in forests.

This study uses indicative figures for the body sizes of ungulate species throughout their range. Ungulates are large animals and few of them show major variability in adult body size (excepting subspecies). Previous work on the distribution of grazer body sizes (Prins & Olff 1998) also used such indicative figures.

Table 4.1. Protected area characteristics. Habitat types were obtained from the WCMC data sheet (WCMC 2001) for each protected area:
1 - primarily savanna/grassland; 2 - primarily forest; 3 - mixed.

Protected area	Country	Source for species list	Area (ha x 10^3)	Grazer species	Habitat type
Comoe	Cote d'Ivoire	2, 5	1150	12	3
Tai	Cote d'Ivoire	3, 5	330	5	2
Kundelungu	Congo (DR)	4	760	16	1
Maiko	Congo (DR)	1, 4, 5	1083	5	2
Virunga	Congo (DR)	4	790	12	3
Kahuzi-Biega	Congo (DR)	4	600	6	2
Upemba	Congo (DR)	4	1173	17	3
Garamba	Congo (DR)	4	492	14	3
Benoue	Cameroon	6	180	12	2
Odzala	Congo	7	126	6	2
Serengeti	Tanzania	8, 9	1476	20	1
Ruaha	Tanzania	8	1295	13	1
Meru	Tanzania	8	87	15	1
Lope	Gabon	7	500	5	2
Mpassa	Gabon	7	15	5	2
Amboseli	Kenya	8	39	14	1
Akagera	Rwanda	1, 5	2500	13	3

Sources: 1 - East (1995); 2 - East (1996); 3 - East (1998); 4 - Anon. (1997); 5 - WCMC data sheets (WCMC 2001); 6 -Tsague (1994); 7 - Hecketsweiler, Doumenge & Mokoko Ikonga (1991); 8 - Williams (1967); 9 - Sinclair & Arcese (eds.) appendix A (1995).

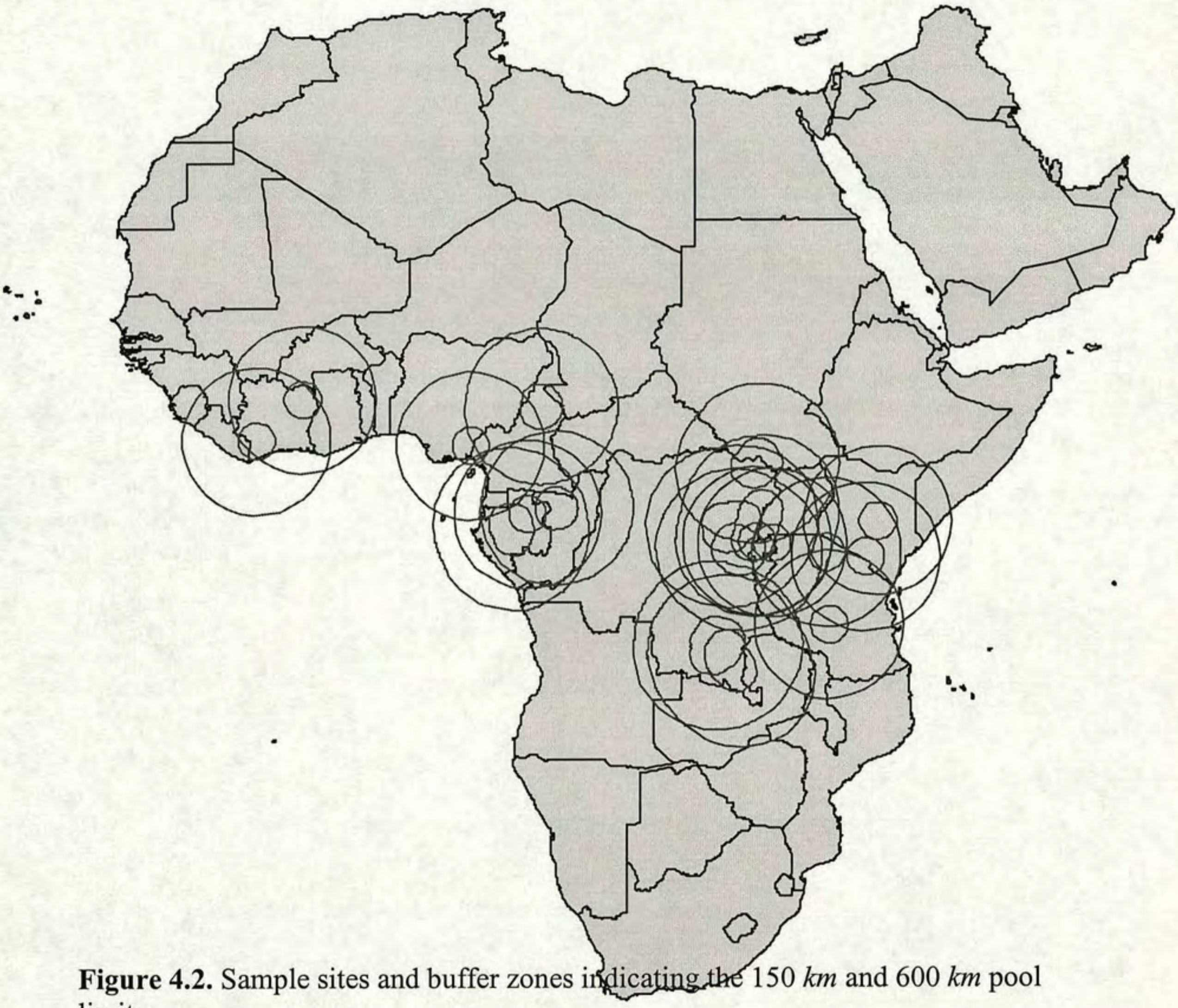


Figure 4.2. Sample sites and buffer zones indicating the 150 *km* and 600 *km* pool limits.

RESULTS

Table 4.2 summarises the results of the Irwin tests and the *Grs* triplets tests. The Irwin tests indicate that four of five savanna communities, plus one of seven forest and one of five mixed communities, have minimum differences in log body weights that are unexpectedly large, supporting a hypothesis of competitive structuring of those communities.

The *Grs* tests are somewhat more conservative. Each regularity hypothesis (evolutionary; ecological with pools at 150 *km* and 600 *km*) is supported in only two communities. However, five of these six significant results are in savanna systems, and the sixth is in a mixed system. Five tests support the opposite hypothesis - that body sizes are clumped together more than expected. Four of these results occur in forest communities.

Table 4.3 provides more information on those tests that indicated significant competitive structure. Three of the significant *Grs* triplets tests were derived from the Serengeti data, which shows highly significant structuring under all three hypotheses. A further two of the six significant *Grs* triplets tests were for Meru, another savanna ecosystem, with significant structure indicated under the evolutionary hypothesis, and the 600 *km* pool ecological hypothesis. The final significant *Grs* triplets test was for Upemba, a mixed habitats ecosystem with significant structuring under the 150 *km* pool ecological hypothesis. Including the Irwin tests, nine of the 12 significant tests occurred in savanna ecosystems, and 11 of the 12 tests were in savanna or mixed savanna/forest ecosystems.

Table 4.2. Results of Irwin and *Grs* triplets statistical tests. # *regular* indicates the number of sites that had unusually regularly spaced body sizes ($P < 0.05$). # *clumped* indicates the number of sites that had unusually clumped body sizes ($P > 0.90$). The Irwin test is significant if the smallest observed log body size difference is unexpectedly large. Results shown are for the *Grs* triplets version of the evolutionary and ecological tests.

Irwin test

	Forest	Savanna	Mixed	all sites
g_1 sig. large	1	4	1	6
n.s.	6	1	4	11
total	7	5	5	17

Significantly large minimum differences in: *Kahuzi-Biega; Upemba; Kundelungu; Amboseli; Meru; Serengeti*

Evolutionary hypothesis

	Forest	Savanna	Mixed	all sites
# *regular*	0	2	0	2
# *clumped*	3	1	0	4
# *n.s.*	4	2	5	11
total	7	5	5	17

Significantly regular body size distributions in: *Serengeti; Meru*

Ecological hypothesis: 150km pool

	Forest	Savanna	Mixed	all sites
# *regular*	0	1	1	2
# *clumped*	0	0	0	0
# *n.s.*	2	3	2	7
total	2	4	3	9

Significantly regular body size distributions in: *Serengeti; Upemba*

Ecological hypothesis: 600km pool

	Forest	Savanna	Mixed	all sites
# *regular*	0	2	0	2
# *clumped*	1	0	0	1
# *n.s.*	6	3	4	13
total	7	5	4	16

Significantly regular body size distributions in: *Serengeti; Meru*

Table 4.3. Summary of significant tests indicating competitive structure (*: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$). Probabilities are for the Fisher log sum combined tests from the *Grs* triplets derived from natural logarithm transformed body sizes of 3 adjacent species on the body size axis. The Kundelungu 150 *km* pool provided too few potential communities to generate a Monte Carlo test (see text). All tests in a further 11 communities were either not significant (36 tests) or not possible because of too few randomised communities (seven 150 *km* pool tests and one 600 *km* pool test).

Site	Main habitat	Irwin test	Ecological H0, 150 *km* pool	Ecological H0, 600 *km* pool	Evolutionary H0
Serengeti	Savanna	***	***	***	**
Meru	Savanna	*		**	**
Amboseli	Savanna	*			
Kundelungu	Savanna	*	*N/A*		
Upemba	Mixed	*	*		
Kahuzi-Biega	Forest	*			

Table 4.4 provides the full results of all tests. In each community, up to 16 tests were carried out:

- the Irwin test of the smallest log body size difference
- five versions of the evolutionary hypothesis regularity test
    - all G_{rs} scores combined in a Fisher log sum
    - G_{rs} scores from adjacent triplets combined
    - the three G_{rs} scores used by Simberloff & Boecklen (1981) combined
    - the Simberloff & Boecklen (1981) criterion: scoring how many of their three G_{rs} scores are significant at $P = 0.05$
    - the Simberloff & Boecklen (1981) criterion: scoring how many of their three G_{rs} scores are significant at $P = 0.30$
- five versions (as above) of the ecological hypothesis regularity test, using a 150 *km* pool
- five versions (as above) of the ecological hypothesis regularity test, using a 600 *km* pool

The best tests, suffering the least from lack of independence while integrating data from the whole community, are the three adjacent triplets tests of the ecological (150 *km* and 600 *km* pools) and evolutionary null hypotheses (see *Discussion*).

In some cases, Monte Carlo estimations could not be carried out because there were too few randomised communities to draw from. For instance, Benoue has 12 species, and the 150 *km* pool has a further two species. There are only 91 combinations of 12 species that can be drawn from a pool of 14 species, and one of those is the observed community, leaving only 90 randomised communities to supply the 1000 random draws for the Monte Carlo estimation.

The results in table 4.4 allow a rough comparison to be made between the Simberloff & Boecklen (1981) method of generating a community-wide test from individual *Grs* probabilities, and the *Grs* triplets method. Table 4.5 summarises the comparison. The Simberloff & Boecklen method takes 3 *Grs* scores into account: $G_{1,n}$, $G_{1,n-1}$ and $G_{2,n}$. If two or all three of these tests are significant, then the community is scored as being structured. Simberloff *and* Boecklen (*ibid.*) repeated the test using $P < 0.05$ and $P < 0.3$. Table 4.5 shows that the test using $P < 0.05$ is more conservative than the *Grs* triplets method, with only two of 42 tests indicating competitive structure for the Simberloff & Boecklen test, compared to six significant test results for the *Grs* triplets. On the other hand, using $P < 0.3$ as the threshold produces a considerably more liberal test, with 16 significant test results.

Table 4.4. Full results of all tests carried out. The Irwin test gives the probability of a g_1 score (smallest difference in log body weights) larger than that observed. Fisher log sum tests combine the probabilities of a set of *Grs* scores to produce a community-wide test of regular differences in log body sizes. Three sets of *Grs* scores were tested: all *Grs* scores from the community; *Grs* scores calculated for all sets of three species adjacent on the body size axis; and the three *Grs* scores specified by Simberloff & Boecklen (1981) ($G_{1,n}$, $G_{1,n-1}$, $G_{2,n}$). The Simberloff & Boecklen criterion counts the number of the latter three *Grs* scores that have $P < 0.05$ or $P < 0.3$. All *Grs* probabilities were estimated by Monte Carlo estimation (1000 simulations per test). Irwin test probability was calculated analytically. *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$; *n.s.*: not significant; +: $P > 0.9$ (significantly clumped body sizes); *N/A*: test not available because too few randomised communities can be generated from the regional pool to carry out the Monte Carlo estimation.

Forest ecosystems:

				Fisher log sum of P's tests:			*Simberloff & Boecklen criterion:*	
Pool	SpR	Test	g_1	All Grs scores	Adjacent triplets	3 Grs scores	$P < 0.05$	$P < 0.3$
Benoue	12	Irwin test	*n.s.*					
150km	14	150km pool		*N/A*	*N/A*	*N/A*	*N/A*	*N/A*
600km	17	600km pool		***	*n.s.*	*	1	3
forest		Evolutionary		*n.s.*	*n.s.*	*n.s.*	0	1
Kahuzi-Biega	6	Irwin test	*					
150km	21	150km pool		*	*n.s.*	*	1	3
600km	28	600km pool		*n.s.*	*n.s.*	*n.s.*	0	3
forest		Evolutionary		*n.s.*	*n.s.*	*n.s.*	0	3
Lope	5	Irwin test	*n.s.*					
150km	7	150km pool		*N/A*	*N/A*	*N/A*	*N/A*	*N/A*
600km	14	600km pool		+	*n.s.*	+	0	0
forest		Evolutionary		+	*n.s.*	+	0	0
Maiko	5	Irwin test	*n.s.*					
150km	16	150km pool		+	*n.s.*	*n.s.*	0	0
600km	26	600km pool		+	+	+	0	0
forest		Evolutionary		+	+	+	0	0

				Fisher log sum of P's tests:			*Simberloff & Boecklen criterion:*	
Pool	SpR	Test	g_1	All Grs scores	Adjacent triplets	3 Grs scores	$P < 0.05$	$P < 0.3$
Mpassa	5	Irwin test	*n.s.*					
150km	6	150km pool		*N/A*	*N/A*	*N/A*	*N/A*	*N/A*
600km	13	600km pool		+	*n.s.*	*n.s.*	0	0
forest		Evolutionary		+	+	+	0	0
Odzala	6	Irwin test	*n.s.*					
150km	7	150km pool		*N/A*	*N/A*	*N/A*	*N/A*	*N/A*
600km	15	600km pool		*n.s.*	*n.s.*	*n.s.*	0	0
forest		Evolutionary		+	+	+	0	0
Tai	5	Irwin test	*n.s.*					
150km	8	150km pool		*N/A*	*N/A*	*N/A*	*N/A*	*N/A*
600km	14	600km pool		*n.s.*	*n.s.*	*n.s.*	0	0
forest		Evolutionary		+	*n.s.*	*n.s.*	0	0

Mixed ecosystems:

				Fisher log sum of P's tests:			*Simberloff & Boecklen criterion:*	
Pool	SpR	Test	g_1	All Grs scores	Adjacent triplets	3 Grs scores	$P < 0.05$	$P < 0.3$
Akagera	13	Irwin test	*n.s.*					
150km	20	150km pool		***	*n.s.*	*	1	3
600km	29	600km pool		*n.s.*	*n.s.*	*n.s.*	0	2
mixed		Evolutionary		*n.s.*	*n.s.*	*n.s.*	0	2
Comoe	12	Irwin test	*n.s.*					
150km	13	150km pool		*N/A*	*N/A*	*N/A*	*N/A*	*N/A*
600km	15	600km pool		*N/A*	*N/A*	*N/A*	*N/A*	*N/A*
mixed		Evolutionary		*n.s.*	*n.s.*	*n.s.*	0	0
Garamba	14	Irwin test	*n.s.*					
150km	16	150km pool		*N/A*	*N/A*	*N/A*	*N/A*	*N/A*
600km	25	600km pool		+	*n.s.*	*n.s.*	0	0
mixed		Evolutionary		+	*n.s.*	*n.s.*	0	0
Upemba	17	Irwin test	*					
150km	20	150km pool		*n.s.*	*	*n.s.*	0	1
600km	23	600km pool		+	*n.s.*	*n.s.*	0	1
mixed		Evolutionary		+	*n.s.*	*n.s.*	0	0
Virunga	12	Irwin test	*n.s.*					
150km	19	150km pool		+	*n.s.*	*n.s.*	0	0
600km	30	600km pool		+	*n.s.*	*n.s.*	0	0
mixed		Evolutionary		+	*n.s.*	*n.s.*	0	0

Savanna ecosystems:

				Fisher log sum of P's tests:			*Simberloff & Boecklen criterion:*	
Pool	SpR	Test	g_1	All Grs scores	Adjacent triplets	3 Grs scores	$P < 0.05$	$P < 0.3$
Amboseli	14	Irwin test	*					
150km	21	150km pool		*	*n.s.*	*n.s.*	0	3
600km	28	600km pool		**	*n.s.*	*n.s.*	0	3
savanna		Evolutionary		***	*n.s.*	*n.s.*	0	3
Kundelungu	16	Irwin test	*					
150km	17	150km pool		*N/A*	*N/A*	*N/A*	*N/A*	*N/A*
600km	24	600km pool		*n.s.*	*n.s.*	*n.s.*	0	3
savanna		Evolutionary		+	+	*n.s.*	0	0
Meru	15	Irwin test	*					
150km	19	150km pool		+	*n.s.*	*n.s.*	0	0
600km	27	600km pool		**	**	*n.s.*	0	2
savanna		Evolutionary		**	**	*n.s.*	0	2
Ruaha	13	Irwin test	*n.s.*					
150km	20	150km pool		*n.s.*	*n.s.*	*n.s.*	0	1
600km	27	600km pool		+	*n.s.*	*n.s.*	0	0
savanna		Evolutionary		+	*n.s.*	*n.s.*	0	0
Serengeti	20	Irwin test	***					
150km	23	150km pool		***	***	***	3	3
600km	28	600km pool		***	***	***	3	3
savanna		Evolutionary		***	**	*	0	3

Table 4.5. Comparison of *Grs* triplets tests with the Simberloff & Boecklen (1981) criterion. The *Grs* triplets test combines the probabilities of all *Grs* scores generated using sets of three species adjacent on the body size axis with a Fisher log sum of probabilities. The Simberloff & Boecklen (1981) criterion scores a community as structured if two out of three *Grs* scores are significant, either at $P < 0.05$, or at $P < 0.3$.

hypothesis	test	savanna	mixed	forest	total
150km pool	*Grs* triplets	1	1	0	2
	S & B: 0.05	1	0	0	1
	S & B: 0.3	2	1	1	4
	# of communities tested	*4*	*3*	*2*	*9*
600km pool	*Grs* triplets	2	0	0	2
	S & B: 0.05	1	0	0	1
	S & B: 0.3	4	1	2	7
	# of communities tested	*5*	*4*	*7*	*16*
Evolutionary	*Grs* triplets	2	0	0	2
	S & B: 0.05	0	0	0	0
	S & B: 0.3	3	1	1	5
	# of communities tested	*5*	*5*	*7*	*17*

Number of significant tests: 6 *Grs* triplets; 2 Simberloff & Boecklen ($P < 0.05$); 16 Simberloff & Boecklen ($P < 0.3$).

Figure 4.3 presents the main results in a more graphical form, illustrating the relative magnitudes of all the *Grs* scores used in the *Grs* triplets tests. Competitive structuring is indicated by larger *Grs* scores, and hence longer bars in the figure.

Figure 4.4 illustrates that there is no significant species/area effect in the data set. Species richness of ecosystems is however highly dependent on the size of the 150 *km* and 600 *km* pools (figures 4.5a and b). About 50% of the variation in local species richness is determined by the size of the 150 *km* pool (figure 4.5a). The 600 *km* pool has little additional direct effect on local species richness. The increase in the explained variance when 600 *km* pool species richness is added to the regression model is not significant. However, the 600 *km* pool strongly controls the diversity of the 150 *km* pool, explaining almost 84% of the variance in the 150 *km* pool species richness (figure 4.5b). A species/area effect does not emerge when the size of regional pools is controlled for ($F = 0.01$, $n = 17$, $R^2_{adj} = 0.0\%$, $P = 0.938$).

Vegetation formation exerts a strong control over grazer species richness (figure 4.4). Local grazer species richness varies with vegetation type ($F = 24.03$, d.f. = [2, 14], $P < 0.0005$), and species richness in forests is significantly lower than in savannas or mixed habitats (Tukey pairwise comparisons, family error rate 0.05, individual error rate 0.0203). Similarly, species richness in the 150 *km* pool varies with vegetation formation (F = 6.73, d.f. = [2, 14], P = 0.009), and species richness in the forests is significantly lower than in savannas (Tukey pairwise comparisons). Species richness in the 600 *km* pool also varies with vegetation formation (F = 4.43, d.f. = [2, 14], P = 0.032), and again species richness in forests is significantly lower than in savannas (Tukey pairwise comparisons).

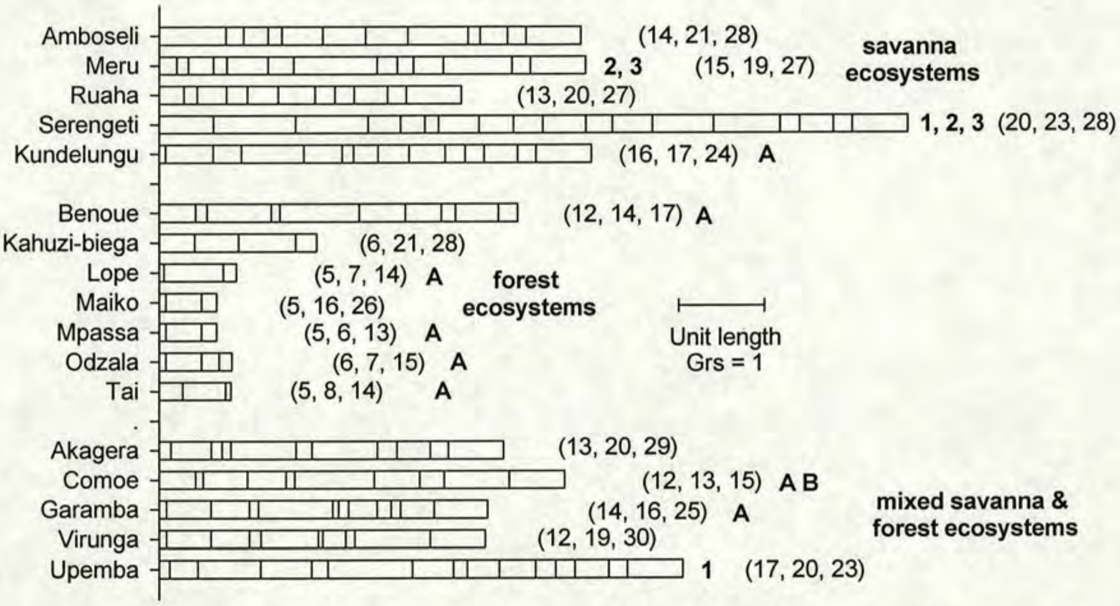


Figure 4.3. Fisher log sum combined probability tests on *Grs* scores of adjacent-sized triplets of grazer species in African protected areas. Each interval on the bar of each protected area represents the *Grs* score for a set of three species that are adjacent on the size rank scale for that community (e.g. 4th, 5th and 6th largest species). *Grs* is the ratio of the smaller log size difference to the larger log size difference. A *Grs* score of 1 indicates that the size difference of these three species is exactly equal. The Fisher combined probabilities test combines the probability of observing each *Grs* score in the community, to produce an overall probability of observing a community with even more regular *G* scores. Three tests were carried out: evolutionary and ecological null hypotheses, with two species pools (150 *km* and 600 *km*) for the ecological null hypothesis. Test results are indicated by bold numerals. **1**: ecological null hypothesis using 150 *km* pool rejected. **2**: ecological null hypothesis using 600 *km* pool rejected. **3**: evolutionary null hypothesis rejected. Figures in brackets give the number of species in the observed community, the number whose extent of occurrence (EO) approaches to within 150 *km* of the protected area, and the number whose EO approaches to within 600 *km*. **A:** too few randomised communities to carry out the 150 *km*, ecological hypothesis test. **B:** too few randomised communities to carry out the 600 *km*, ecological hypothesis test.

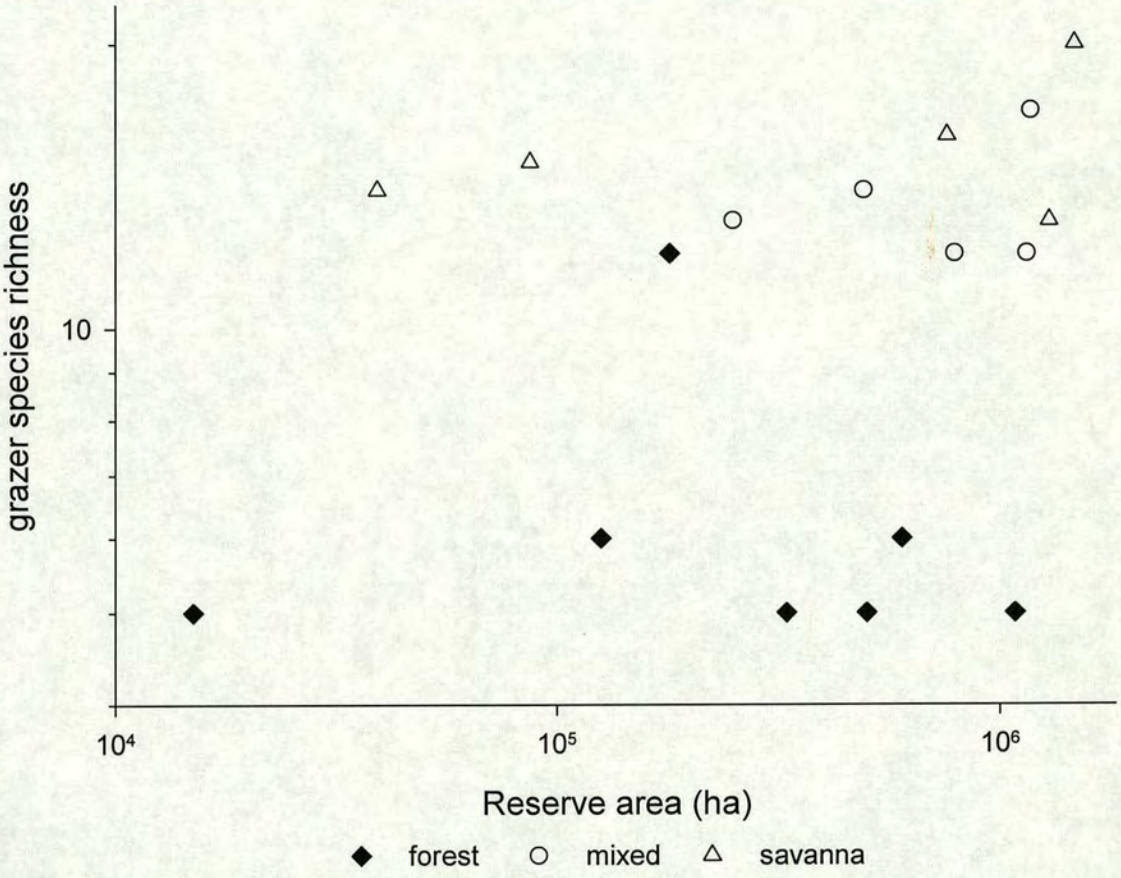


Figure 4.4. Species richness *vs.* area of grazer communities, stratified by major vegetation formation. There is no species/area relationship ($y = 8.841 + 0.03838\ x$; $F = 2.52$, $n = 17$, $R^2_{adj} = 8.3\%$, $P = 0.133$).

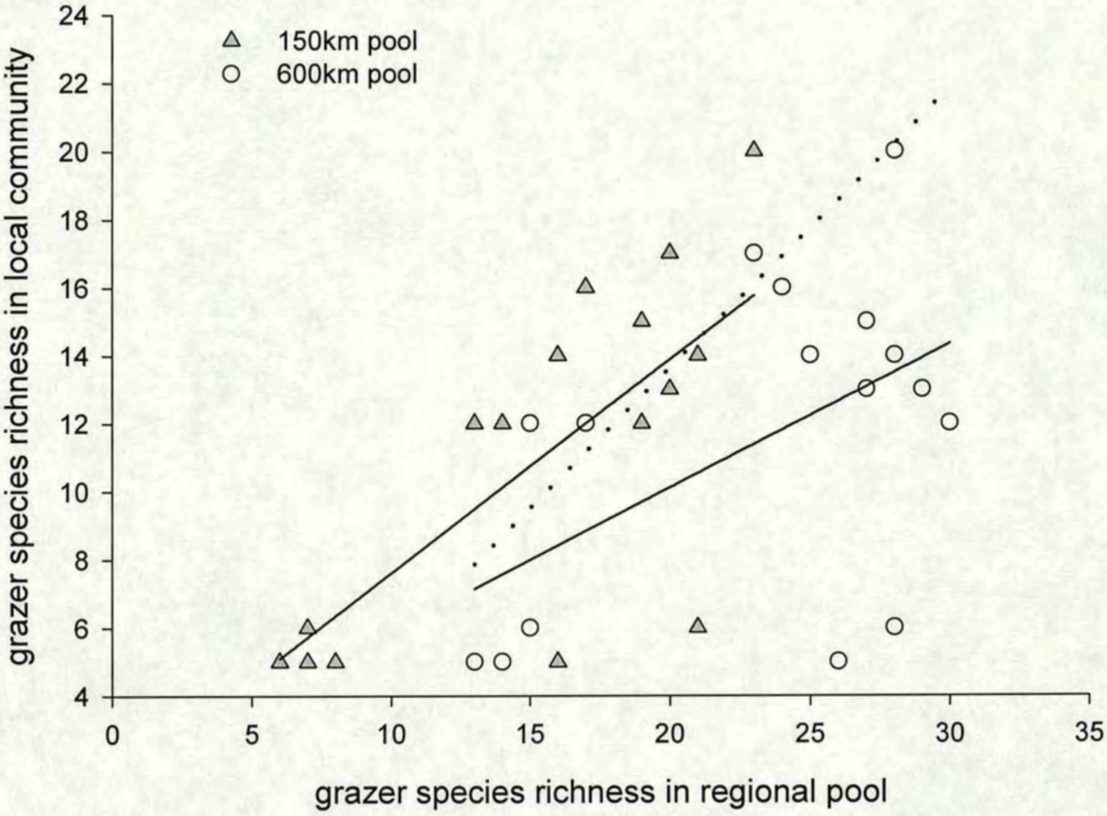


Figure 4.5a. Influence of regional biotas on local species richness. Local community grazer species richness is a positive function of 150 *km* pool species richness (y = 1.324 + 0.6273 x; F = 16.30, n = 17, R^2_{adj} = 48.9%, P = 0.001) and less strongly, of 600 *km* pool species richness (y = 1.623 + 0.4241 x; F = 6.34, n = 17, R^2_{adj} = 25.0%, P = 0.024). The regression line for 150 *km* pool *vs.* 600 *km* pool species richness is shown for comparison (see figure 4b). Including both 150 *km* and 600 *km* species richness in a multiple regression model of local species richness does not significantly increase the explained variance (localSpR = 5.20 + 1.25 × 150kmSpR - 0.607 × 600kmSpR; F = 11.13, n = 17, R^2_{adj} = 55.9%, P = 0.001. Increase in R^2 = 9.3%, F_s = 3.373, d.f. = [1, 14], P > 0.05). F test for increase in (non-adjusted) variance explained from Sokal & Rohlf (1995).

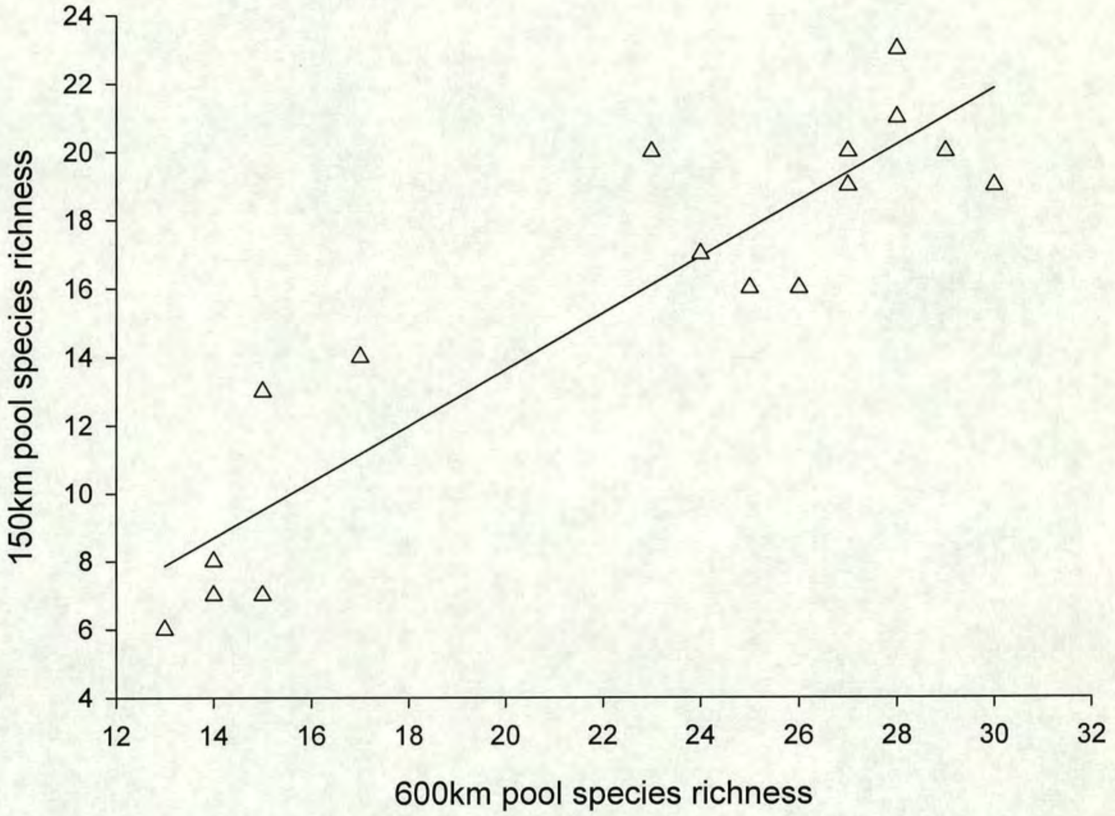


Figure 4.5b. Species richness is positively related across spatial scales ($y = -2.858 + 0.8240\ x$; $F = 83.09$, $n = 17$, $R^2_{adj} = 83.7\%$, $P < 0.0005$).

DISCUSSION

Criticisms of the statistical tests

The Barton & David test has been criticised on various grounds. The null hypothesis is a log uniform random distribution, but body sizes of many groups of species are log normally distributed, often with a long tail (Schoener 1984, Colwell & Winkler 1984). However, as described in the *Introduction*, when species lists are broken down into guilds, and/or generated for local communities, the body size distribution often becomes log uniform, and this is the case for African grazers (data in Prins & Olff 1998). Furthermore, Boecklen & NeSmith (1985) demonstrated that using the

Barton & David test on data that are in fact log normally distributed has a negligible effect on the accuracy of the test.

The test has been criticised for having low power (Losos, Naeem & Colwell 1989, Pleasants 1990), therefore being unacceptably likely to fail to reject a false null hypothesis. When Losos, Naeem & Colwell (*ibid.*) re-analysed the data of Simberloff & Boecklen (1981), but combined tests in multiple assemblages reported within each study using Fisher's log sum of probabilities, they found a much higher rate of rejection of the null hypothesis. In the work described here, a specific subset of the G_{rs} scores was combined using Fisher's log sum in a similar attempt to increase power (see *Methods*).

Pleasants (1990) concluded that the test had low power as a result of simulation models in which he generated competitively structured communities and claimed that the G_{rs} tests failed to identify the structure. Arita (1993) demonstrated that the simulations of Pleasants (*ibid.*) were flawed because body sizes were limited to integer values. When the tests were repeated with real number body sizes, the G_{rs} tests were found to be reliable.

More fundamentally, Pleasants (1990, 1994) criticised the Barton & David and Irwin tests because they rely on data from a subset of the species making up the community. The tests therefore are not community-wide, but the hypotheses are. For example, the Irwin test relies on just the two species adjacent on the character axis that happen to produce the smallest difference in character sizes (g_1). This will fail to reject a false null hypothesis whenever a single species, very similar in character value to another species, can successfully coexist within the community perhaps due to some specialisation entirely unrelated to the general ecological situation under scrutiny. This species will mask any effect of community-wide competition among the rest of the species.

With respect to the Barton & David test, the standard practice of using only a subset of three of the possible G_{rs} values similarly opens the test to inaccuracy caused by one or two unusual species being included in the community. If we imagine a community that displays an unexpectedly large minimum size ratio, then a little examination will show that ratio constancy is then also likely to be supported, and therefore the two hypotheses are not independently tested. With an unusually large g_1, all the G_{1s} are likely to be unusually large also. Since there are more G_{1s} values than any other G_{rs} values for any $r > 1$, then ratio constancy is likely to be supported. Thus if limiting similarity is operating, then ratio constancy is likely to be supported even if the only non-random feature of the community was that the smallest size difference was unexpectedly large.

This consideration illustrates why simply using all the P[G_{rs}] values in a combined test (*e.g.* using the Fisher log sum of probabilities to test the probability of observing all the $P[G_{rs}]$) is unsatisfactory: the $P[G_{rs}]$ are not fully independent. The procedure described in the *Methods* of combining G_{rs} scores for triplets of species adjacent on the log body size axis minimises the repeated use of data from the same species, but uses data from all species to provide an acceptably independent, powerful, and appropriate test of the hypotheses.

The tests implemented here were in fact Monte Carlo analogues of the Barton & David test. The evolutionary null hypothesis however still depends on the assumption of a log uniform random distribution of body sizes, which has been defended above. The ecological null hypotheses used regional species pools to provide the underlying distribution of body sizes, which cannot be done with the analytical Barton & David test.

Using a species pool to generate random communities has been criticised (Harvey *et al.* 1983, Gilpin & Diamond 1984) because the species pool may itself have been structured by competition. Any random community selected from the pool will therefore be likely to exhibit competitive structuring, and only real communities with even more extreme structure will be able to generate rejections of the null hypothesis. This is a valid criticism of the ecological hypothesis tests. In effect, the null hypothesis is that the local community is not more structured than the regional pool. The ecological hypothesis tests are searching for evidence that local communities are subject to more powerful competitive interactions than regional pools are.

Conclusions

The Irwin test relies on data from only the two most similar species, plus the species richness of the community, and is therefore highly susceptible to bias. The regularity tests using all available G_{rs} scores suffer badly from non-independence, especially in more diverse communities, because each species contributes to many G_{rs} scores. The G_{rs} triplets test suffers from a degree of non-independence, as an individual species can contribute to up to three of the G_{rs} scores used in the test, but has the advantage of using data from the entire community. The test using only the three G_{rs} scores specified by Simberloff & Boecklen (1981) is independent in diverse communities, but fails to use all the data available. In species-poor communities, data from the same species are used repeatedly just as with the G_{rs} triplets test. Finally, applying the Simberloff & Boecklen criterion to their three G_{rs} scores is either extremely conservative (with $P < 0.05$) or rather liberal (using $P < 0.3$) when compared to the Fisher log sum of probabilities.

These considerations suggest that the best test to use is the G_{rs} triplets test. The degree of non-independence is limited, and comparable to that of the original Simberloff & Boecklen (1981) test as applied to species-poor communities (as in the vast majority of studies using this test). In more diverse communities, lack of independence remains about the same for the G_{rs} triplets test, but all data are used, producing a true community-wide test. The Simberloff & Boecklen trio of G_{rs} scores will become more independent as diversity increases, but uses a smaller and smaller proportion of the available data, becoming susceptible to biases similar to the Irwin test.

In the ecological hypothesis tests, the Monte Carlo procedure of drawing samples from a regional pool will be less powerful if the pool itself is structured (composed of regular body sizes). The test is in fact assessing whether the local community is even more structured than the regional pools.

Species richness of assemblages

The area of an ecosystem has no detectable effect on grazer species richness (figure 4.4). Soulé, Wilcox & Holtby (1979) and Burkey (1995) predicted that if African game reserves became completely insularised, rapid local extinction of many species would take place. This prediction was made by analogy with the extinction of large mammals as the Malay archipelago formed at the end of the Pleistocene. The mechanism of extinction from island biotas is competitive (MacArthur & Wilson

1963, MacArthur 1972), and assumes that there is a limit to the number of species that can coexist when the ecosystem becomes insularised.

The lack of a species-area relationship in the current data set suggests three possible explanations. The range of areas sampled may be too small. Figure 4.4 shows that only two orders of magnitude of ecosystem size were sampled, which is too little to show up all but the strongest of species-area relationships (Lomolino 1989). The ecosystems may not be sufficiently isolated from surrounding regions, and are in fact smaller portions of larger, contiguous ecosystems of unknown extent. This seems likely for the central African forest ecosystems, and possibly for the western African forests and mixed systems as well. Finally, competition may not be intense enough to exclude species. This is supported by the general lack of evidence in this chapter that grazer communities are structured. Forest ecosystems support a much lower number of grazer species than savannas and mixed systems, but this is probably due to lack of grazing habitat rather than by competition. There is no evidence in the current analysis that such exclusion has led to competitive structuring of the remaining grazer species. The exclusion of grazer species from forest ecosystems is probably directly due to lack of suitable habitat, leading to small grazer population sizes that are susceptible to random (at least with respect to the presence of other grazer species) extinctions. The small sizes of forest grazer populations, and their low density due to dispersal to rare habitat patches, would severely constrain the potential for negative interactions among them, counteracting any tendency to deplete resources and enter into direct resource competition.

Species richness of local grazer assemblages is highly dependent on the diversity of the regional grazer biota (figures 4.5a & b). There is no indication that the relationship between local grazer diversity and 150 *km* pool diversity becomes asymptotic at higher diversity. This suggests that most local assemblages are not saturated, because where there are more potential immigrant species, there are proportionally more coexisting local species (Cornell & Lawton 1992, Cornell & Karlson 1996, Hugueny *et al.* 1997). If local assemblages are not saturated, then competition among grazers is likely to be weak. Competitive explanations of variation in species richness, such as resource partitioning, spatial and temporal heterogeneity in habitat characteristics, and limiting similarity, are not sufficient because they all act at the local scale (Karlson & Cornell 1998), whereas figures 4.5a & b show that local diversity is largely controlled at the regional scale.

Rarity of competitive structuring in African grazer assemblages

In 42 G_{rs} triplets tests, in 17 grazer communities from across Africa, only six significant deviations from random expectations, in just three communities, were found. With an alpha of 0.05, about two false significant results would be expected, potentially reducing the number of true significant results even further. Competitive structure appears to be rare in African grazer communities.

As discussed above, forest communities have a low diversity of grazers (figure 4.4). Forests afford few opportunities for grazers, and competition among these rather distributed, low density populations is likely to be limited, explaining the lack of any significant G_{rs} triplets tests in forest ecosystems.

Savanna and mixed habitats grazer communities are more diverse, reflecting the greater extent of suitable habitat. Savanna grazer communities can also have much higher population densities. In two of the five savanna communities, Serengeti and Meru, there is strong evidence of competitive structure.

Much of the literature on competition in ungulates reviewed in chapter 1 focuses on savanna communities. In general however, there is little direct evidence that African ungulate communities are structured by competition (McNaughton & Georgiadis 1986). Most populations are in flux, under the control of extrinsic environmental factors rather than density dependent competition. Competition, when it does occur, is likely to be concentrated in a delimited season when food is scarce (Sinclair 1975). The evidence of this chapter suggests that competition can only become important in ungulate communities under rare conditions of unusually high diversity and population densities.

The results of this chapter strongly contrast with those of Prins & Olff (1998), who found overwhelming support for limiting similarity in their tests. As described in the *Introduction* however, their null hypothesis was flawed by not using log transformed body weights. Their null model was a uniform random distribution of body weights, which generates a monotonic increasing, asymptotic curve when log body weights are plotted against size rank (see their figure 17.7). Observed data lay roughly along straight lines, which they took to support a hypothesis of constant weight ratios. However, these straight lines in fact coincide with a null model of a uniform random distribution of *log* body weights (see figure 4.1).

The Prins & Olff (*ibid.*) test could be modified by examining the spread of ranked log body weights around the straight line. If the points remained closer to the line than a random uniform distribution would be expected to, then limiting similarity and an unexpectedly constant ratio would be supported. This would be equivalent to the variance test of Poole & Rathcke (1979), which was shown to be less powerful than the Barton & David (1956) test by Simberloff & Boecklen (1981).

Competition in the Serengeti

The tests on the Serengeti community show very strong evidence of competitive structure (table 4.3 and figure 4.3). The Serengeti is also the most diverse community in the data set, with 20 grazer species, many of which are present in high densities. The tests reported in this chapter show that these 20 species have not been assembled at random. They are regularly spaced out on a log body weight axis (the evolutionary test), and they are more regularly spaced than either the 150 *km* pool or the 600 *km* pool (the ecological tests).

There is ample evidence that grazer populations in the Serengeti are limited by food availability during part of the year, establishing the potential for competitive interactions. In some cases, competition has been directly demonstrated, and there are many other data suggesting that competition is important (reviewed in chapter 1). The Serengeti is probably the most intensively studied grazer community in Africa, and impressions gained there inform ecologists' ideas about grazer communities in general. The results of the tests reported here suggest that the grazer community of the Serengeti may be organised in quite a different way from most other communities.

Conclusions

Several lines of evidence presented in this chapter argue that competition is generally unimportant in structuring African grazer communities:

- Species richness is independent of area. If ecosystems are insularised, then competition should exclude more species from smaller areas. This evidence is however weak because ecosystems are probably not often isolated.
- Competition among grazers in forests is likely to be weak because of their low diversity, and because their low density populations are dispersed among small patches of habitat.
- Plots of local *vs.* regional species richness are not asymptotic. Local communities are probably not saturated, except possibly for the most diverse communities.
- There is little evidence of competitive structuring of body sizes (limiting similarity) except in a few cases. This result contrasts with the only published analysis of African grazer body sizes.

Competition does appear to have structured communities in the savannas, particularly Serengeti and Meru. This is probably due to the high number of species, and their high population densities.

Grazer communities do not display a pattern of competitive structuring wherever they occur. Rather, where habitats can support a high diversity and density of grazers, competition is likely. Elsewhere, with fewer species and individuals, other factors become much more important.

APPENDIX 4.1. PRESENCE / ABSENCE DATA AND SPECIES AND PROTECTED AREA CHARACTERISTICS

Body size data were extracted from Estes (1991), Kingdon (1989, 1992a, 1992b, 1997), Skinner & Smithers (1990), Jarman (1974) and www.ultimateungulate.com (for *Potamochoerus porcus*). *Phacochoerus africanus* was assumed to have the same body size as *Phacochoerus aethiopicus*.

Feeding style data were obtained from Estes (1991), Kingdon (1992a, 1992b), Gordon & Illius (1988), and www.ultimateungulate.com (for *Hexaprotodon liberiensis*).

Species characteristics and presence/absence data

name	common name	weight (kg)	feeding style
Addax nasomaculatus	addax	100	grazer
Aepyceros melampus	impala	52.5	mixed
Alcelaphus buselaphus	hartebeest; Coke's h,; kongoni;	134	grazer
Antidorcas marsupialis	springbok	28.65	mixed
Ceratotherium simum	white rhino	2950	grazer
Connochaetes gnou	black wildebeest	132.25	grazer
Connochaetes taurinus	common, blue and white-bearded w.beest	181.5	grazer
Damaliscus hunteri	hirola/Hunter's hartebeest	80	grazer
Damaliscus lunatus	topi/tsessebe/tiang/korrigum	119	grazer
Damaliscus pygargus	blesbok and bontebok	66.5	grazer
Equus africanus	African wild ass	275	grazer
Equus burchellii	plains or Burchell's zebra	235	grazer
Equus grevyi	Grevy's zebra	408	grazer
Equus zebra	mountain zebra	287	grazer
Gazella dama	dama or addra gazelle	73	mixed
Gazella granti	Grant's gazelle	55	mixed
Gazella soemmerringi	Sommerring's gazelle	40	mixed
Gazella thomsonii	Thomson's gazelle	20.5	mixed
Hexaprotodon liberiensis	pygmy hippo	264	mixed
Hippopotamus amphibius	hippo	1900	grazer
Hippotragus equinus	roan antelope	270	grazer
Hippotragus niger	sable	227.5	grazer
Hylochoerus meinertzhageni	giant forest hog	205	mixed
Kobus ellipsiprymnus	waterbuck	211	grazer
Kobus kob	kob	78.5	grazer
Kobus leche	lechwe	91	grazer
Kobus megaceros	Nile lechwe	86	grazer
Kobus vardonii	puku	69.3	grazer
Loxodonta africana	African elephant	3900	mixed
Loxodonta africana africana	savanna elephant	3900	mixed
Loxodonta africana cyclotis	forest elephant	2500	mixed
Oryx dammah	scimitar-horned oryx	204	grazer
Oryx gazella	oryx/gemsbok	169	grazer
Ourebia ourebi	oribi	14.1	grazer
Pelea capreolus	vaal rhebok	20	mixed
Phacochoerus aethiopicus	desert warthog	73.5	mixed
Phacochoerus africanus	common warthog	73.5	mixed
Potamochoerus larvatus	savanna bushpig	84.5	mixed
Potamochoerus porcus	red river hog; forest bushpig	82.5	mixed
Raphicerus campestris	steenbok	11.1	mixed
Redunca arundinum	common reedbuck	58	grazer
Redunca fulvorufula	mountain reedbuck	29.4	grazer
Redunca redunca	bohor reedbuck	44.75	grazer
Sigmoceros lichtensteinii	Lichtenstein's hartebeest	171.7	grazer
Syncerus caffer	buffalo	631	grazer
Syncerus caffer caffer	black buffalo; savanna buffalo	631	grazer
Syncerus caffer nanus	red buffalo; forest buffalo	300	grazer
Taurotragus derbianus	giant or Derby eland	559	mixed
Taurotragus oryx	eland	496	mixed
Tragelaphus angasii	nyala	84.6	mixed
Tragelaphus spekii	sitatunga	76.75	mixed

Akagera	Akagera 150	Akagera 600	Amboseli	Amboseli 150	Amboseli 600	Benoue	Benoue 150	Benoue 600
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Comoe	Comoe 150	Comoe 600	Garamba	Garamba 150	Garamba 600
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Mpassa	MPassa 150	MPassa 600	Maiko	Maiko 150	Maiko 600	Meru	Meru 150	Meru 600
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Yes	Yes	Yes	No	No	Yes	No	Yes	Yes

Tai	Tai 150	Tai 600	Upemba	Upemba 150	Upemba 600	Virunga	Virunga 150	Virunga 600
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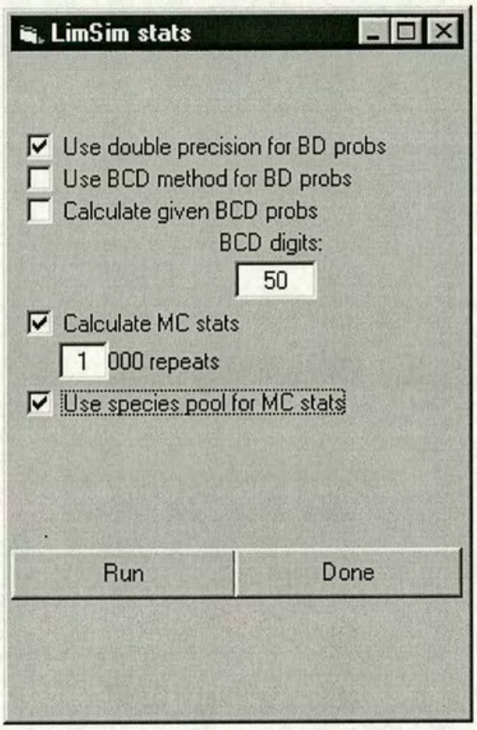
APPENDIX 4.2. EXAMPLE OUTPUT FROM THE LIMSIM PROGRAM



☑ Use double precision for BD probs
☐ Use BCD method for BD probs
☐ Calculate given BCD probs

BCD digits: 50

☑ Calculate MC stats

1 000 repeats

☑ Use species pool for MC stats

The **first line of output** lists the data file(s) used as input for the analysis.

Columns in the first table:

Rank: value (e.g. body size) ranking, smallest to largest.

Value: ordered data from the community file.

g score: ordered list of the differences in the log (base 10) values of adjacent species. Therefore g score (rank = 1) is the smallest g score, not the g score between species 1 and 2.

Irwin prob: the probability of observing a minimum g score larger than the one observed. If this probability is small, then the observed g score is unexpectedly large, supporting a hypothesis of minimum difference.

small sp; large sp: pairs of adjacent-value species (i.e. 1 & 2, 2 & 3 etc.).

g score rank: rank of the g score for the given pair of adjacent species.

g score: g scores rearranged from column 3 to correspond with their species pairs.

r for Grs; s for Grs: r and s are the ranks of g scores. These ranks identify the Grs scores that are associated with adjacent triplets of species on the value axis. Later in the analysis, these r and s values are used to retrieve the Grs data for each species triplet.

The **next line of output** records the number of repeats used in the Monte Carlo models. This was set at 1000 in all the analyses discussed in this chapter.

Columns in the second table:

r & s: ranks of g scores used to calculate Grs scores.

Grs scores: Grs = $g(r) / g(s) < 1$ since $g(r) < g(s)$ by definition.

BD Prob: probability of observing an even larger Grs, calculated using double precision arithmetic according to Barton and David (1956). See text for the errors associated with these calculations in species rich communities.

BCD BD Prob: as above, but using arbitrary precision arithmetic from the BCD (Binary Coded Decimal) routines in the ProMath 3.0 programming library (Block, Shakir & Smith 1998). This output was not used in the analyses of this chapter, as even using 50 decimal places failed to reduce the cumulative rounding errors to an acceptable degree.

MC (evol) Count: the number of simulated communities (evolutionary null hypothesis) that had an even larger Grs score than the observed community. If there are very few such communities, the observed Grs score is unusually large.

MC (ecol) Count: the number of simulated communities (ecological null hypothesis) that had an even larger Grs score than the observed community. If there are very few such communities, the observed Grs score is unusually large.

The next line of output gives the degrees of freedom (= twice the number of Grs values) for the Fisher log sum test of all the Grs data. This test violates the assumption of independence of P values.

The **third table** calculates test statistics for each of the probability calculations (BD and BCD if carried out; Monte Carlo evolutionary and ecological hypotheses). Advice is supplied about which statistic to use: Fisher log sum probabilities if d.f. <= 100, Z score if d.f. > 100.

The **fourth table** lists the species pool data in order, if a species pool was supplied to the program.

The next several tables re-arrange the Grs scores, BD (and BCD if carried out) probabilities, and the Monte Carlo scores in matrix format. This data can then be graphed in Excel. This visual output is useful for illustrating the non-independence of the data.

The **final table** excerpts Grs scores, probabilities and Monte Carlo counts for the species triplets identified in the first table, and calculates test statistics for this data set.

```
Community file: Garamba.txt   / Pool file: Garamba 150.txt

Rank       Value     g score    Irwin Prob       small sp   large sp   g score    g score    r for Grs  s for Grs
                                [g1 > obs(g1)]                         rank
        1     44.75  9.79E-03          0.195191          1          2         11  0.215494
        2      73.5  1.25E-02                            2          3          3  1.88E-02           3         11
        3     76.75  1.88E-02                            3          4          1  9.79E-03           1          3
        4      78.5  2.16E-02                            4          5          4  2.16E-02           1          4
        5      82.5  5.26E-02                            5          6         10  0.210651           4         10
        6       134  0.107081                            6          7          8  0.184649           8         10
        7       205  0.121243                            7          8          2  1.25E-02           2          8
        8       211  0.184649                            8          9          6  0.107081           2          6
        9       270  0.191068                            9         10         12  0.316048           6         12
       10       559  0.210651                           10         11          5  5.26E-02           5         12
       11       631  0.215494                           11         12         13  0.478724           5         13
       12      1900  0.316048                           12         13          9  0.191068           9         13
       13      2950  0.478724                           13         14          7  0.121243           7          9
       14      3900

Repeats = 1000

r          s         Grs        BD Prob          BCD BD     MC (evol)  MC (ecol) Count
                     scores                      Prob       Count
        1          2  0.781514         0.205127 /                 159          0
        1          3  0.521061         0.200813 /                 187          0
        1          4   0.45363         0.127795 /                 112          0
        1          5  0.186084         0.365665 /                 378        364
        1          6  9.14E-02         0.534721 /                 628        359
        1          7  8.08E-02         0.495648 /                 543        186
        1          8  0.053026         0.564651 /                 632        531
        1          9  5.12E-02         0.504831 /                 498        474
        1         10  4.65E-02         0.464564 /                 429        392
        1         11  4.54E-02         0.391822 /                 357         50
        1         12  3.10E-02         0.436239 /                 420         36
        1         13  2.05E-02         0.453186 /                 385        202
```

2	3	0.666732	0.51806 /	506	279
2	4	0.58045	0.320244 /	273	37
2	5	0.238107	0.683358 /	708	499
2	6	0.117001	0.83496 /	879	587
2	7	0.103335	0.797644 /	836	506
2	8	6.79E-02	0.849227 /	904	729
2	9	6.56E-02	0.79825 /	871	703
2	10	0.059476	0.758232 /	822	606
2	11	5.81E-02	0.678173 /	720	387
2	12	3.96E-02	0.722595 /	774	187
2	13	2.62E-02	0.733043 /	738	413
3	4	0.870589	0.296578 /	244	120
3	5	0.357125	0.806504 /	820	631
3	6	0.175484	0.92373 /	951	677
3	7	0.154987	0.89077 /	916	444
3	8	0.101766	0.927173 /	956	771
3	9	9.83E-02	0.885108 /	931	752
3	10	8.92E-02	0.847622 /	897	609
3	11	8.72E-02	0.766919 /	781	280
3	12	5.95E-02	0.808543 /	819	303
3	13	3.93E-02	0.813992 /	789	459
4	5	0.410211	0.951701 /	965	878
4	6	0.201569	0.983359 /	1000	759
4	7	0.178026	0.968149 /	982	731
4	8	0.116894	0.980446 /	996	824
4	9	0.112966	0.960938 /	983	801
4	10	0.102465	0.939609 /	972	735
4	11	0.100162	0.886718 /	922	640
4	12	6.83E-02	0.910862 /	949	622
4	13	4.51E-02	0.909206 /	932	599
5	6	0.491379	0.941249 /	958	498
5	7	0.433986	0.863111 /	853	458
5	8	0.28496	0.916918 /	940	697
5	9	0.275386	0.832699 /	847	667

5	10	0.249786	0.754046 /	745	567
5	11	0.244171	0.597035 /	575	373
5	12	0.166486	0.677798 /	638	377
5	13	0.109912	0.692521 /	611	352
6	7	0.883199	0.405388 /	312	23
6	8	0.579918	0.698727 /	645	706
6	9	0.560434	0.477504 /	407	645
6	10	0.508336	0.351776 /	321	564
6	11	0.49691	0.179804 /	121	8
6	12	0.338813	0.304612 /	250	7
6	13	0.223681	0.365221 /	265	519
7	8	0.656611	0.860926 /	845	964
7	9	0.634551	0.623824 /	622	844
7	10	0.575562	0.462933 /	463	733
7	11	0.562626	0.241731 /	216	190
7	12	0.383621	0.387391 /	404	98
7	13	0.253262	0.444213 /	370	596
8	9	0.966403	0.142976 /	121	120
8	10	0.876565	0.114892 /	86	178
8	11	0.856863	2.66E-02 /	3	0
8	12	0.584244	0.171119 /	109	0
8	13	0.385711	0.263488 /	140	48
9	10	0.907038	0.354505 /	308	409
9	11	0.886652	0.089791 /	59	0
9	12	0.604555	0.327617 /	317	0
9	13	0.39912	0.409905 /	279	239
10	11	0.977524	8.83E-02 /	34	63
10	12	0.666515	0.46765 /	407	21
10	13	0.440025	0.521235 /	381	311
11	12	0.68184	0.76432 /	710	231
11	13	0.450143	0.718914 /	640	780
12	13	0.660188	0.651589 /	527	841

```
d.f. =          156
          Fisher    Z score:
          log sum
          P:
BD:         108.7028   -2.89051
MC          125.4468   -1.79557
(evol):
MC          259.4363   5.143584
(ecol):
d.f. > 100, so use Z score as test statistic

rank      Species pool
         1       14.1
         2      44.75
         3       73.5
         4      76.75
         5       78.5
         6       82.5
         7        119
         8        134
         9        205
        10        211
        11        270
        12        559
        13        631
        14       1900
        15       2950
        16       3900



Matrix: Grs (column=s, row=r)
                  2          3                 4         5         6          7         8         9        10        11        12        13
         1  0.781514  0.521061           0.45363  0.186084  9.14E-02  8.08E-02  0.053026  5.12E-02  4.65E-02  4.54E-02  3.10E-02  2.05E-02
         2            0.666732           0.58045  0.238107  0.117001  0.103335  6.79E-02  6.56E-02  0.059476  5.81E-02  3.96E-02  2.62E-02
         3                              0.870589  0.357125  0.175484  0.154987  0.101766  9.83E-02  8.92E-02  8.72E-02  5.95E-02  3.93E-02
```

4	0.410211	0.201569	0.178026	0.116894	0.112966	0.102465	0.100162	6.83E-02	4.51E-02
5		0.491379	0.433986	0.28496	0.275386	0.249786	0.244171	0.166486	0.109912
6			0.883199	0.579918	0.560434	0.508336	0.49691	0.338813	0.223681
7				0.656611	0.634551	0.575562	0.562626	0.383621	0.253262
8					0.966403	0.876565	0.856863	0.584244	0.385711
9						0.907038	0.886652	0.604555	0.39912
10							0.977524	0.666515	0.440025
11								0.68184	0.450143
12									0.660188

Matrix: P(Grs) (column=s, row=r); double precision BD calculation

	2	3	4	5	6	7	8	9	10	11	12	13
1	0.205127	0.200813	0.127795	0.365665	0.534721	0.495648	0.564651	0.504831	0.464564	0.391822	0.436239	0.453186
2		0.51806	0.320244	0.683358	0.83496	0.797644	0.849227	0.79825	0.758232	0.678173	0.722595	0.733043
3			0.296578	0.806504	0.92373	0.89077	0.927173	0.885108	0.847622	0.766919	0.808543	0.813992
4				0.951701	0.983359	0.968149	0.980446	0.960938	0.939609	0.886718	0.910862	0.909206
5					0.941249	0.863111	0.916918	0.832699	0.754046	0.597035	0.677798	0.692521
6						0.405388	0.698727	0.477504	0.351776	0.179804	0.304612	0.365221
7							0.860926	0.623824	0.462933	0.241731	0.387391	0.444213
8								0.142976	0.114892	2.66E-02	0.171119	0.263488
9									0.354505	0.089791	0.327617	0.409905
10										8.83E-02	0.46765	0.521235
11											0.76432	0.718914
12												0.651589

Matrix: Monte Carlo (evol) (column=s, row=r)

	2	3	4	5	6	7	8	9	10	11	12	13
1	159	187	112	378	628	543	632	498	429	357	420	385
2		506	273	708	879	836	904	871	822	720	774	738
3			244	820	951	916	956	931	897	781	819	789
4				965	1000	982	996	983	972	922	949	932

5	958	853	940	847	745	575	638	611
6		312	645	407	321	121	250	265
7			845	622	463	216	404	370
8				121	86	3	109	140
9					308	59	317	279
10						34	407	381
11							710	640
12								527

Matrix: Monte Carlo (ecol) (column=s, row=r)

	2	3	4	5	6	7	8	9	10	11	12	13
1	0	0	0	364	359	186	531	474	392	50	36	202
2		279	37	499	587	506	729	703	606	387	187	413
3			120	631	677	444	771	752	609	280	303	459
4				878	759	731	824	801	735	640	622	599
5					498	458	697	667	567	373	377	352
6						23	706	645	564	8	7	519
7							964	844	733	190	98	596
8								120	178	0	0	48
9									409	0	0	239
10										63	21	311
11											231	780
12												841

Adjacent species triplets data

r	s	Grs	BD P(Grs)	BCD P(Grs)	MC count(evol)	MC count (ecol)
3	11	8.72E-02	0.766919	/	781	280
1	3	0.521061	0.200813	/	187	0
1	4	0.45363	0.127795	/	112	0
4	10	0.102465	0.939609	/	972	735

```
         8        10  0.876565        0.114892 /                86        178
         2         8  6.79E-02        0.849227 /               904        729
         2         6  0.117001         0.83496 /               879        587
         6        12  0.338813        0.304612 /               250          7
         5        12  0.166486        0.677798 /               638        377
         5        13  0.109912        0.692521 /               611        352
         9        13   0.39912        0.409905 /               279        239
         7         9  0.634551        0.623824 /               622        844

d.f. =            24
          Fisher     Z score:
          log sum
          P:
BD:         19.61338  -0.59253
MC          21.80903  -0.25126
(evol):
MC          53.10704  3.450367
(ecol):
d.f. <= 100, so use Fisher log sum as test statistic
```

APPENDIX 4.3. LIMSIM SOURCE CODE

1. Global settings
2. Main control code
3. Functions
4. Statistical calculations
5. Not included: ProMath 3.0 code used for extended decimal place precision calculations

1. Global settings

```
Attribute VB_Name = "modGlobal"
Option Base 1

Global Const PmArrayBase = 1                'First element of array
Global Const Pi = 3.14159265358979            'Global Pi Constant
Global Const Pi2 = Pi / 2#                    'Global Pi/2 Constant

Global DupsRemoved%

Public LeftLen%
Public RightLen%

Public CurrentVarName$
Public ErrCode%, ValuesFile$, WorkDir$ ', SaveDir$


Sub swap1(I1#, I2#)

    tmp = I1
    I1 = I2
    I2 = tmp

End Sub
```

2. Main control code

[Interface graphic description code omitted].

```
Option Explicit
Option Base 1
Dim optWeights As Boolean

Private Sub cmdRun_Click()

    Dim i%, Repeats%, r%, s%, n%, Length%, PGrs#, SpPoolFile$,
ListOfFiles$
    Dim OrdWeights As New Collection
    Dim Ord_gScs As New Collection
    Dim Grs As New Collection
    Dim MCScoresEcol As New Collection
    Dim MCScoresEvol As New Collection
    Dim BCDMCScores As New Collection
    Dim ProbsGrs As New Collection
    Dim gScosSeq As New Collection
    Dim gScosOrd As New Collection
    Dim TempCol2 As New Collection
    Dim MCScoresAll As New Collection
    Dim ThreeGrs As New Collection
    Dim BCDgScosOrd As New Collection
    Dim BCDGrs As New Collection
    Dim Grs2 As New Collection
    Dim Probs As New Collection
    Dim BCDProbs As New Collection
    Dim SpeciesPool As New Collection
    Dim gScosInfo As New Collection

    CheckVis
    Length = Val(txtBCDLen.Text)
    LeftLen = Length
    RightLen = Length

    lblStatus.Caption = ""
    lblStatus2.Caption = ""
    comdlgReadWts.filename = ""

    'read assemblage species list
    comdlgReadWts.InitDir = WorkDir
    comdlgReadWts.DialogTitle = "Assemblage list file..."
    comdlgReadWts.ShowOpen
    If comdlgReadWts.filename = "" Then Exit Sub
    ValuesFile = ExtractFileName(comdlgReadWts.filename) & "." &
ExtractExtension(comdlgReadWts.filename)
    WorkDir = ExtractPath(comdlgReadWts.filename) & "\"
    frmRun.Caption = ValuesFile
    Set OrdWeights = GetWeights(WorkDir & ValuesFile)
    If DupsRemoved > 0 Then
        MsgBox DupsRemoved & " duplicate value(s) removed from " &
ValuesFile, vbOKOnly, "Checking input data"
    End If
    n = OrdWeights.Count - 1
```

```
    'read species pool data if required
    If chkPool Then
        comdlgSpeciesPool.InitDir = WorkDir
        comdlgSpeciesPool.DialogTitle = "Species pool file..."
        comdlgSpeciesPool.ShowOpen
        If comdlgSpeciesPool.filename = "" Then Exit Sub
        SpPoolFile = ExtractFileName(comdlgSpeciesPool.filename) &
"." & ExtractExtension(comdlgSpeciesPool.filename)
        WorkDir = ExtractPath(comdlgSpeciesPool.filename) & "\"
        Set SpeciesPool = GetWeights(WorkDir & SpPoolFile)
            If DupsRemoved > 0 Then
                MsgBox DupsRemoved & " duplicate value(s) removed
from " & SpPoolFile, vbOKOnly, "Checking input data"
            End If
    End If

    lblStatus.Caption = "Calculating g scores..."
    Set gScosOrd = gScores(OrdWeights)
    Set gScosInfo = gScoresInfo(OrdWeights)

    lblStatus.Caption = "Calculating Grs scores..."
    Set Grs = GrsScores(gScosOrd)

    If chkBCDrs Then
        lblStatus.Caption = "Calculating BCDProbGrs (r,s)..."
        DoEvents
        i = 0
        For r = 1 To n - 1
        For s = r + 1 To n
            i = i + 1
            If r = Val(txtr) And s = Val(txts) Then
                PGrs = BCDProbGrs(n, Grs(i), r, s)
                r = n - 1
                s = n
            End If
        Next s
        Next r
        lblStatus.Caption = "DONE."
        lblStatus2.Caption = "BCDProbGrs = " & PGrs
        PGrs = 0
        Exit Sub
    End If

    If chkDbl Then
        lblStatus.Caption = "Calculating BD probs..."
        i = 0
        For r = 1 To n - 1
        For s = r + 1 To n
            lblStatus2.Caption = "r = " & r & ": s = " & s
            i = i + 1
            PGrs = ProbGrs(n, Grs(i), r, s)
            Probs.Add PGrs
        Next s
        Next r
    End If

    If chkBCD Then
        lblStatus.Caption = "BCD probabilities..."
```

```
        i = 0
        For r = 1 To n - 1
            For s = r + 1 To n
                DoEvents
                lblStatus2.Caption = "r = " & r & "/" & n & " :s = "
& s & "/" & n
                i = i + 1
                BCDProbs.Add BCDProbGrs(n, Grs(i), r, s)
            Next s
        Next r
    End If

    If chkMC Then
        lblStatus.Caption = "Running Monte Carlo simulation
(evol)..."
        Repeats = 1000 * Val(tBoxRepeats)
        Set MCScoresEvol = MonteCarlo(Grs, Repeats, OrdWeights)
'evolutionary hypothesis
        'ecological hypothesis
            If chkPool Then
                lblStatus.Caption = "Running Monte Carlo simulation
(ecol)..."
                Set MCScoresEcol = MonteCarloEcol(Grs, Repeats,
OrdWeights, SpeciesPool)
            End If
    End If
    'MCScores is organised as r, s, MC score...

    lblStatus.Caption = "Saving output..."
    If chkPool Then
        ListOfFiles = "Community file: " & ValuesFile & "   / Pool
file: " & SpPoolFile
    Else: ListOfFiles = "Community file: " & ValuesFile
    End If
    SaveResults OrdWeights, gScosOrd, gScosInfo, Grs, ListOfFiles,
MCScoresEcol, SpeciesPool, MCScoresEvol, Probs, BCDProbs

    lblStatus.Caption = "DONE."
    lblStatus2.Caption = ""
    lblMCCount.Caption = ""

End Sub

Private Sub SaveResults(Wts As Collection, gScs As Collection,
gScsInfo As Collection, _
    GrsScs As Collection, FileList$, Optional MCScsEcol As
Collection, _
    Optional PoolWts As Collection, Optional MCScsEvol As
Collection, Optional PGrs As Collection, _
    Optional BCDPGrs As Collection)

    Dim i%, r%, s%, outfile$, Reps%, SpR%, BDLogSumP#, df%
    Dim MCEcolZscore#, MCEvolZscore#, BDZscore#
    Dim MCEcolLogSumP#, MCEvolLogSumP#, MCEcolProb#, MCEvolProb#
    Dim MCProbEcol#, MCProbEvol#
    Dim MCec$, MCev$, PG$
    Dim BCDLogSumP#, BCDP$, BCDZscore#
    Dim rsForAdjSpp As New Collection
```

```
    SpR = Wts.Count

    'Create output file and directory.
    outfile = "LS_" & ValuesFile
    If Not CheckDirExists(WorkDir & "\results") Then
        MkDir (WorkDir & "results\")
    End If
    Open WorkDir & "results\" & outfile For Output As #1
    Write #1, FileList
    Write #1,

    'Calculate Irwin test value
    Dim IrwinP#
    If gScs(1) <= 1 / (SpR - 1) Then
        IrwinP = Power(1 - (SpR - 1) * gScs(1), SpR - 2)
    Else: IrwinP = 0
    End If

    'Write input data, g scores, and Irwin P
    Write #1, "Rank", "Value", "g score", "Irwin Prob [g1 >
obs(g1)]", "small sp", "large sp", "g score rank", "g score", "r for
Grs", "s for Grs"
    Write #1, 1, Wts(1), gScs(1), IrwinP, gScsInfo(1), gScsInfo(2),
gScsInfo(3), gScsInfo(4)
    For i = 2 To SpR - 1
        r = WorksheetFunction.Min(gScsInfo(4 * i - 1), gScsInfo(4 *
(i - 1) - 1))
        s = WorksheetFunction.Max(gScsInfo(4 * i - 1), gScsInfo(4 *
(i - 1) - 1))
        rsForAdjSpp.Add r
        rsForAdjSpp.Add s
        Write #1, i, Wts(i), gScs(i), , gScsInfo(4 * i - 3),
gScsInfo(4 * i - 2), gScsInfo(4 * i - 1), gScsInfo(4 * i), r, s
    Next i
    Write #1, SpR, Wts(SpR)

    'Write Grs scores, MC scores, BD and BCD probs. Calculate log
sum P's
    Write #1,
    Reps = 1000 * Val(tBoxRepeats)
    Write #1, "Repeats = " & Reps
    Write #1,
        Write #1, "r", "s", "Grs scores", "BD Prob", "BCD BD Prob",
"MC (evol) Count", "MC (ecol) Count"
        i = 0
        For r = 1 To SpR - 2
            For s = r + 1 To SpR - 1
                i = i + 1
                If chkMC Then
                    MCProbEvol = MCScsEvol(3 * i) / Reps
                    If MCProbEvol = 0 Then MCProbEvol = 1 / Reps
                    MCEvolLogSumP = MCEvolLogSumP + Log(MCProbEvol)
                    MCev = Str(MCScsEvol(3 * i))
                Else: MCev = "/"
                End If
                If chkPool Then
                    MCProbEcol = MCScsEcol(3 * i) / Reps
                    If MCProbEcol = 0 Then MCProbEcol = 1 / Reps
                    MCEcolLogSumP = MCEcolLogSumP + Log(MCProbEcol)
```

```
                    MCec = Str(MCScsEcol(3 * i))
                Else: MCec = "/"
                End If
                If chkDbl Then
                    If (PGrs(i) > 0) And (PGrs(i) < 1) Then
                        BDLogSumP = BDLogSumP + Log(PGrs(i))
                        PG = Str(PGrs(i))
                    Else: PG = "ERROR"
                    End If
                Else: PG = "/"
                End If
                If chkBCD Then
                    If (BCDPGrs(i) > 0) And (BCDPGrs(i) < 1) Then
                        BCDLogSumP = BCDLogSumP + Log(BCDPGrs(i))
                        BCDP = Str(BCDPGrs(i))
                    Else: BCDP = "ERROR"
                    End If
                Else: BCDP = "/"
                End If
                Write #1, r, s, GrsScs(i), PG, BCDP, MCev, MCec
            Next s
        Next r
    Write #1,

    'Calculate test stats and write
    df = 2 * i
    If chkDbl Or chkBCD Or chkMC Or chkPool Then
        Write #1,
        Write #1, "d.f. = ", df
        Write #1, , "Fisher log sum P:", "Z score:"
    End If
    If chkDbl Then
        BDLogSumP = -2 * BDLogSumP
        BDZscore = Sqr(2 * BDLogSumP) - Sqr(2 * df - 1)
        Write #1, "BD:", BDLogSumP, BDZscore
    End If
    If chkBCD Then
        BCDLogSumP = -2 * BCDLogSumP
        BCDZscore = Sqr(2 * BCDLogSumP) - Sqr(2 * df - 1)
        Write #1, "BCD:", BCDLogSumP, BCDZscore
    End If
    If chkMC Then
        MCEvolLogSumP = -2 * MCEvolLogSumP
        MCEvolZscore = Sqr(2 * MCEvolLogSumP) - Sqr(2 * df - 1)
        Write #1, "MC (evol):", MCEvolLogSumP, MCEvolZscore
    End If
    If chkPool Then
        MCEcolLogSumP = -2 * MCEcolLogSumP
        MCEcolZscore = Sqr(2 * MCEcolLogSumP) - Sqr(2 * df - 1)
        Write #1, "MC (ecol):", MCEcolLogSumP, MCEcolZscore
    End If
    If df > 100 Then
        Write #1, "d.f. > 100, so use Z score as test statistic"
    Else: Write #1, "d.f. <= 100, so use Fisher log sum as test
statistic"
    End If

    If chkPool Then
        Write #1,
```

```
    Write #1, "rank", "Species pool"
    For i = 1 To PoolWts.Count
      Write #1, i, PoolWts(i)
    Next i
  End If

  'Print results [Grs, P(Grs), MCEvol(rs), MCEcol(rs)] in matrix
formats
  Write #1,
  Write #1, "Matrix: Grs (column=s, row=r)"
  PrintMatrix GrsScs, SpR, False

  If chkDbl Then
  Write #1,
  Write #1, "Matrix: P(Grs) (column=s, row=r); double precision BD
calculation"
  PrintMatrix PGrs, SpR, False
  End If

  If chkMC Then
  Write #1,
  Write #1, "Matrix: Monte Carlo (evol) (column=s, row=r)"
  PrintMatrix MCScsEvol, SpR, True
  End If

  If chkPool Then
  Write #1,
  Write #1, "Matrix: Monte Carlo (ecol) (column=s, row=r)"
  PrintMatrix MCScsEcol, SpR, True
  End If

  'print list of Grs scores and stats for triplets of adjacent
species
  Dim j%, selectr%, selects%, selectGrs#, selectPGrs$,
selectBCDPGrs$, selectMCevol$, selectmcecol$
  Dim tempval#
  Write #1,
  Write #1, "Adjacent species triplets data"
  Write #1, "r", "s", "Grs", "BD P(Grs)", "BCD P(Grs)", "MC
count(evol)", "MC count  (ecol)"
  MCEvolLogSumP = 0
  MCEcolLogSumP = 0
  BDLogSumP = 0
  BCDLogSumP = 0
  df = 0
  For i = 1 To SpR - 2
    j = 0
    selectr = rsForAdjSpp(i * 2 - 1)
    selects = rsForAdjSpp(i * 2)
    For r = 1 To SpR - 2
      For s = r + 1 To SpR - 1
      j = j + 1
      If (r = selectr) And (s = selects) Then
        df = df + 2
        selectGrs = GrsScs(j)
        If chkDbl Then
          selectPGrs = Str(PGrs(j))
          If (PGrs(j) > 0) And (PGrs(j) < 1) Then
            BDLogSumP = BDLogSumP + Log(PGrs(j))
```

```
                End If
            Else: selectPGrs = "/"
            End If
            If chkBCD Then
                selectBCDPGrs = Str(BCDPGrs(j))
                If (BCDPGrs(j) > 0) And (BCDPGrs(j) < 1) Then
                    BCDLogSumP = BCDLogSumP + Log(BCDPGrs(j))
                End If
            Else: selectBCDPGrs = "/"
            End If
            If chkMC Then
                selectMCevol = Str(MCScsEvol(j * 3))
                MCProbEvol = MCScsEvol(3 * j) / Reps
                If MCProbEvol = 0 Then MCProbEvol = 1 / Reps
                MCEvolLogSumP = MCEvolLogSumP + Log(MCProbEvol)
            Else: selectMCevol = "/"
            End If
            If chkPool Then
                selectmcecol = Str(MCScsEcol(j * 3))
                MCProbEcol = MCScsEcol(3 * j) / Reps
                If MCProbEcol = 0 Then MCProbEcol = 1 / Reps
                MCEcolLogSumP = MCEcolLogSumP + Log(MCProbEcol)
            Else: selectmcecol = "/"
            End If
            Write #1, selectr, selects, selectGrs, selectPGrs, _
                selectBCDPGrs, selectMCevol, selectmcecol
        End If
        Next s
    Next r
Next i

'Calculate test stats and write
If chkDbl Or chkBCD Or chkMC Or chkPool Then
    Write #1,
    Write #1, "d.f. = ", df
    Write #1, , "Fisher log sum P:", "Z score:"
End If
If chkDbl Then
    BDLogSumP = -2 * BDLogSumP
    BDZscore = Sqr(2 * BDLogSumP) - Sqr(2 * df - 1)
    Write #1, "BD:", BDLogSumP, BDZscore
End If
If chkBCD Then
    BCDLogSumP = -2 * BCDLogSumP
    BCDZscore = Sqr(2 * BCDLogSumP) - Sqr(2 * df - 1)
    Write #1, "BCD:", BCDLogSumP, BCDZscore
End If
If chkMC Then
    MCEvolLogSumP = -2 * MCEvolLogSumP
    MCEvolZscore = Sqr(2 * MCEvolLogSumP) - Sqr(2 * df - 1)
    Write #1, "MC (evol):", MCEvolLogSumP, MCEvolZscore
End If
If chkPool Then
    MCEcolLogSumP = -2 * MCEcolLogSumP
    MCEcolZscore = Sqr(2 * MCEcolLogSumP) - Sqr(2 * df - 1)
    Write #1, "MC (ecol):", MCEcolLogSumP, MCEcolZscore
End If
If df > 100 Then
    Write #1, "d.f. > 100, so use Z score as test statistic"
```

```
    Else: Write #1, "d.f. <= 100, so use Fisher log sum as test
statistic"
    End If


    Close #1

End Sub

Private Sub PrintMatrix(Col As Collection, n%, MCData As Boolean)

Dim MatRow$, MatRowLead$, i%, j%, r%, s%

MatRow = ""
For i = 2 To n - 1
    MatRow = MatRow & "," & i
Next i
Print #1, MatRow
MatRow = ""
i = 0
For r = 1 To n - 2
    MatRow = ""
    For s = r + 1 To n - 1
        i = i + 1
        If MCData Then
        MatRow = MatRow & "," & Str(Col(3 * i))
        Else: MatRow = MatRow & "," & Str(Col(i))
        End If
    Next s
    MatRowLead = ""
    If r = 1 Then
        MatRowLead = ""
    Else
        For j = 1 To r - 1
            MatRowLead = MatRowLead & ","
        Next j
    End If
    Print #1, r, MatRowLead, MatRow
Next r

End Sub

Private Sub txts_Change()

    If Val(txts) <= Val(txtr) Then txts = Str(Val(txtr) + 1)

End Sub

Private Sub txtr_Change()

    If Val(txts) <= Val(txtr) Then txts = Str(Val(txtr) + 1)

End Sub

Private Sub chkBCD_Click()

CheckVis

End Sub
```

```
Private Sub CheckVis()

If chkBCDrs Then
    chkMC.Value = 0
    chkBCD.Value = 0
    lbls.Visible = True
    lblr.Visible = True
    txtr.Visible = True
    txts.Visible = True
End If

If chkBCDrs = 0 Then
    lbls.Visible = False
    lblr.Visible = False
    txtr.Visible = False
    txts.Visible = False
End If

If chkBCD Then
    chkBCDrs.Value = 0
End If


If chkMC Then
    chkBCDrs.Value = 0
    tBoxRepeats.Visible = True
    lblRepeats.Visible = True
    chkPool.Visible = True
End If

If chkMC = 0 Then
    tBoxRepeats.Visible = False
    lblRepeats.Visible = False
    chkPool.Visible = False
End If


End Sub

Private Sub chkBCDrs_Click()

CheckVis

End Sub

Private Sub chkMC_Click()

CheckVis

End Sub

Private Sub Form_Load()

Dim num#

    WorkDir = GetSetting(App.Title, Name, "Start Dir", CurDir)

    CheckVis
```

```
End Sub

Private Sub Form_Unload(Cancel As Integer)

    SaveSetting App.Title, Name, "Start Dir", WorkDir

End Sub

Public Sub cmdDone_Click()
    Unload Me
    End
End Sub
```

3. Functions

```
Attribute VB_Name = "modFunctions"
Option Explicit

Public Function GetWeights(PathToFile$) As Collection

    Dim Weight#
    Dim WeightList As New Collection, OrderedWeights As New
Collection
    Dim WeightList2 As New Collection

    Open PathToFile$ For Input As #1
    Do While Not EOF(1)
        Input #1, Weight
        WeightList.Add Weight
    Loop
    Close #1

    Set WeightList2 = RemoveDuplicates(WeightList)
    Set GetWeights = SortCol(WeightList2)

End Function

Private Function RemoveDuplicates(Col As Collection) As Collection

Dim i%, j%, testval#

DupsRemoved = 0

For i = 1 To Col.Count
    If i > Col.Count Then
        Set RemoveDuplicates = Col
        Exit Function
    End If
    testval = Col(i)
    For j = 1 To Col.Count
        If j > Col.Count Then GoTo jumpout
        If (Col(i) = Col(j)) And (i <> j) Then
            Col.Remove (i)
            DupsRemoved = DupsRemoved + 1
        End If
    Next j
jumpout:
Next i

Set RemoveDuplicates = Col

End Function

Public Function SortCol(ByVal ColToSort As Collection) As Collection
    'Sorts the items of a collection by
    'ascending size

    Dim i As Integer, j As Integer
    Dim Small As Variant
    Dim ItemCount As Integer
```

```
    Dim tempCol As New Collection
    Dim ItemNo As Integer

    ItemCount = ColToSort.Count

    For j = 1 To ItemCount

    Small = 999999999

    For i = 1 To ColToSort.Count 'ColToSort.Count <> ItemCount after
the 1st iteration
        If ColToSort(i) < Small Then
            Small = ColToSort(i)
            ItemNo = i
        End If
    Next i

    tempCol.Add Small
    ColToSort.Remove (ItemNo)

    Next j

    Set SortCol = tempCol

End Function

Public Function Combin(Numbers As Integer, Choose As Integer) As
Double

    Combin = Factor(Numbers) / (Factor(Choose) * Factor(Numbers -
Choose))

End Function

Public Function Factor(Number As Integer) As Double

    Dim i As Double

    Factor = 1

    For i = 1 To Number
        Factor = i * Factor
    Next i

End Function

Public Function Log10(Number As Double) As Double

Log10 = Log(Number) / Log(10)

End Function

Public Function Exponent(Number As Double) As Integer

Exponent = Int(Log10(Number))

End Function

Public Function Mantissa(Number As Double) As Double
```

```
Mantissa = Number / Power(10, Exponent(Number))

End Function

Public Function Power#(Number#, Exponent#)

If Int(Exponent) = Exponent And Exponent > 0 Then
    Power = PowerIntExp(Number, Int(Exponent))
    'I think this is much faster than the Excel function
Else
    Power = WorksheetFunction.Power(Number, Exponent)
End If

End Function

Public Function PowerIntExp(Number As Double, Exponent As Integer)
As Double
'NOTE THAT THIS IS ONLY FOR ***INTEGER*** EXPONENT

    Dim i%

    If Exponent = 0 Then
        PowerIntExp = 1
        Exit Function
    End If

    PowerIntExp = 1
    For i = 1 To Exponent
    PowerIntExp = Number * PowerIntExp
    Next i

End Function

Public Function ExtractExtension(strIn As String)
'Returns the extension from strIn, (ie string after first .)
'Called by projectFileExtension in this mod

    Dim intLen As String
    Dim strOUT As String

    intLen = InStr(strIn, ".") 'check to see if a full stop exists

    If intLen Then 'if a full stop is found in the passed string
       strOUT = Mid(strIn, intLen + 1) 'get the extension
    End If

    ExtractExtension = strOUT 'return the extension to the user

End Function

Public Function ExtractFileName(strPath As String) As String
'Purpose: returns the filename from the given input string
'Called by: ProjectName, mifMain_OpenProject

    Dim pos As Integer, lastpos As Integer
    pos = InStr(1, strPath, "\", 1)
    'Find last \
    Do While pos > 0
```

```
        DoEvents
        lastpos = pos
        pos = InStr(lastpos + 1, strPath, "\", 1)
    Loop
    'Find last "." if there is one before the last \ - work back
from the end
    pos = Len(strPath)
    Do While pos > lastpos
        DoEvents
        If (Mid(strPath, pos, 1) = ".") Then Exit Do
        pos = pos - 1
    Loop
    'If don't find one, set pos to one longer than the string length
    If pos = lastpos Then pos = Len(strPath) + 1

    ExtractFileName = Mid(strPath, lastpos + 1, pos - lastpos - 1)

End Function

Public Function ExtractPath(strIn As String)
' _
Purpose: _
    strips a valid path out from a "\filename.ext"-ended string. _
Inputs: invalid string _
Outputs: valid string _
Uses: _
Call:   frmSplash FindDefaultSettings and _
        modGlobal ProjectFolder

    Dim i As Integer
    Dim strOUT As String

    If InStr(strIn, "\") Then 'check to see if a forward slash
exists
       For i = Len(strIn) To 1 Step -1 'step though until full name
is extracted
           DoEvents
           If Mid(strIn, i, 1) = "\" Then
              strOUT = Left(strIn, i)
              Exit For
           End If
       Next i
    ElseIf InStr(strIn, ":") = 2 Then 'otherwise, check to see if a
colon exists
       strOUT = CurDir(strIn)
       If Len(strOUT) = 0 Then
          strOUT = CurDir
       End If
    Else
       strOUT = CurDir 'otherwise, return the current directory
    End If

    ExtractPath = Left(strOUT, Len(strOUT) - 1) 'return the
filenames path to the user

End Function

Public Function CheckDirExists(DirToCheck As String) As Boolean
```

```
Dim MyName$
CheckDirExists = True

' Display the names in PathToDir that represent directories:
MyName = Dir(DirToCheck, vbDirectory)    ' Retrieve the first entry.
If MyName = "" Then CheckDirExists = False


End Function
```

4. Statistical calculations

```
Attribute VB_Name = "modCalculations"
Option Explicit

Public Function gScores(OrdWts As Collection) As Collection

    Dim tempgScs As New Collection
    Dim i%, Big#, Small#

    For i = 1 To OrdWts.Count - 1
        DoEvents
        Big = OrdWts(i + 1)
        Small = OrdWts(i)
        tempgScs.Add (Log10(Big) - Log10(Small))
    Next i

    Set gScores = SortCol(tempgScs)

End Function

Public Function gScoresInfo(OrdWts As Collection)

    Dim tempgScs As New Collection
    Dim gScsOrd As New Collection
    Dim i%, j%, Big#, Small#, Rank%, g#

    Set gScsOrd = gScores(OrdWts)

    For i = 1 To OrdWts.Count - 1
        DoEvents
        Big = OrdWts(i + 1)
        Small = OrdWts(i)
        g = (Log10(Big) - Log10(Small))
        tempgScs.Add i
        tempgScs.Add i + 1
        For j = 1 To gScsOrd.Count
            If g = gScsOrd(j) Then Rank = j
        Next j
        tempgScs.Add Rank
        tempgScs.Add g
    Next i

    Set gScoresInfo = tempgScs

End Function

Public Function GrsScores(gScs As Collection) As Collection

    Dim r%, s%, Grs#
    Dim tempGrs As New Collection

    For r = 1 To gScs.Count - 1
    For s = r + 1 To gScs.Count
        DoEvents
        Grs = gScs(r) / gScs(s)
        tempGrs.Add Grs
```

```
    Next s
    Next r

    Set GrsScores = tempGrs

End Function

Public Function MonteCarlo(GrsScore As Collection, Reps%, Weights As
Collection) As Collection
'Calculates Monte Carlo counts (probabilities)
'n = no. of species
'Reps = no. of repeats
'This is the evolutionary hypothesis

    Dim r%, s%, i%, j%, n%, MC%, Wt#, MaxWt#, MinWt#
    Dim TestGrsScore#, Score#, ObsGrs#, GIndex%, Progress$
    Dim SortRandWts As New Collection
    Dim TempRandWts As New Collection
    Dim EmptyCol As New Collection
    Dim gScoresMC As New Collection
    Dim gScoresMCSort As New Collection
    Dim tempScrs As New Collection

    n = Weights.Count

'    MaxWt = 0
'    MinWt = 10000
'    For i = 1 To n
'        Wt = Weights(i)
'        If Wt > MaxWt Then MaxWt = Wt
'        If Wt < MinWt Then MinWt = Wt
'    Next i
    MaxWt = Weights(n)
    MinWt = Weights(1)

    For r = 1 To n - 2
    For s = r + 1 To n - 1
        Progress = "r = " & r & "/" & n - 2 & ": s = " & s & "/" & n
- 1
        frmRun.lblStatus2.Caption = Progress
        GIndex = GIndex + 1

        For MC = 1 To Reps      'calculate random communities
            frmRun.lblMCCount = Str(MC)
            DoEvents
            Set TempRandWts = EmptyCol
            For i = 2 To n - 1  'each community has n species
                Randomize
                TempRandWts.Add Exp(((Log(MaxWt) - Log(MinWt)) * Rnd
+ Log(MinWt)))
            Next i
            TempRandWts.Add MinWt
            TempRandWts.Add MaxWt
            Set SortRandWts = SortCol(TempRandWts)
        'calculate g scores:  g = log10(big) - log10(small)
            For i = 1 To n - 1
                gScoresMC.Add (Log10(SortRandWts(i + 1)) -
Log10(SortRandWts(i)))
            Next i
```

```
                Set gScoresMCSort = SortCol(gScoresMC)
            'now test Grs against obs(Grs) = a
                ObsGrs = GrsScore(GIndex)
                TestGrsScore = gScoresMCSort(r) / gScoresMCSort(s)
                If TestGrsScore > ObsGrs Then Score = Score + 1
            Next MC
        tempScrs.Add r
        tempScrs.Add s
        tempScrs.Add Score
        Score = 0
        Next s
        Next r

        Set MonteCarlo = tempScrs
        'MonteCarlo has structure: r, s, MCscore

    End Function

    Public Function MonteCarloEcol(GrsScore As Collection, Reps%,
    Weights As Collection, SpPool As Collection) As Collection
    'Calculates Monte Carlo counts (probabilities)
    'n = no. of species in test community
    'Reps = no. of repeats
    'This is the ecological hypothesis

        Dim n%, r%, s%, GIndex%, PoolSpr%, MC%, PickSp%, g#
        Dim i%, TestGrsScore#, Score#, ObsGrs#, Progress$
        Dim Big#, Small#
        Dim SpPoolSort As New Collection
        Dim PickedSpp As New Collection
        Dim SortPickedSpp As New Collection
        Dim EmptyCol As New Collection
        Dim gScoresMC As New Collection
        Dim gScoresMCSort As New Collection
        Dim tempScrs As New Collection
        Dim TempRandWts As New Collection

        n = Weights.Count
        PoolSpr = SpPool.Count
        If n >= PoolSpr Then
            MsgBox "SpR (inventory) >= SpR (pool): aborting", vbOKOnly,
    "Data error"
            End
        End If

        For r = 1 To n - 2
        For s = r + 1 To n - 1
            Progress = "r = " & r & "/" & n - 2 & ": s = " & s & "/" & n
    - 1
            frmRun.lblStatus2.Caption = Progress
            GIndex = GIndex + 1

            For MC = 1 To Reps      'calculate random communities
                frmRun.lblMCCount = Str(MC)
                DoEvents
                Set TempRandWts = EmptyCol
                Set PickedSpp = EmptyCol
                For i = 1 To n   'each community has n species
                    Randomize
```

```
                PickSp = Int(PoolSpr * Rnd + 1)
                If AlreadyPicked(PickedSpp, PickSp) Then
                    i = i - 1
                Else: PickedSpp.Add PickSp
                End If
            Next i
            Set SortPickedSpp = SortCol(PickedSpp)
        'calculate g scores:  g = log10(big) - log10(small)
            For i = 1 To n - 1
                Big = SpPool(SortPickedSpp(i + 1))
                Small = SpPool(SortPickedSpp(i))
                g = (Log10(Big) - Log10(Small))
                If g = 0 Then
                    MsgBox "Zero g score encountered in species
pool: aborting.", vbOKOnly, "Error"
                    frmRun.cmdDone_Click
                End If
                gScoresMC.Add g
            Next i
            Set gScoresMCSort = SortCol(gScoresMC)
        'now test Grs against obs(Grs) = a
            ObsGrs = GrsScore(GIndex)
            TestGrsScore = gScoresMCSort(r) / gScoresMCSort(s)
            If TestGrsScore > ObsGrs Then Score = Score + 1
        Next MC
    tempScrs.Add r
    tempScrs.Add s
    tempScrs.Add Score
    Score = 0
    Next s
    Next r

    Set MonteCarloEcol = tempScrs
    'MonteCarloEcol has structure: r, s, MCscore


End Function
Private Function AlreadyPicked(Col As Collection, It As Integer) As
Boolean

Dim i%

AlreadyPicked = False
For i = 1 To Col.Count
    If It = Col(i) Then AlreadyPicked = True
Next i

End Function

Public Function ProbGrs#(n%, A#, r%, s%)
'n is the number of g scores

Dim Comb1#, Comb2#, Comb3#, Comb4#
Dim Mult#, Denom#, Numer#
Dim i%, iTerm#, iSum#
Dim j%, jTerm#, jSumPos#, jSumNeg#
Dim zero#, strTemp#, Prob1#
Dim testp#
```

```
Comb1 = Combin(n, s)
Comb2 = Combin(s, r + 1)
Mult = Comb1 * Comb2

iSum = 0
iTerm = 0
jTerm = 0
jSumPos = 0
jSumNeg = 0
For i = 0 To r - 1
    Comb3 = Combin(r - 1, i)
For j = 0 To s - r - 1
    DoEvents
    Comb4 = Combin(s - r - 1, j)
    Numer = Comb3 * Comb4
    Denom = (n - s + j + 1) * ((s - r + i - j) * A + (n - s + j +
1))
    jTerm = Numer / Denom

    testp = Power(-1, i + j)
    If Power(-1, i + j) = 1 Then jSumPos = jSumPos + jTerm
    If Power(-1, i + j) = -1 Then jSumNeg = jSumNeg + jTerm
Next j
Next i

iSum = jSumPos - jSumNeg

strTemp = Mult * iSum
Prob1 = strTemp * A * r * (r + 1)

ProbGrs = 1 - Prob1

End Function
```

5. COMPETITION AND FACILITATION IN THE SERENGETI

INTRODUCTION

The prevalence of interspecific interactions within communities of African ungulates, and their influence on community structure, is unclear (Murray & Illius 1996) and has been debated for some time. Some authors argue that active competition is important (Murray & Illius 1996), others that active competition and facilitation are both important (Prins & Olff 1998), others that facilitation is important (Vesey-Fitzgerald 1960, 1965, Bell 1970, 1971), and still others that niche separation has evolved to the degree that little active competition actually occurs (Bell 1970, 1971, Jarman 1974, Owen-Smith 1989). Past competition has led to the evolution of a community that largely avoids the costs of competition (Connell 1980).

Some argue from general principles that major herbivore guilds are never limited by their food supply (and therefore are never structured by interspecific resource competition) because they consume such a small proportion of the available biomass (Hairston, Smith & Slobodkin 1960, Slobodkin, Smith & Hairston 1967). However, a range of information presented by Sinclair and co-authors has shown that the food supply does regulate the Serengeti herbivore community as a whole (Sinclair 1975), but that individual species are regulated by a range of different factors (chapter 1). For instance, wildebeest and buffalo (Sinclair 1974, Dublin *et al.* 1990, Mduma, Sinclair & Hilborn 1999) are regulated by the availability of food in the dry season. This regulation operates mainly through intraspecific competition in wildebeest, but for buffalo, competition with wildebeest contributes an important source of mortality. Buffalo are also excluded from wildebeest grazing lawns generated on their wet season range in the south east Serengeti plains (Murray & Illius 1996, 2000). Topi are excluded from wildebeest dry season range in the Masai Mara (Sinclair 1985).

For other species, and for different populations of the same species, interspecific interactions are less important and disease, predation, poaching and other external perturbations prevent the system from approaching close enough to equilibrium for competition to become limiting. Poaching reduced the buffalo population in the western Serengeti between 1970 and 1986 (Dublin *et al.* 1990). Predation may explain the stability of the zebra population during the 20 year eruption of wildebeest (Sinclair and Norton-Griffiths 1982), although poaching occurring when the zebra are outside the boundaries of the park may be more important, since wildebeest are easier prey than zebra (M. Murray *pers. comm.*). Individual species such as gazelle may be limited by competition in some situations, during part of the year, in certain years (Sinclair and Norton-Griffiths 1982), but in general neither competition nor, in particular, facilitation, are thought to be important.

In chapter 4, the Serengeti ecosystem was identified as a rare example where competition strongly influences the structure of a community of grazers. This chapter investigates in detail the influences of competition, facilitation and the food supply on the community dynamics of ungulates foraging on the short grass plains of the Serengeti National Park during the wet season. Expected outcomes of pairwise interactions between species under varying resource supply conditions are synthesised into hypotheses about how ungulate community parameters are expected to vary with the food supply. These hypotheses are tested using monthly aerial survey data collected by the Serengeti Ecological Monitoring Programme (SEMP) during three complete seasons from 1969 to 1972.

Mechanisms of interaction - ungulate foraging strategies and their influences on community dynamics

The interactions discussed in this chapter relate solely to resource use. Species interact by changing the properties of resource supplies used by other species. The aim of this discussion is to describe the effects different kinds of forager are likely to have on different resource scenarios, and then to predict the influence those changes will have on other kinds of forager. Foraging strategies were discussed in detail in chapter 2. Here the emphasis is on predicting the community dynamics associated with those strategies - how a community of ungulates responds to changes in resource supply characteristics, as well as how the animals themselves actually change resource supply characteristics.

There is ample evidence that ungulates, particularly grazers, can have a large impact upon their environment at a variety of scales. At a very broad scale, the recovery of wildebeest populations after the eradication of rinderpest in the Serengeti changed the burning regime in the south east plains. Before the recovery, these plains burned almost every year because of the build-up of fuel during the wet season. When the wildebeest populations recovered, they consumed up to 80% of the primary productivity of these plains, leaving nothing to burn (Sinclair 1975).

At a much more local scale, grazers can inflict subtle yet important modifications on the characteristics of the resource base. Illius & Gordon (1987) predicted that the ability of smaller animals to graze a sward closer to the ground than larger animals could allow them to capture a sward. This effect could be so subtle that even within a species (red deer), they predicted that the smaller females should be able to exclude the larger males from preferred, high quality grazing patches.

Experimental support for this prediction has come from studies of grazing by wildebeest and topi (Murray & Brown 1993, Murray & Illius 2000, see chapter 2). Although of similar body size, wildebeest are adapted to crop grass very close to the ground, and can reduce the available resource to below the threshold required by topi. The particularly wide incisor arcade of the wildebeest allows them to maintain a positive net energy intake on this sward, so excluding the topi. Topi, however, can exert a different modification upon the vegetation. By preferentially selecting the green leaf component of the sward, they can reduce the quality of the sward to the unselective wildebeest to the point where wildebeest cannot achieve a positive net energy intake, and yet the topi can.

At a scale intermediate between these scenarios, the annual Serengeti migratory succession starts with an early invasion by bulk grazers such as wildebeest and zebra. These prepare the way for smaller species such as gazelle by grazing down the mature, tall, low quality swards. Fresh growth of the sward is more suitable for the smaller grazers, which follow afterwards and benefit from the modified foraging conditions (Bell 1970, 1971).

Modification of resources is important because it provides a mechanism for species interactions. If 1) the modifications effected by different species, and 2) the population responses to these modifications by different species, can be specified, then community dynamics can be predicted. Extrapolating these processes to make predictions about ungulate community dynamics is not simple, because the experimental work (mostly on processes to do with competition) has been carried out under controlled resource supply conditions (*e.g.* Duncan *et al.* 1990, Murray 1991, 1993, Murray & Brown 1993, Van Soest 1994, Murray & Illius 2000). What happens when these processes operate in a spatially extensive, heterogeneous, temporally variable environment that is responsive to the influences of herbivore feeding is much more difficult to predict. The approach adopted here is to identify the range of inter-specific interactions that take place between foraging ungulates, to describe each in isolation from the others as far as is possible, and to attempt to reconstruct community dynamics from these individual elements.

From this analysis, a set of specific hypotheses will be derived, testing the overall hypothesis that grazer community structure is shaped by competition for resources. The hypotheses will be tested using aerial monitoring data from the Serengeti Wildlife Monitoring Programme.

Competitive exclusion and resource partitioning

The following foraging strategies can be understood both as mechanisms through which interspecific competition for resources can take place, but also as descriptions of species characteristics that define niche partitioning in the herbivore guild and can potentially operate to avoid resource competition. Evidence that species partition a range of resources among themselves is not sufficient proof that current competition takes place, although it is consistent with a hypothesis of evolutionary adaptation under competitive pressures (Connell 1980) and provides *prima facie* evidence that competition is possible.

Traditionally, two main lines of evidence have been used to support or reject hypotheses of active competition. The direct line of evidence is to measure the influence one species has on the population of another species. The indirect line is to compare community organisation with predictions generated from competition theory. Chapter 1 reviewed the published work reporting studies of competition in African ungulates, and chapter 4 used indirect evidence to test and support a hypothesis of competition in the Serengeti (and reject it in many other ecosystems). In this chapter, direct evidence of population interactions will be tested.

The Bell-Jarman hypothesis provides a mechanism for resource partitioning in ungulates. A community of ungulates of different body sizes can partition the available resources according to digestibility and abundance (see chapters 1 and 2). Species that are sufficiently different in body size are able to avoid competition and can stably coexist (chapter 4). However, there is also potential for smaller species to capture a sward by maintaining it in a short, close cropped state, and there may therefore also be a limit to the *difference* (as well as a limit to the similarity) in body sizes that can stably coexist (as discussed in chapter 2).

In the following discussion, the consequences for community dynamics of a number of foraging strategies are described. Facilitation is similarly analysed. Finally, predictions are made about community dynamics in relation to resource supply characteristics, and a number of testable hypotheses are derived.

Diet selectivity

Diet selectivity in part varies as a function of body size, with smaller species both able and obliged to search out the higher quality components of the vegetation. However, selectivity also varies among species of similar body size, allowing selectivity *per se* to become the basis of niche partitioning or of competitive interactions, independently of body size. In ungulates, selectivity depends upon the width of the incisor arcade (Illius & Gordon 1987, Gordon & Illius 1988, Murray & Illius 2000, Pérez-Barbería & Gordon 2000), with a narrower incisor arcade allowing more selective feeding, but entailing a cost of reduced intake rate.

Figure 9.5 in Murray & Illius (1996) shows that among mid-sized grazers in the Serengeti, there is variation in incisor arcade breadth that is not related to body size. This suggests that some similar-sized ungulates may partition resources, or else competitively interact, via differences in selective ability.

Consequences for community dynamics

Murray & Brown (1993) and Murray & Illius (2000) describe how a more selective grazer (topi) is able to deplete a sward of its green leaf component to below the level required by a more generalist grazer (wildebeest) (see also chapter 2). Conversely, the generalist is able to graze the sward down to a height below which the selective forager is able to maintain a net positive energy intake. Within a patch therefore, similar-sized selective and generalist feeders cannot stably coexist. However, across a landscape, the two species are able to coexist because each is capable of capturing the sward within a patch - of modifying it to such an extent that the other species cannot invade (chapter 2). This sward capture is independent of initial vegetation conditions, depending in fact on which species enters the patch first. Coexisting species can generate spatial heterogeneity in resources, rather than depending on pre-existing heterogeneity to support coexistence.

Digestive strategy

The lack of diversity in hind-gut fermenters in African ecosystems has been a puzzle, but may in fact be due to the success of the strategy (Demment & van Soest 1985, Duncan *et al.* 1990). Hind-gut fermentation reduces the passage rate limit on the functional response. The animal can continue processing large amounts of food when it is available, subjecting it to a more rapid and therefore less complete digestion, but profiting from a larger net energy intake because of the enhanced throughput. The hind-gut digestive strategy is likely to be more profitable than fore-gut digestion for any quality of forage, so long as the forage is abundant.

The much greater diversity of fore-gut fermenters (Demment & van Soest 1985) is probably due to the frequency of food shortages experienced either within years (*i.e.* seasonal shortages) or between years (*e.g.* after droughts). The fore-gut strategy extracts a greater proportion of the nutrients from a given amount of food, and if food quantity is limiting, the hind-gut strategy will not be successful.

Consequences for community dynamics

The main African species that use a hind-gut strategy are the zebras. In the Serengeti, zebra populations are largely migratory, moving in synchrony with the wildebeest. They therefore track the most abundant resources, allowing them to maintain a high intake rate and to experience a relatively constant resource supply rate. Fore-gut fermenters are better able to survive variable conditions and temporary shortages of food.

Intake vs. utilisation efficiency

Murray (unpublished MS) has suggested a further possible foraging strategy. Noting that competitive strategies in plants are often described in terms of differing tolerances to low nutrient levels, Murray (*ibid.*) extended the idea to ungulates. Some species are known to have markedly lower metabolic rates than others, and therefore can tolerate a lower energy intake than other ungulates of similar body size. Murray (*ibid.*) discusses further examples of differences among ungulates in the efficiency with which they use different resources and nutrients.

Some species, Murray suggests, have a high utilisation efficiency, achieving positive net energy budgets on limited resources. Other species, such as wildebeest, are much more efficient at harvesting resources, and may be thought of as maximising intake efficiency. The extra work involved in gathering such a large amount of food reduces their utilisation efficiency.

Consequences for community dynamics

Murray (*ibid.*) argues that a community of ungulates controlled by this kind of competition will be unstable. The intake maximiser is necessarily less selective than the utilisation efficiency maximiser, since its strategy is to consume a larger proportion of the available forage. The utilisation efficiency maximiser consumes a lower bulk of material per unit time, and can therefore be more selective. The two strategies therefore deplete the resource base in different ways. A more selective, utilisation efficiency maximiser such as topi, can reduce the proportion of green leaf in the sward to below the level required by a less selective intake maximiser such as wildebeest. Conversely, wildebeest can deplete the standing biomass of a sward to below that required by topi (Murray & Brown 1993, Murray & Illius 2000). Each species is therefore capable of reducing the level of the resource that is limiting to the other species, and depending upon starting conditions, each species can exclude the other from a sward. Stable coexistence is not possible.

This scenario requires that species differ in their selective ability as well as metabolic rates, and may therefore be understood simply as a development of the selectivity strategy, with more selective species adapted to require fewer resources. However, Murray (*ibid.*) developed the scenario and generated unique predictions that could potentially be used to test whether competition is mediated by utilisation efficiency or by digestive and intake constraints. No tests of this hypothesis were designed in the current analysis, but these are considered further in the *Discussion*.

Facilitation

Facilitation has been proposed largely as a result of observations of the temporal sequence of grazing species that pass through a plot of land, either during major migrations, or during more nomadic movements between different patches of habitat. Vesey-Fitzgerald (1960, 1965) described a grazing succession whereby larger species initially colonised an area, trampling and grazing down the tall grasses and stimulating new growth. These habitat modifications then allowed smaller species to follow the larger species onto these ranges. Bell (1971) described this process for a succession consisting of zebra first, then wildebeest and finally Thomson's gazelle. Similar sequences were reported both for small scale inter-patch movements by resident populations in the western Serengeti, and for the larger scale movements of migratory populations moving onto their wet season ranges.

Although the grazing succession is seen as a form of niche separation, minimising competition (Vesey-Fitzgerald 1960, 1965, Maddock 1979), it seems likely that the beneficiaries are the smaller species, and that ultimately they force the larger species off depleted grazing lawns and back on the road to search for taller patches of grass.

Local movements - patch selection

Bell (1970, 1971) described the sequence of movements by species occupying the gently undulating region in the western Serengeti. On the tops of the hills, soils were sandy and well drained. After rains, short but high quality grazing would develop on these sandy tops, attracting many species. However, the forage would be grazed down rapidly, forcing the largest species to move down the hillside looking for ungrazed patches. As the grazing became more depleted on the hill tops, successively smaller species would be forced to leave.

Meanwhile, in the wet hollows at the bottom of the hills, tall, fibrous swards had developed. This grazing is unsuitable for smaller species, but larger animals such as buffalo are able to feed on this grass. The larger grazers reduce the height of this sward, allowing smaller species to feed there, and the sequence of larger species leaving the hill tops is followed by one of smaller species successively colonising the wet hollows.

The interaction at the top of the hills is clearly competitive exclusion, but the sequence of colonisation of the less-preferred habitat is facilitation.

Long distance movements - migrations

The larger scale migrations follow a similar sequence (Bell 1971, Pennycuick 1975, Maddock 1979, Murray 1995), with the largest species being the first to be forced off a depleted resource (grasses in the woodlands) and on to an abundant but less preferred resource (the well developed, tall and fibrous grasses that dominate the short-grass plains at the beginning of the wet season). Once this old growth is broken down by the larger species, subsequent new flushes of growth that come with the rains can be used by smaller species, and a heterogeneous, patchy distribution of grass heights and qualities develops and is maintained by the different grazing species occupying the short-grass plains in the wet season.

Consequences for community dynamics

Facilitation extends the spatial extent over which smaller species can occur. They can invade patches that are suitable, or patches that are currently unsuitable but are in the process of being modified by larger species. If facilitation is important, there may be a feedback process whereby large densities of smaller species capture a large proportion of the swards, forcing the larger species away. This in turn reduces the amount of habitat modification occurring, and after rainfall the sward may grow quickly enough to escape control by the smaller species. They in turn may be forced to migrate, or may starve, reducing their density and allowing the larger species to return.

If smaller species respond to the facilitatory potential of larger species, then the presence of small species in tall swards may be correlated to the presence or abundance of larger species. Conversely, larger species may avoid shorter swards if there are already smaller species present on it. These hypotheses predict a positive correlation between small and large grazer densities on tall swards, and a negative correlation on short swards.

Predicting community dynamics

To predict how community parameters (species richness, mean body size, size ratios *etc.*) vary with resource parameters (supply rate, quality, spatial and temporal heterogeneity) under the influence of competition (-ve interaction), facilitation (+ve interaction) and neutrality (no interaction), first of all the expected interactions of pairs of species under varying resource conditions are specified in table 5.1. These interactions are generalised and covariation of herbivore community and resource supply parameters is predicted in table 5.4. These predictions are then used to generate a set of specific, testable hypotheses.

Table 5.1. Predicted responses of pairs of coexisting grazers to changes in resource characteristics (supply, quality and spatial heterogeneity). Supply and quality are assumed to vary independently. The neutral scenario predicts the population response of each species living separately from the other. The response indicated under each interaction (facilitation, neutral or competition) indicates population responses attributable purely to that interaction in isolation from the others.

a) Smaller vs. larger species

		facilitation		**neutral**		**competition**	
		smaller species	larger species	smaller species	larger species	smaller species	larger species
change in resources	S +	+	0	+	+	-	+
	S -	-	0	-	-	+	-
	Q +	-	0	+	+	+	-
	Q -	+	0	-	-	-	+
	H +	0	0	0	0	+	+
	H -	0	0	0	0	-	-

b) More selective and less selective species, both equal sized. Facilitation between these species is assumed not to occur

		neutral		**competition**	
		selective species	unselective species	selective species	unselective species
change in resources	S +	+	+	+	-
	S -	-	-	-	+
	Q +	+	+	-	+
	Q -	-	-	+	-
	H +	0	0	+	+
	H -	0	0	-	-

c) Foregut fermenter and hindgut fermenter, both equal sized

		facilitation		neutral		competition	
		foregut	hindgut	foregut	hindgut	foregut	hindgut
change in resources	S +	+	0	+	+	-	+
	S -	-	0	-	-	+	-
	Q +	-	0	+	+	-	+
	Q -	+	0	-	-	+	-
	H +	0	0	0	-	+	+
	H -	0	0	0	+	-	-

d) Utilisation efficiency maximizer (UEM) vs. intake maximiser (IM), both equal sized

		facilitation		neutral		competition	
		UEM	IM	UEM	IM	UEM	IM
change in resources	S +	+	0	+	+	+	-
	S -	-	0	-	-	-	+
	Q +	-	0	+	+	-	+
	Q -	+	0	-	-	+	-
	H +	0	0	0	0	+	+
	H -	0	0	0	0	-	-

S = resource supply; Q = resource quality; H = resource heterogeneity.
Changes to H assume no change in mean S or Q.
+ = benefit to species (e.g. more food, less competition, more facilitation)
- = disadvantage to species.
Note that the magnitudes of +'s and -'s are not necessarily equal.

Notes on the predictions in table 5.1

a) smaller vs. larger species

Under the neutral scenario (isolated populations), more resources (S+) or better resources (Q+) benefits either species. More variable resources (H+, with mean S and Q unaffected) has no overall effect, since deficits in low Q or S patches are offset by benefits in high Q or S patches.

Predicting the competitive responses of the species under varying S is more difficult. The negative correlation of S and Q must be ignored, and the basic effect of having more or less food is addressed under the neutral scenario. In the table, the larger species is predicted to benefit from reduced competition when S increases because the smaller species is less able to exploitatively reduce resource availability. The smaller species suffers increased competition because of the relatively greater population growth rate of the larger species.

When quality increases, the smaller species is able to consume more of the available resources, and therefore experiences a benefit and imposes a competitive cost on the larger species. Increases in heterogeneity benefit both species because there are more patches where they can escape competition.

The larger species experiences no costs or benefits associated with facilitation because this interaction depends only on the responses of the smaller species to resource modifications effected by the larger species. When the supply increases, the facilitation enjoyed by the smaller species increases because the larger species has a relatively greater impact. When quality increases, the high quality regrowth stimulated by the larger species' foraging is not so much better than ungrazed vegetation, and the facilitation effect is weaker. When resources are more variable, facilitation is stronger in some patches and weaker in others, producing no overall change in the interaction.

b) More selective and less selective species, both equal sized

Facilitation is likely to be very weak or non-existent among similar sized species, and no predictions are made. The neutral scenario has the same predictions as before. The outcomes under competition however are a mirror image of those for a smaller and larger species.

When S increases, it is more difficult to feed selectively, and the quality of the diet of the less selective species falls more rapidly than that of the more selective species. Conversely, when quality increases, the advantages of feeding selectively are reduced. Outcomes under varying heterogeneity are as before.

c) Fore-gut fermenter and hind-gut fermenter, both equal sized

Despite being of equal size, the bulk feeding strategy of the hindgut fermenter allows a facilitatory interaction to occur, with the same outcomes as for a smaller and a larger species. However, the strength of any facilitation is likely to be weak.

The response of the hind-gut fermenter in the neutral scenario under varying heterogeneity is different from all other species described. Hind-gut fermenters are more sensitive to food restrictions than other species, because of their fast throughput (relative to body size) and less complete digestion. They therefore suffer an unsymmetrical, intensified cost in patches with lower than average supply rates.

Under competition, the ability of the hind-gut fermenter to process large volumes of food gives it a competitive advantage when S increases. When S falls, the ability of the fore-gut fermenter to extract more nutrients from a restricted intake confers an advantage. When quality increases, the more complete digestion of fore-gut fermenters is less of an advantage, whereas the hind-gut strategy is more efficient at extracting nutrients rapidly from more digestible forage.

d) Utilization efficiency maximizer (UEM) vs. intake maximizer (IM), both equal sized

The interactions predicted here are identical to those between a more selective species and a less selective one. Facilitation has been allowed, but again is likely to be weak.

Predicting community responses to variable resources

Table 5.1 is intended as an aid to thinking about the complexities of the multiple interactions that can occur in ungulate communities. It is unrealistic to make predictions based on one interaction (*e.g.* facilitation) without taking into account the concurrent community responses occurring as a result of the others (*e.g.* competition and neutrality). Furthermore, table 5.1 does not indicate the relative magnitudes of responses, so that a negative response under one scenario and a positive response under another cannot be balanced against each other. What the table does is emphasise the complexity of community interactions and clarify the range of possible outcomes. Some form of synthesis can now be attempted by considering the range of community responses to changes in the three resource supply characteristics: supply rate, quality, and spatial heterogeneity.

Resource supply rate (S) and community dynamics

An increase in the supply rate of resources may lead to an increase in the prevalence of hind-gut fermenters. These species are limited in particular by the availability of forage. Larger species will also be able to occupy taller swards. Facilitation interactions can intensify because the larger species are supported, so that the abundance and diversity of smaller species becomes more strongly linked to the presence of larger, facilitating species. This interaction acts in opposition to the competitive disadvantage smaller species experience on taller swards.

Resource quality (Q) and community dynamics

Increased forage quality will have a strong influence on smaller species, allowing them to occupy swards that would otherwise provide food of too low digestibility. If a large proportion of the forage becomes available to the smaller species, they may even be able to capture the sward, competitively excluding larger species. Facilitation will reduce, but this is likely to be of secondary importance to the smaller species. Higher quality swards should also be more advantageous to hind-gut fermenters, if sward height is sufficient. These species digest their food less completely than fore-gut fermenters, and are therefore more sensitive to forage quality.

Resource heterogeneity (H) and community dynamics

When heterogeneity changes for two competing species, both gain a benefit if H increases, and both suffer a disadvantage if H decreases. When H increases, both competing species can escape to their preferred patch type, avoiding or reducing competition. When H decreases, any competitive interaction between the species becomes more intense, since there are fewer patches to which each species can escape.

If the two coexisting species are instead in a facilitatory interaction, then changes in H (up or down) have no overall effect on either species. Some patches will allow a stronger interaction, increasing the advantage to the recipient, whereas in other patches the strength of the interaction is weaker.

For hind-gut fermenters, increased heterogeneity increases the likelihood of encountering patches where food intake is limited by availability. The hind-gut strategy depends upon high intake rates, and therefore hind-gut fermenters are negatively impacted by increased heterogeneity. The major response of these species - principally zebras - is migration, which allows them to maintain high intake rates throughout the year.

Correlations among S, Q and H

In the real world, resource supply rates and quality are negatively correlated. Small species derive overall benefits from increases in resource supply, and overall disadvantages from decreases in quality. The competitive outcome of an increase in supply with a concomitant decrease in quality depends on how much the increased competition from larger species impacts upon the smaller species, and upon how sensitive the smaller species is to reduced quality forage. When resource supply increases and quality decreases, the larger species benefits both from the increased food supply (neutral interaction) and from reduced competition from the smaller species. The larger species suffers a cost of reduced quality under the neutral interaction, and therefore the limit to the increase in resource supply that benefits the larger species is set by its sensitivity to low quality forage. For the community as a whole, increased supply and decreased quality will see the abundance and diversity of larger species increase, and of smaller species decrease.

Ungulate ecologists have not discussed the impacts of any correlation between productivity and spatial heterogeneity. If Tilman's (1980, 1982, 1986) assumption is correct, then heterogeneity is negatively correlated to productivity and overall species richness should fall in productive habitats.

Table 5.2. Resource supply modifications and inter-specific responses to different foraging styles.

Feeding style	Modifications	Responses
1. large, generalist grazer e.g. buffalo	depletes biomass in tall swards	i. excluded from short swards by (4) ii. excluded from medium swards by (3) iii. not affected by (2)
2. medium, selective feeder e.g. topi	depletes quality in medium/tall swards	i. excluded by (4) ii. facilitated by (1) iii. excluded by (3)
3. medium, generalist grazer e.g. wildebeest or zebra	depletes biomass in medium/tall swards	i. excluded by (2) ii. excluded by (4) iii. facilitated by (1)
4. small, selective feeder e.g. Thomson's gazelle	maintains low biomass in short swards	i. facilitated by (1) and (3).

These considerations can be summarised in a matrix of expected inter-specific influences (table 5.3). The table shows the influence of the column species upon the row species (0 = no influence, - = competition, + = facilitation):

Table 5.3. Inter-specific competitive and facilitatory interactions.

	1. buffalo	**2. topi**	**3. wildebeest**	**4. Thomson's gazelle**
1. buffalo		0	-	-
2. topi	+		-	-
3. wildebeest	+	-		-
4. Thomson's gazelle	+	0	+	

These expected influences interact with the food resources supplied by the environment. Despite the fact that buffalo appear to suffer a negative or at best zero influence from all the other species, their ability to achieve a positive net energy intake on the most abundant but poor quality forages is sufficient to make buffalo an important if not dominant component of many herbivore assemblages. Conversely, Thomson's gazelle require unusually rich grazing to achieve a positive net energy intake, so that despite benefiting from facilitation by many species they never represent a large proportion of the herbivore biomass. However, by exploiting the left-overs (modified habitats) of a number of other species, Thomson's gazelle do achieve a presence in a great diversity of habitats across a large species range.

The predicted correlations in table 5.3 for individual species could be tested directly, but they ignore the important influence of resource supply dynamics. The foregoing discussion, and particularly the responses predicted in table 5.1, can be summarised in a set of predictions about how diverse communities of ungulates will respond to various changes in resource characteristics (table 5.4). This table provides the basis for the generation of a set of specific, testable hypotheses.

Table 5.4. Predicted responses of a community of herbivores to changes in resource characteristics (supply, quality and spatial heterogeneity).

Change in resources	Community responses
S +	Total abundance and biomass increase.
S -	Total abundance and biomass decrease.
Q +	Total abundance and biomass increase.
Q -	Total abundance and biomass decrease.
H +	Species richness increases, particularly in relatively unproductive habitat. Abundance of hind-gut fermenters decreases.
H -	Species richness falls. Abundance of hind-gut fermenters increases.
S + and Q -	Large-bodied abundance, biomass and diversity increase; small-bodied species decrease. Average body size increases. Diversity of small-bodied species is positively correlated to diversity of large-bodied species.
S - and Q +	Small-bodied species more abundant and diverse, large-bodied species less. Average body size decreases. Correlation of small-bodied species richness to large-bodied species richness diminishes or even becomes negative.

The predictions of table 5.4 and the preceding discussion can now be framed in a set of specific hypotheses designed to test some of the mechanistic theories of ungulate community organisation discussed in this thesis.

STATEMENT OF HYPOTHESES

H1. Herbivore biomass is correlated to vegetation productivity

This provides a baseline expectation. If confirmed, classical competition theory predicts that species richness should also be positively correlated to vegetation productivity, since species richness should increase with herbivore abundance. This contrasts with the predictions of resource competition theory (see H5). If herbivore biomass is positively correlated to vegetation productivity and species richness is not, then some other process (*i.e.* not classical competition) must be invoked to explain herbivore community dynamics.

Productivity and quality: the Bell-Jarman hypothesis

H2. Biomass of large herbivores is high, and of small herbivores is low, in productive, low quality swards

The quality and quantity of available forage are typically negatively correlated. In well developed swards, with a high biomass of mature, fibrous grass, larger animals are expected to predominate. The Bell-Jarman hypothesis predicts that larger species will prefer more productive swards, and smaller species will prefer higher quality, less productive swards.

H3. Typical body size is high in productive, low quality swards

This hypothesis is closely related to H2, placing the emphasis upon body size rather than on biomass in different body size classes. The Serengeti dataset allows several tests of this hypothesis, based on average body sizes of individuals or of species present.

H4. Species richness of large species is high, and of small species is low, in productive, low quality swards

This is a further test of the Bell-Jarman hypothesis, that well-developed swards are preferred habitat for large species.

H4A. Any increase in the diversity of larger species is due to increased numbers of larger animals on well developed swards. This would support the Bell-

Jarman idea that the food supply for larger animals increases more than that for small animals as the sward develops.

The resource-ratio hypothesis

H5. Species richness falls in productive, low quality swards

This provides a weak test of Tilman's model of competition, in that diversity is predicted to fall at high levels of productivity, rather than to increase as classical competition theory would predict.

H5A. Any observed reduction in diversity could also be explained if the number of individuals falls (*i.e.* herbivore biomass is concentrated in a smaller number of large animals). The Bell-Jarman hypothesis predicts that herbivore biomass will be concentrated in larger species as productivity increases (see H2, H3 and H4).

Facilitation

H6. On tall swards, the presence and abundance of smaller species depends on habitat modifications carried out by larger species

The idea of facilitation is that larger species deplete tall, low quality swards, stimulating the production of higher quality new growth that is suitable for smaller species. This hypothesis predicts a positive correlation between small and large species, on tall swards.

H6A. On short swards, the presence of large animals depends on the absence of smaller animals. A negative correlation between large and small animals is predicted.

Some further hypotheses not tested in this chapter

The south east plains during the wet season were chosen because of the very high density of grazers and the high consumption efficiency achieved by this aggregation (see *Methods*). Because of the season and study region chosen, insufficient quadrants were burned (generating heterogeneity) to allow testing of hypotheses 7 and 8. These two hypotheses would provide a more powerful test of resource-ratio theory. The index of spatial heterogeneity to be used for these tests was whether part of the quadrant had recently burned or not. Because the season chosen was the wet season, during which the grass is less likely to burn, and the high densities of grazing herbivores prevent the build-up of fuel to burn, there were in fact only 19 records (out of 1444) that indicated burning. If the analysis was extended to other parts of the ecosystem, these hypotheses could be tested.

H7. Increased spatial heterogeneity allows more species to coexist

This is a general expectation of classical competition theory. Spatial heterogeneity provides refuges from direct competition, therefore reducing the local rate of competitive exclusion.

H8. Increased heterogeneity will have a greater influence on species richness in unproductive habitat

This directly tests the resource-ratio theory of community dynamics. Tilman (1982) predicts that at low productivity, a limited range of variation in resource supply rates will have a large influence on the range of resource ratios existing in the habitat. This range of resource ratios can support a large diversity of species, albeit at low density.

METHODS

The Serengeti migratory ecosystem

The Serengeti-Mara ecosystem extends to some 25-35,000 km^2, bounded to the west by human populations on the eastern shore of Lake Victoria, and to the east by the Loliondo highlands and the Rift Valley. The ecosystem is traditionally defined as the region occupied by the migratory herds of wildebeest and other species (Murray 1995, McNaughton & Banyikwa 1995). These populations spend the wet season (November to May) concentrated on a region of short grass plains in the south east of the ecosystem. Around the time the rains end, the migratory wildebeest, together with significant populations of zebra and Thomson's gazelle, move westwards and northwards, dispersing into the woodlands and woody savannas in the north of the ecosystem (Pennycuick 1975, Maddock 1979, Murray 1995). These populations return to the south east plains in May, coinciding with the beginning of the next wet season and the first flush of new grass growth on the short plains.

There is a rainfall gradient across the ecosystem, with the northwest receiving over 1000 *mm* of rainfall annually, and the south east falling to below 400 *mm*. There is also a gradient in the pattern of rainfall. In the north and west, rainfall is more evenly spread throughout the year, with significant amounts of rain falling in the dry season (June to October). In the south east plains, rainfall is largely concentrated in the wet season months (Murray 1995) and rainfall and grass growth are virtually nil during the dry season (McNaughton & Banyikwa 1995).

The growth form of the grasses on the southern plains is typically short, because the grass develops during a restricted flush in the wet season. This rapid growth means that the grass has a high concentration of protein relative to the fibre content, and is therefore easily digestible and highly palatable (Murray & Illius 1996).

The migration onto the south east plains coincides with the beginning of a period of rapid grass growth. This increased food supply may explain the migratory movements, although it also seems that specific requirements for nutrients that are present in higher concentrations in the short plains swards may be important, especially for lactating females (Murray 1995, McNaughton & Banyikwa 1995).

Although the migratory movements of several species of ungulates onto the short grass plains are spectacular, several other species move onto the plains from surrounding areas during the wet season. Very few species remain resident year-round because of the lack of drinking water and the low rainfall and hence grass growth in the dry season. Resident ungulates rarely occur in regions of the ecosystem receiving less than about 700 *mm* rainfall annually (McNaughton & Banyikwa 1995).

Data source

During 1969, 1970, 1971 and 1972, the Serengeti Ecological Monitoring Programme (SEMP) carried out monthly reconnaissance flights, surveying animal populations and vegetation parameters for the entire Serengeti ecosystem (K. Campbell, M. Murray *pers. comm.*, S. Huish *in litt.*). The data from these flights were originally used to describe the Serengeti migration, but since their acquisition very few analyses have been carried out on the data. Indeed, the data were almost lost when it was found that the original magnetic tapes that contained the transcribed data could no longer be read by modern computers. However, the computer coding forms used to enter the data onto the tapes were located, and were used in a repeat exercise in the late 1980's to enter the data back into computerised form. The original raw data no longer existed, and indeed now the computer coding forms have been lost as well.

Despite these travails, the database is almost entirely complete, missing only the first two flights. No recces were flown in Sep 1970, Dec 1971, Feb and Apr 1972, and so data exist for the following months:

1969:								Aug,	Sep,	Oct,	Nov,	Dec
1970:	Jan,	Feb,	Mar,	Apr,	May,	Jun,	Jul,	Aug,		Oct,	Nov,	Dec
1971:	Jan,	Feb,	Mar,	Apr,	May,	Jun,	Jul,	Aug,	Sep,	Oct,	Nov	
1972:	Jan,		Mar,		May,	Jun,	Jul,	Aug				

No detailed account of the methods employed for the recces has been found. A brief description of the flights is appended to the data files (Huish 1989 *in litt.*). Each month, several aircraft took part in the surveys, following flight paths along the grid lines used by SEMP to map the ecosystem. Each grid cell is 10 x 10km, and observations were recorded for each 5 x 5 *km* quadrant of each grid cell. Animal species abundance estimates were recorded as classes.

Abundance class	**Abundance range**
1	1 - 25
2	26 - 250
3	251 - 2500
4	2501 +
5	not specified

In addition to the species abundances, vegetation conditions were recorded. For each quadrant, burnt and unburnt ground were treated separately. Estimates were made of the percent of the quadrant burnt, how long ago the burn occurred, the height of regrowth and the height of unburnt vegetation, and the greenness of both regrowth and unburnt vegetation.

A further extensive database of monthly rainfall records during the survey period from a large number of rain gauges situated throughout the Serengeti ecosystem is also available, although not used in the current analysis.

The above information was compiled from a summary of what is known about the recce flights (Huish 1989 *in litt.*), and from information supplied by Ken

Campbell, who managed the re-entering of the data onto computer in the late 1980's (K. Campbell *pers. comm.*). Because so little is known about the data, references in the literature to the data have been summarised in appendix 5.1.

Data extraction

The complete database consists of 33 files, one for each survey. These were restructured and combined into a single file containing 42,982 records. Each record stores data on the vegetation parameters and animal counts described above, indexed by recce date and grid square & quadrant. Records for grid square quadrants within the study area (the south-east plains within the bounds of the Serengeti National Park) and the study season (wet season - November to May inclusive) were extracted for analysis, reducing the database to 1,452 records. Of these records, only three recorded a vegetation height class of 5. These records were removed. Five of the remaining records contained cattle, and these records were also removed. Three of the remaining records showed evidence of human activity (two with bomas and one with cultivation) but these records were not removed. The final database therefore consisted of 1,444 records, covering 2,875 km^2 in 115, 5x5 km quadrats, each quadrat surveyed an average of 12.6 times (minimum 8) during three consecutive wet seasons (1969/70, 1970/71 & 1971/72).

Analyses

Definitions of variables

Vegetation height is scored in the database as the *height of regrowth* for burnt ground, and *height of unburnt grass* for unburnt ground: 0 = bare ground; 1 = short; 2 = short & medium; 3 = medium; 4 = medium & long; 5 = long. The proportion of burnt ground in the quadrat is scored as: 0 = none burnt; 1 = 0-25% burnt; 2 = 25-50% burnt; 3 = 50-75% burnt; 4 = 75-100% burnt; 5 = 100% burnt. The algorithm used to estimate **vegetation biomass** within a quadrant is:

vegetation biomass = (percent burnt) x (height of burnt) +
(percent unburnt) x (height of unburnt)

where the % burnt scores are taken as: 0 - 1 = 0%; 1 - 2 = 20%; 2 - 3 = 40%; 3 - 4 = 60%; 4 - 5 = 80%; 5 = 100%

Greenness is derived from the greenness scores in the database. A greenness score is recorded for burnt and unburnt grass in each quadrat. These scores are: 0 = dry and parched; 1 = few green patches; 2 = poor flush; 3 = good flush; 4 = lush. The algorithm for greenness is:

greenness of quadrant = (percent burnt) x (greenness of burnt) + (percent unburnt) x (greenness of unburnt)

and the contributions of burnt and unburnt grass are scored as for vegetation biomass.

In fact, only 19 quadrants in the extracted data had been burned, because the study was restricted to the wet season, when fuel cannot accumulate because the migratory ungulate herds continually graze it down, and because the grass is not dry.

Herbivore biomass was estimated by multiplying the body size of each species present by the mid-point of the abundance class, then summing over all species present.

Mean body size was calculated as the mean of ln(body size) of those species present in the quadrant (*i.e.* not weighted by the relative abundances of species):

$$\text{mean body size} = \frac{1}{SpR}\sum_{i=1}^{SpR}\ln(W_i).$$

Weighted mean body size is mean body size weighted by abundance:

$$\text{weighted mean body size} = \frac{\text{herbivore biomass}}{\text{total abundance}}$$

Species richness, herbivore biomass, and abundance were calculated for all species, and within body size classes. Two body size classifications were used: small, medium, large & mega and smaller & larger (see figure 5.1).

Hypothesis testing

Vegetation biomass is recorded as ordinal classes, and therefore hypotheses relating a variable to vegetation height were tested using ANOVA, with vegetation biomass class as the factor. Differences between classes were assessed using *post-hoc* Tukey pairwise contrasts (Zar 1996) because competing hypotheses make different predictions about differences between vegetation height classes. *Post-hoc* tests allow every possible comparison to be made (in this case, the variable value in each vegetation height class is compared to all other height classes). This is less powerful than testing *a priori* hypotheses, where only a subset of comparisons is of interest. An overall probability of 0.05 that any one of these comparisons falsely indicates a significant difference from random (type I error) was chosen. With five vegetation classes, there are 10 pairwise comparisons, and each comparison must have a type I error rate < 0.00642 to satisfy the overall type I error rate of < 0.05. *A priori* testing would be more powerful because the hypothesis itself rejects a number of the possible comparisons.

ANCOVA was used to test whether the relationship between the abundance (or biomass, or species richness) of smaller species and larger species changes according to the vegetation height class of the quadrant (H6: facilitation). ANCOVAs (including pairwise *post-hoc* Tukey tests) were programmed into Excel 97 worksheets (Microsoft Corporation 1997), using formulae in Sokal & Rohlf (1995, box 14.9) and Zar (1996, table 17.1) for unbalanced designs. For ANOVA and ANCOVA analyses, unbalanced designs were used because the sample sizes varied among the vegetation height classes. Non-parametric correlations, Chi-square tests, ANOVAs and Tukey pairwise comparisons in ANOVAs were carried out using Minitab release 12.1 software (Minitab Inc. 1998).

RESULTS

Body size classes

Figure 5.1 shows the body size distribution of Serengeti herbivores. An arbitrary classification of body sizes is indicated. A second classification of "smaller" (= small & medium) and "larger" (= large & mega) is also used in the analyses. Body sizes were obtained from the literature as documented in chapter 4 (appendix 4.1).

Vegetation quality

The aerial surveys provide estimates of vegetation greenness as well as height. Greenness scores were positively correlated with vegetation height (figure 5.2), as indicated by a Chi-square test and non-parametric correlation. Greenness scores therefore cannot be used directly as an index of vegetation quality. The data are ordinal, and therefore regression analysis (allowing residuals to be used to measure quality) is inappropriate.

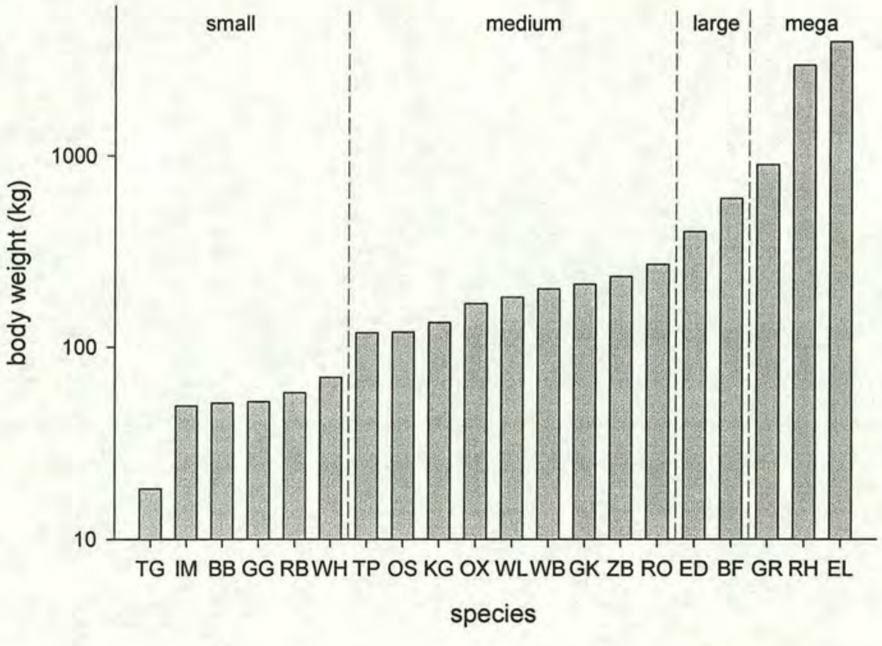


Figure 5.1. Body size distribution of Serengeti herbivores. Data from various sources. Arbitrary classification of body sizes is indicated. A second classification into 'smaller' (small and medium) and 'larger' (large and mega) was also used. Species codes: TG - Thomson's gazelle; IM - impala; BB - bushbuck; GG - Grant's gazelle; RB - reedbuck; WH - warthog; TP - topi; OS - ostrich; KG - kongoni; OX - oryx; WL - wildebeest; WB - waterbuck; GK - greater kudu; ZB - zebra; RO - roan; ED - eland; BF - buffalo; GR - giraffe; RH - rhino; EL - elephant.

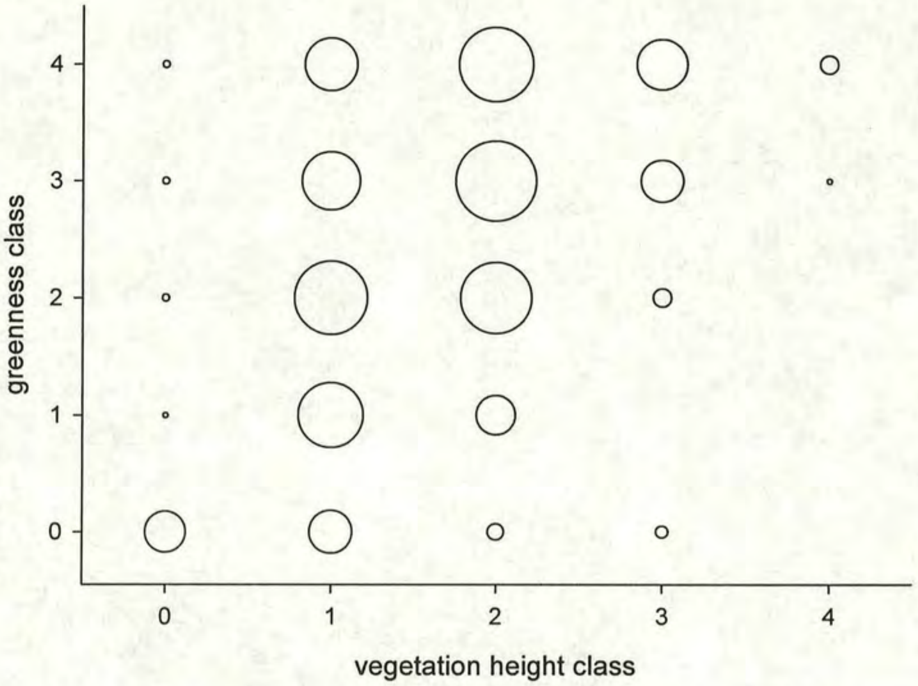


Figure 5.2. Greenness scores do not provide an independent estimate of vegetation quality. Circles are proportional to the square root of the number of quadrants recorded with the particular vegetation height and greenness class. The positive association between vegetation class and greenness class is tested with a Chi-square test and a Spearman rank correlation coefficient. One cell with a greenness score of 5 was omitted from the analysis.

Chi-Square Test

Expected counts are printed below observed counts:

		greenness score					
		G0	G1	G2	G3	G4	Total
vegetation height score	VH0	57	1	2	2	2	64
		5.85	8.52	15.79	17.30	16.54	
	VH1	61	139	176	113	93	582
		53.24	77.44	143.58	157.30	150.44	
	VH2	9	52	167	215	182	625
		57.17	83.16	154.19	168.92	161.56	
	VH3	5	0	11	59	85	160
		14.64	21.29	39.47	43.24	41.36	
	VH4	0	0	0	1	11	12
		1.10	1.60	2.96	3.24	3.10	
	Total	132	192	356	390	373	1443

Chi-Square = 779.368, d.f. = 16, $P << 0.001$ (5 out of 25 cells have expected frequencies < 5, which is borderline acceptable according to Sokal & Rohlf, 1995). There is a non-random association between the two categories. The association is positive: the Spearman rank correlation coefficient between vegetation height class and greenness class is $r_s = 0.467$, $n = 1444$, $P << 0.001$. Note that *n* varies between the two tests because a single quadrant with a greenness score of 5 was excluded from the Chi-square analysis.

Hypothesis testing

H1. Herbivore biomass is positively correlated to vegetation productivity

Figure 5.3 suggests that herbivore biomass in fact falls with increasing vegetation height, except in height class 0. Height class 0 indicates almost bare ground, and it is therefore not surprising that herbivore biomass should be low.

Variation in herbivore biomass classes is significant (one-way ANOVA: F = 4.93, d.f. = 4, P = 0.001). However, pairwise unplanned comparisons indicate that the only significant differences are that herbivore biomass in height classes 1 and 2 is higher than in height class 0.

Figures 5.4 and 5.5 show that herbivore abundance and biomass both predict species richness.

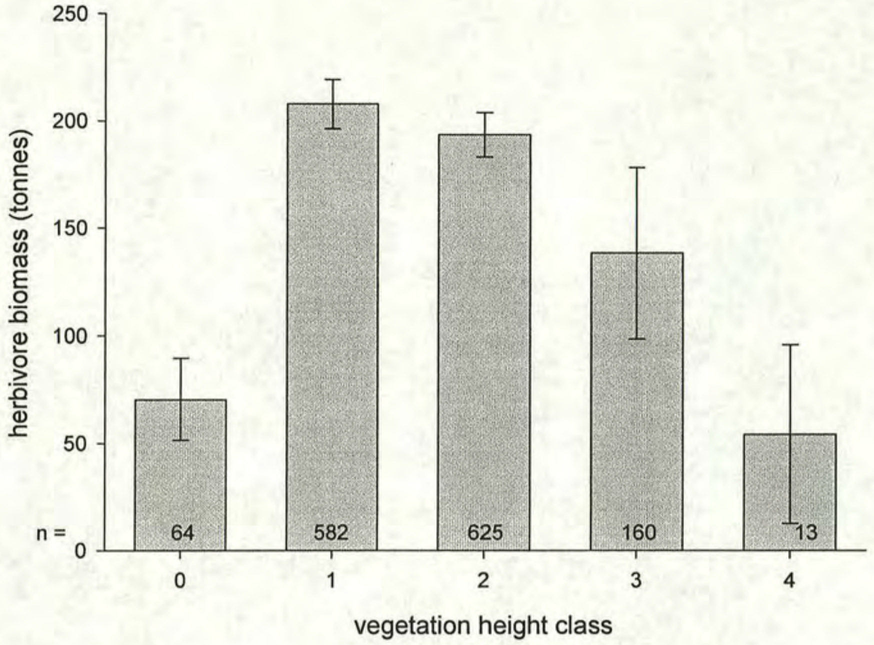


Figure 5.3. Herbivore biomass is not positively correlated to vegetation biomass. Variation in herbivore biomass among vegetation height classes is significant (F = 4.93, d.f. = 4, *n* = 1444, P = 0.001). The only significant differences are that herbivore biomass in height class 0 is significantly lower than in height classes 1 and 2 (Tukey unplanned pairwise comparisons, family error rate = 0.05, individual error rate = 0.00642). Error bars represent +/- 1 s.e.

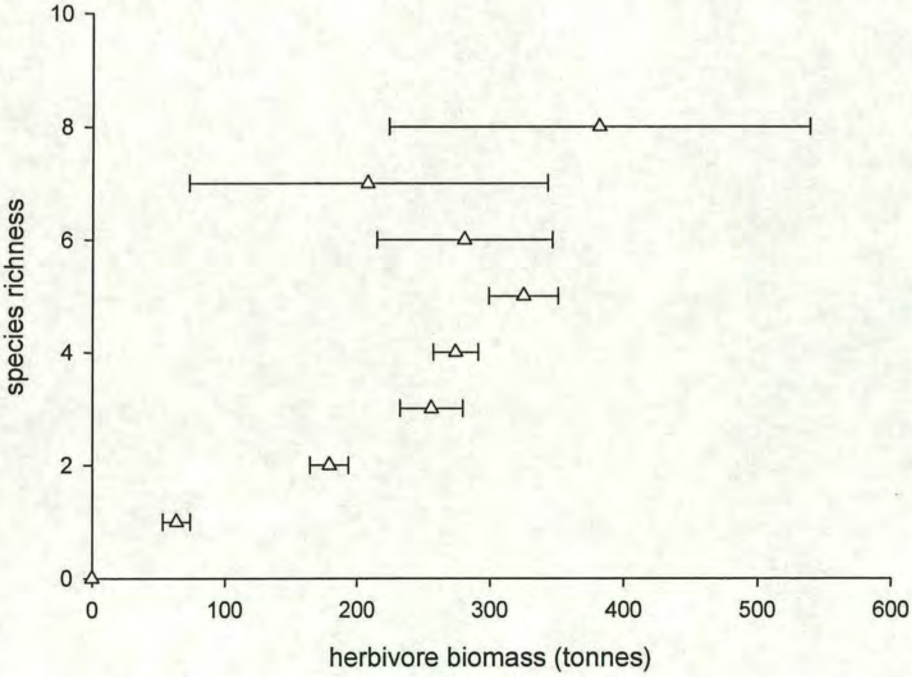


Figure 5.4. Herbivore biomass predicts species richness. Spearman rank correlation coefficient = 0.817, *P* = 0.007, *n* = 9. Excluding (0,0) and the 3 data with wide error bars (due to low sample sizes of 21, 3 and 3): $r_s = 1.000$. Error bars represent +/- 1 s.e.

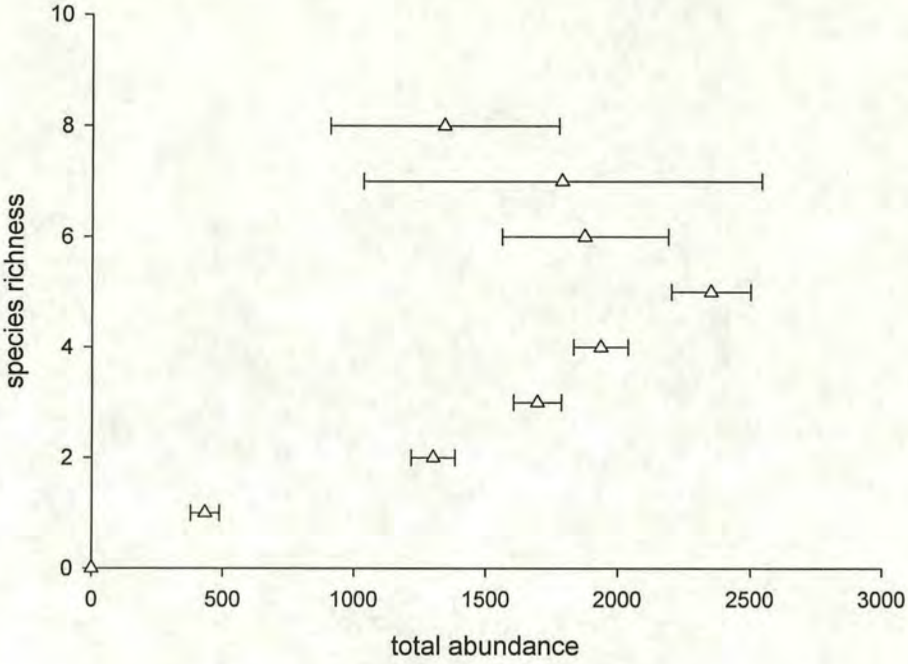


Figure 5.5. Herbivore abundance predicts species richness. Spearman rank correlation coefficient = 0.600, $P = 0.088$, $n = 9$. Excluding (0,0) and the 3 with wide error bars (due to low sample sizes of 21, 3 and 3): $r_s = 1.000$. Error bars represent +/- 1 s.e.

H2. Biomass of large herbivores is high, and of small herbivores is low, in productive, low quality swards

This tests the Bell-Jarman hypothesis that large herbivores are adapted to tall, poor quality swards, and small herbivores to short, high quality swards.

Figures 5.6a and 5.6b show the relationship between vegetation height class and herbivore biomass in 4 body size classes. Figure 5.6b repeats the data of figure 5.6a in a different format. Figures 5.7a and 5.7b show the data when analysed for two body size classes.

Vegetation height classes 1 to 4 represent a gradient of increasing vegetation biomass and decreasing quality or digestibility. Height class 0 is separate from this gradient, as it represents a barren state, with virtually no vegetation. Any vegetation that is present is likely to be of very low quality. These quadrants have experienced extremely heavy grazing, and only the most indigestible material is left behind.

Within vegetation height classes 1 to 4, figure 5.6b shows that small and medium sized ungulate biomass falls as vegetation height rises. Conversely, large and mega herbivores become more dominant. Figure 5.7b shows the same pattern, with body sizes classed as 'smaller' or 'larger'. Table 5.5 summarises the significant differences in biomass within body size classes, between vegetation height classes, as shown in figures 5.6a and 5.7a. Ignoring vegetation height class 0, it is clear that smaller size classes have lower biomasses in the taller vegetation classes, and that the larger size classes have higher biomasses in the taller vegetation classes.

An alternative explanation for the trend could be that as vegetation height increases, smaller species become less visible to aerial observers. However, this does not explain the increase in large and mega herbivore biomass as seen in figure 5.6a, and seems unlikely for medium sized (119 to 270 *kg*) animals.

Small herbivore biomass appears to increase in vegetation height class 4 in figure 5.6b. However, this increase in the proportion of the biomass contributed by small species is due to the lack of any large herbivores in this height class, and to the low total biomass in vegetation height class 4 (see figure 5.3). Figure 5.6a shows that small herbivore biomass is in fact at a minimum in height class 4.

The lack of large herbivores in height class 4 is anomalous. This may in part be due to the inclusion of only two species in this class (eland and buffalo - see figure 5.1).

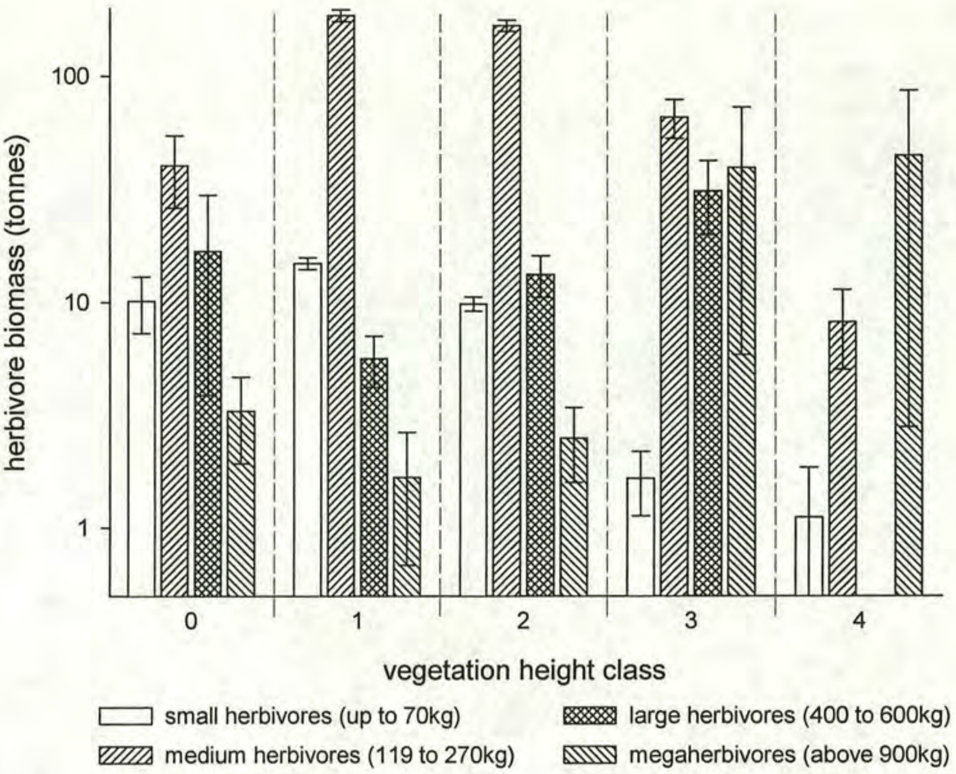


Figure 5.6a. Variation in herbivore biomass in four body size classes with vegetation height class. Error bars represent +/- 1 s.e.

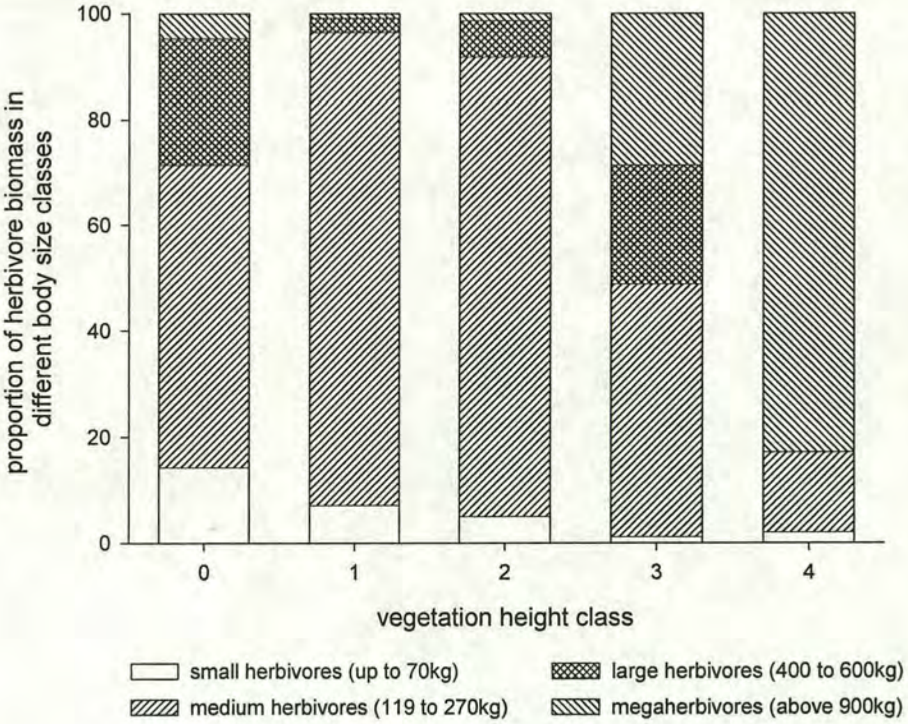


Figure 5.6b. Variation in the proportion of herbivore biomass in four body size classes with vegetation height class.

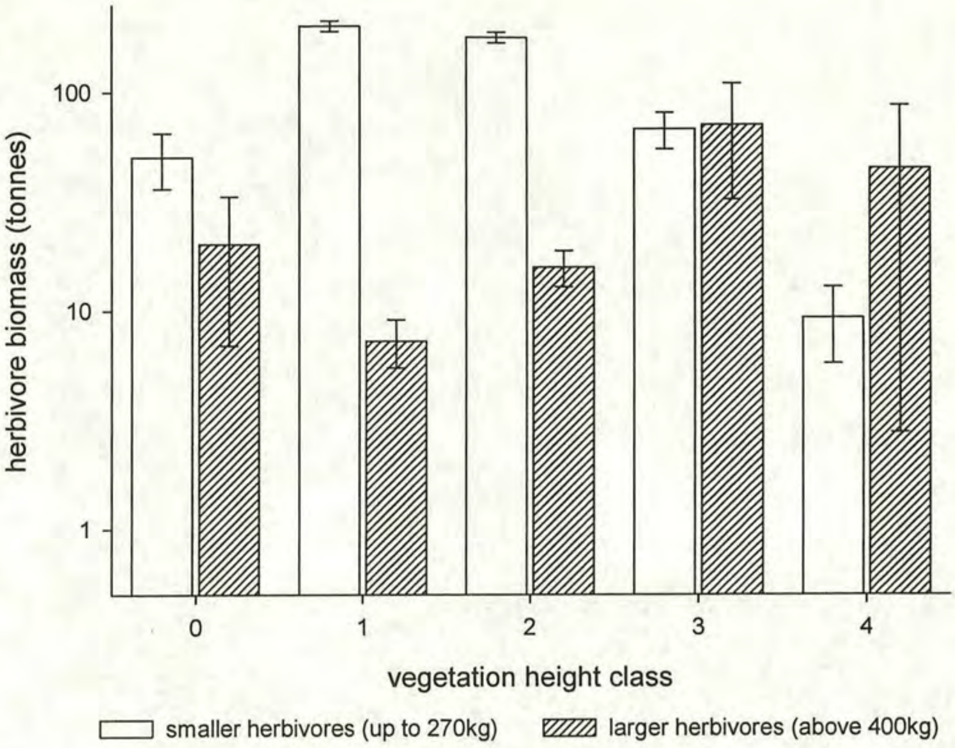


Figure 5.7a. Variation in herbivore biomass in two body size classes with vegetation height class. Error bars represent +/- 1 s.e.

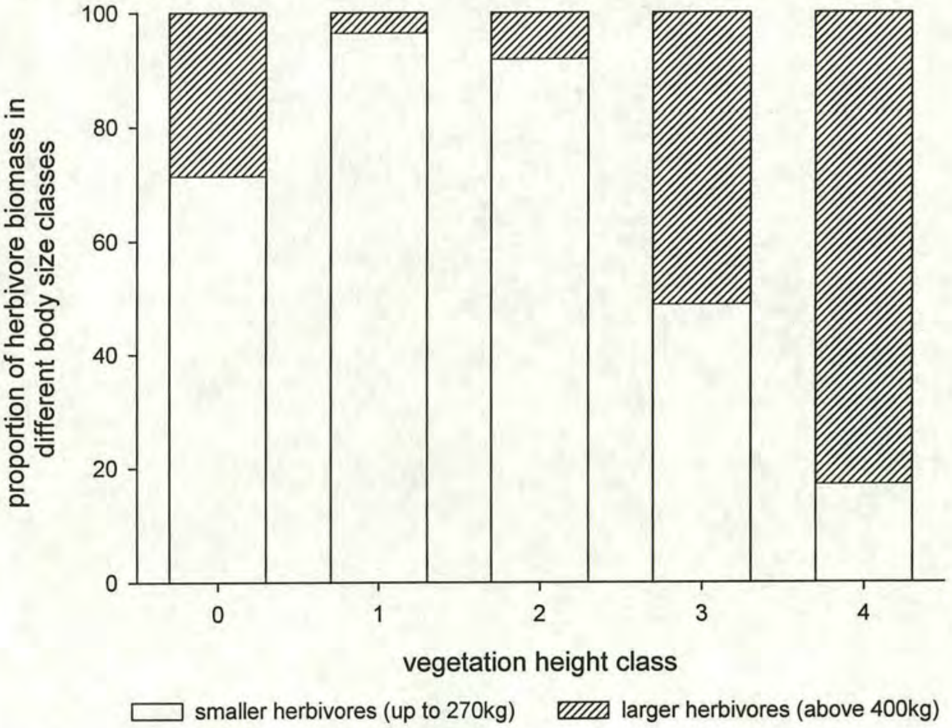


Figure 5.7b. Variation in the proportion of herbivore biomass in two body size classes with vegetation height class.

Table 5.5. Significant differences in herbivore biomass within body size classes, between vegetation height classes. Two classifications of herbivore body size were used: one of four classes (small, medium, large and mega, see figure 5.1) and 'smaller' (= small & medium) or 'larger' (= large & mega). An entry in the table identifies the body size class for which biomass is lower in the column vegetation height class than the row vegetation height class. Each body size class was analysed in a separate one-way ANOVA. Significance of differences was assessed using Tukey pairwise unplanned comparisons, with family error rate = 0.05 (individual error rate = 0.00642).

		lower herbivore biomass				
		VH0	**VH1**	**VH2**	**VH3**	**VH4**
higher herbivore biomass	**VH0**				small	
	VH1	medium smaller		small	small medium smaller	smaller
	VH2	medium smaller			small medium smaller	
	VH3		large mega larger	large mega larger		
	VH4					

H3. Typical body size is high in productive, low quality swards

'Typical' body size can be measured in several ways - species richness of different body size classes, mean body size of species present, or mean body size of individuals present. An inverse measure can also be used, counting the number of animals per unit herbivore biomass.

In figures 5.8a and 5.8b, species richness in different size classes is compared across vegetation height classes (four body size classes in figure 5.8a, and two size classes in figure 5.8b). Table 5.6 summarises the significant differences in species richness within body size classes, between vegetation height classes, as shown in figures 5.8a and b. Again ignoring vegetation class 0, larger and mega herbivores show higher species richness in taller vegetation classes, while small, medium and smaller size classes show reduced species richness in the taller vegetation classes.

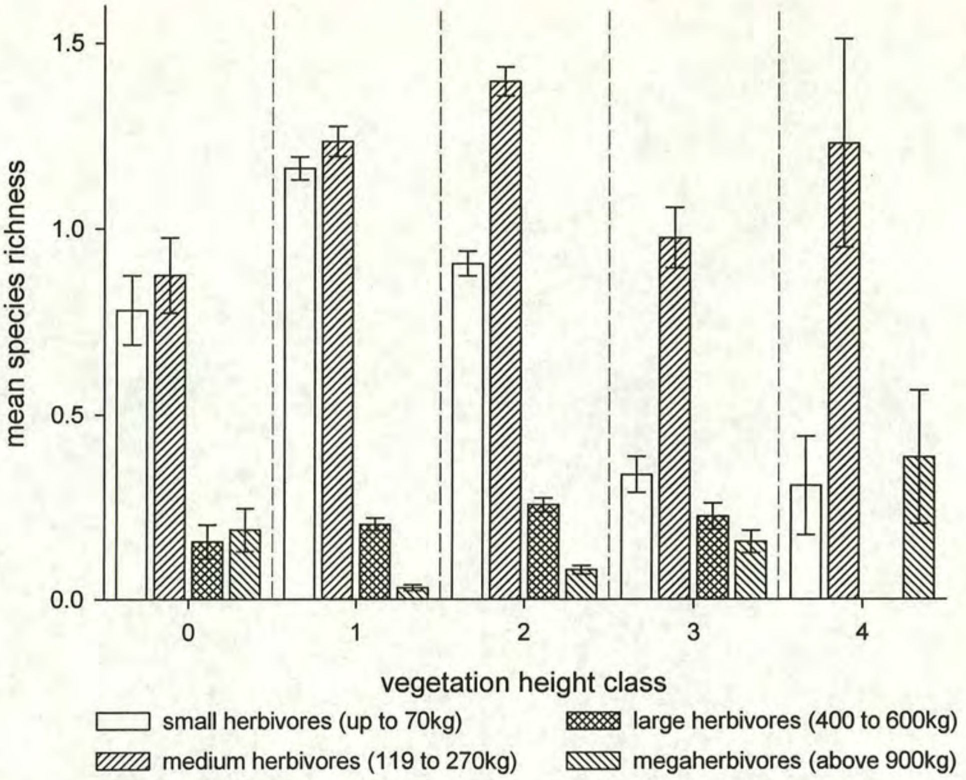


Figure 5.8a. Variation in herbivore species richness in four body size classes with vegetation height class. Error bars represent +/- 1 s.e.

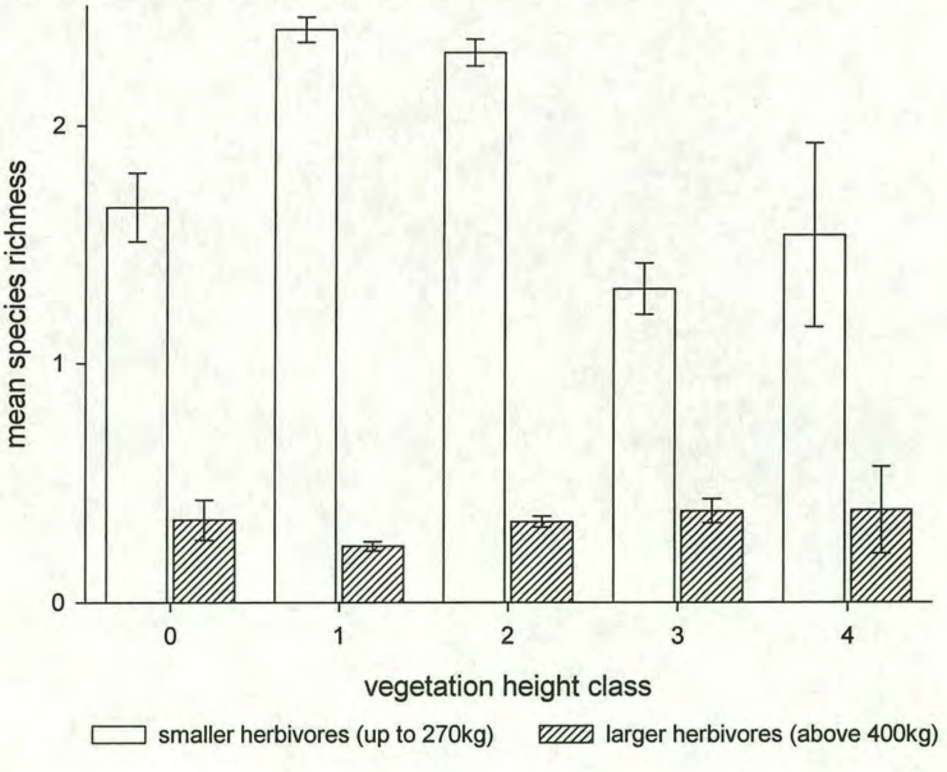


Figure 5.8b. Variation in herbivore species richness in two body size classes with vegetation height class. Error bars represent +/- 1 s.e.

Table 5.6. Significant differences in herbivore species richness within body size classes, between vegetation height classes. Two classifications of herbivore body size were used: one of four classes (small, medium, large and mega, see figure 5.1) and 'smaller' (= small & medium) or 'larger' (= large & mega). An entry in the table identifies the body size class for which species richness is lower in the column vegetation height class than the row vegetation height class. Each body size class was analysed in a separate one-way ANOVA. Significance of differences was assessed using Tukey pairwise unplanned comparisons, with family error rate = 0.05 (individual error rate = 0.00642).

		lower herbivore species richness				
		VH0	**VH1**	**VH2**	**VH3**	**VH4**
higher herbivore species richness	**VH0**		mega	mega	small	
	VH1	small medium smaller		small	small medium smaller	small
	VH2	medium smaller	medium mega larger		small medium smaller	small
	VH3		mega larger	mega		
	VH4		mega	mega	mega	

Mean body sizes of species and individuals present are shown in figures 5.9a and 5.9b respectively. There is no support for the hypothesis that mean body size should increase with vegetation height.

The figures are very similar because the expected mean body size of individuals is the same as the mean body size of species. This is a consequence of using look-up tables to convert abundance classes into abundance values. The real world variation that could potentially lead to mean body sizes of species differing from mean body sizes of individuals is lost because only five different abundance values are possible. Figure 5.9c shows the relationship between mean body size for species and for individuals in the data set.

Figure 5.10 and table 5.7 show that the number of individuals per tonne of herbivore biomass falls in taller swards, as predicted by the Bell-Jarman hypothesis.

$$\text{mean body size (species)} = \frac{1}{SpR}\sum_{i=1}^{SpR}\ln(W_i)$$

$$\text{mean body size (individuals)} = \frac{1}{N}\sum_{j=1}^{N}\ln\left(W_j\right)$$

$$= \frac{1}{N}\sum_{i=1}^{SpR}A_i\ln\left(W_i\right)$$

However,

$$E\left(\frac{A_i}{N}\right) = \frac{1}{SpR}\sum_{i=1}^{SpR}\frac{A_i}{N} = \frac{1}{SpR}\frac{1}{N}N = \frac{1}{SpR}$$

and E[mean body size (individuals)] = mean body size (species)

$SpR =$ no. of species present in the quadrat
$A_i =$ abundance of species i
$N =$ total abundance
$W_i =$ body size (*kg*) of species i

A is taken from a lookup table of abundance scores:

abundance score	*A*
0	0
1	12.5
2	138
3	1375.5
4	3000

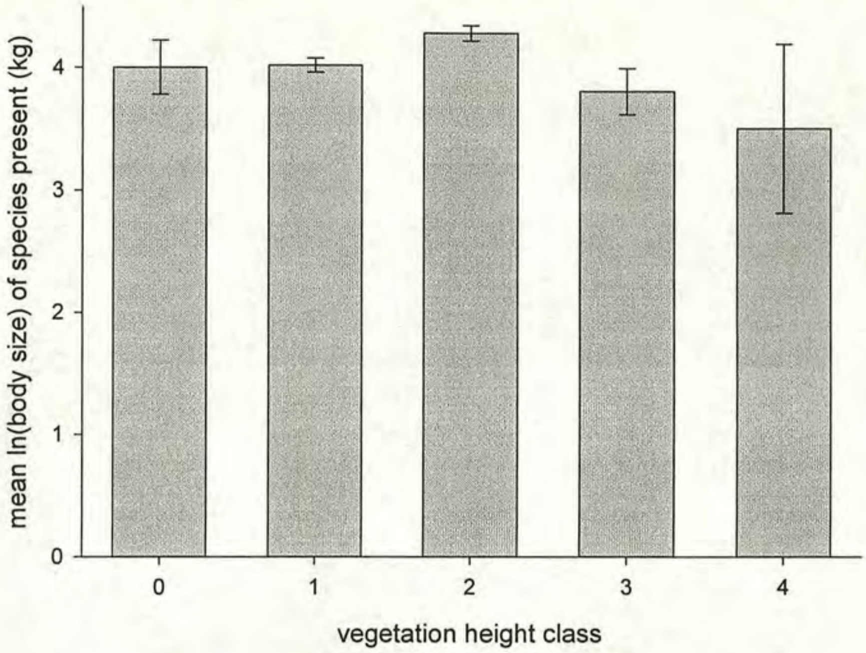


Figure 5.9a. Mean body size of species present in a quadrant varies with vegetation height (one-way ANOVA: F = 4.09, d.f. = 4, n = 1444, P = 0.003). Tukey pairwise unplanned comparisons show that mean body size of species is higher in vegetation height class 2 than in classes 1 or 3 (family error rate = 0.05, individual error rate = 0.00642). Error bars represent +/- 1 s.e.

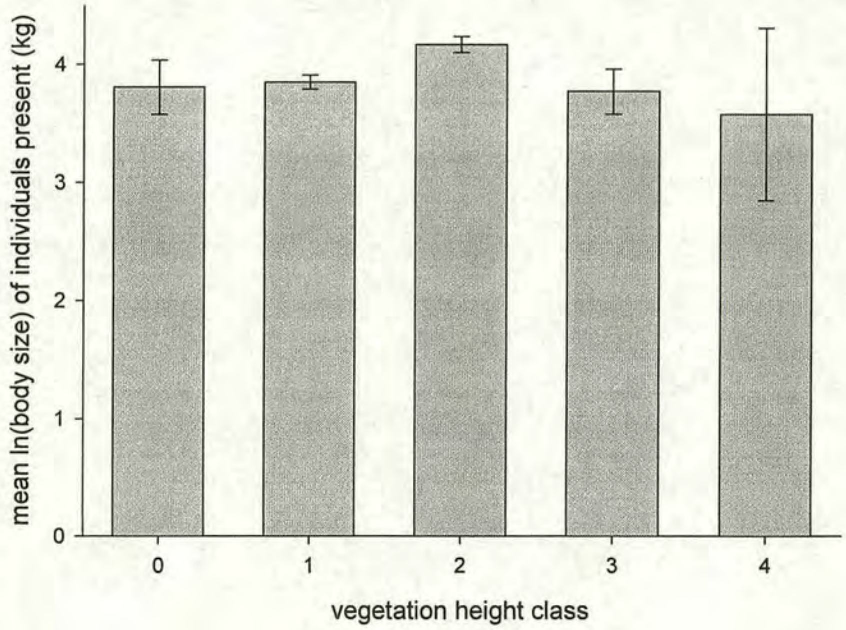


Figure 5.9b. Mean body size of individuals present in a quadrant varies with vegetation height (one-way ANOVA: F = 10.84, d.f. = 4, n = 1444, P = 0.005). Tukey pairwise unplanned comparisons show that mean body size of species is higher in vegetation height class 2 than in class 1 (family error rate = 0.05, individual error rate = 0.00642). Error bars represent +/- 1 s.e.

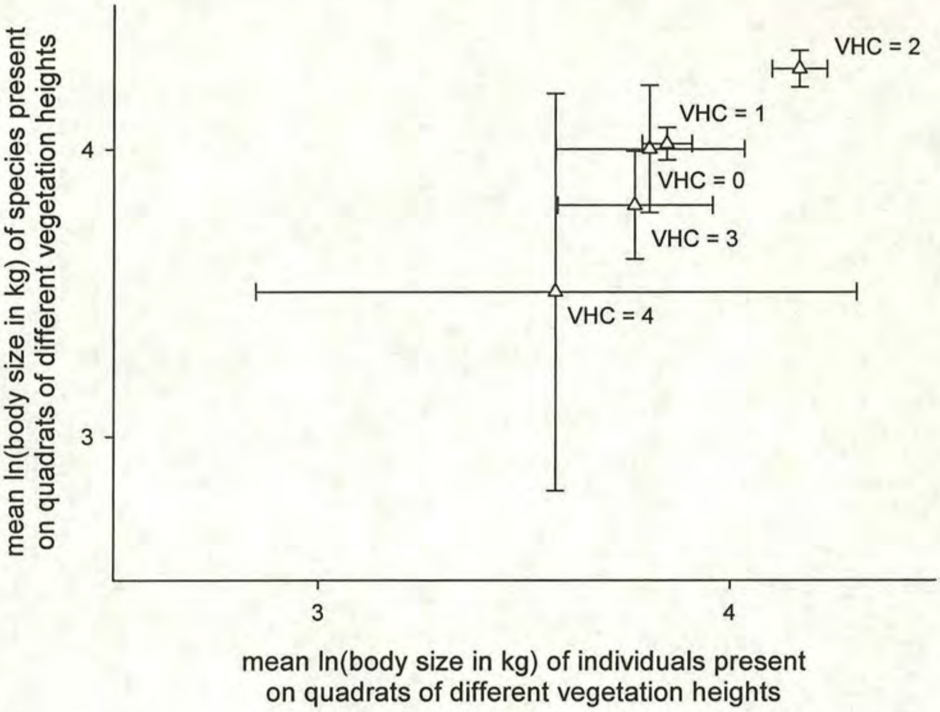


Figure 5.9c. Mean body sizes of individuals and species present in quadrants varying in vegetation height class are highly correlated (*r* = 0.948, *n* = 5, P = 0.0141). VHC = vegetation height class. The closeness of the correlation is probably an anomaly of the data preparation (see text). Error bars represent +/- 1 s.e.

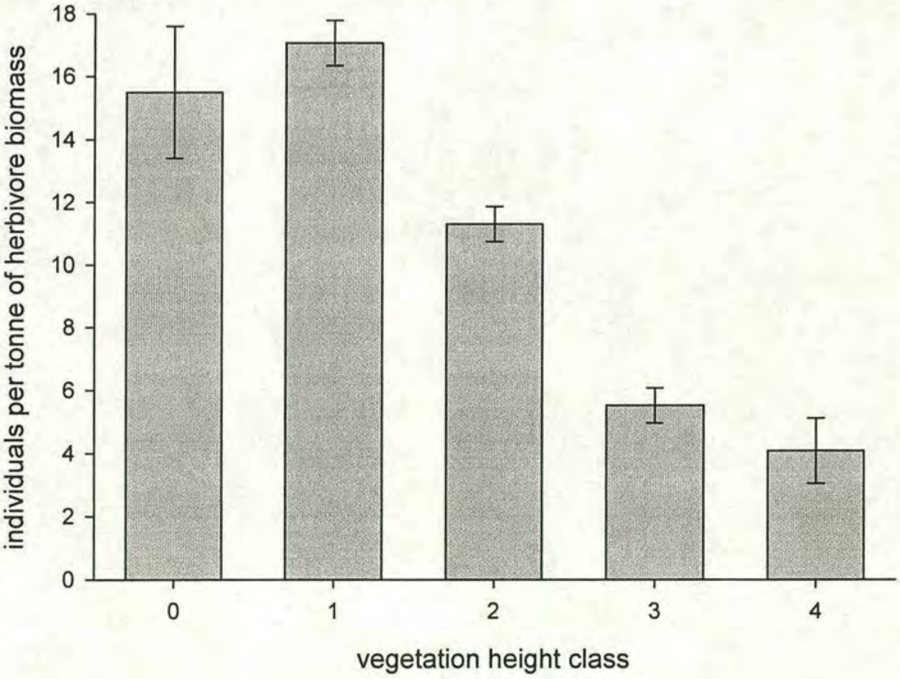


Figure 5.10. Individuals per tonne of herbivore biomass falls in tall swards (one-way ANOVA: F = 24.24, d.f. = 4, *n* = 1444, P << 0.001. Tukey pairwise unplanned comparisons are summarised in table 5.7. Error bars represent +/- 1 s.e.

Table 5.7. Significant differences in the number of individuals per tonne of herbivore biomass, between vegetation height classes. Significance of differences was assessed using Tukey pairwise unplanned comparisons, with family error rate = 0.05 (individual error rate = 0.00642).

		fewer individuals per tonne				
		VH0	**VH1**	**VH2**	**VH3**	**VH4**
more individuals per tonne	**VH0**				X	
	VH1			X	X	X
	VH2				X	
	VH3					
	VH4					

H4. Species richness of large species is high, and of small species is low, in productive, low quality swards

Figures 5.8a and b and table 5.6 have already shown that species richness in larger body size classes increases, and in smaller body size classes decreases, in taller swards.

To investigate whether this variation in species richness is due to changes in abundance, figures 5.11 and 5.12 plot abundance of herbivores in different body size classes against vegetation height classes. Figures 5.11a and b show the data for the four body size classes, and figures 5.12a and b for the 'smaller' and 'larger' classes. Table 5.8 summarises the significant differences in abundance within body size classes, between vegetation height classes, as shown in figures 5.11 and 5.12. Ignoring vegetation class 0 (for reasons discussed above), the smaller size classes (small, medium and 'smaller') are less abundant in the taller swards than in the shorter, and the larger size classes are less abundant in the short swards than in the longer swards of vegetation height class 3. Changes in abundance, as predicted by the Bell-Jarman hypothesis, explain the observed variation in species richness within body size classes, between vegetation height classes.

Table 5.8. Significant differences in herbivore abundance within body size classes, between vegetation height classes. Two classifications of herbivore body size were used: one of 4 classes (small, medium, large and mega, see figure 5.1) and 'smaller' (= small & medium) or 'larger' (= large & mega). An entry in the table identifies the body size class for which abundance is lower in the column vegetation height class than the row vegetation height class. Each body size class was analysed in a separate one-way ANOVA. Significance of differences was assessed using Tukey pairwise unplanned comparisons, with family error rate = 0.05 (individual error rate = 0.00642).

		lower herbivore abundance				
		VH0	**VH1**	**VH2**	**VH3**	**VH4**
higher herbivore abundance	**VH0**				small	
	VH1	medium smaller		small smaller	small medium smaller	small smaller
	VH2	medium smaller			small medium smaller	smaller
	VH3		large mega larger	mega larger		
	VH4					

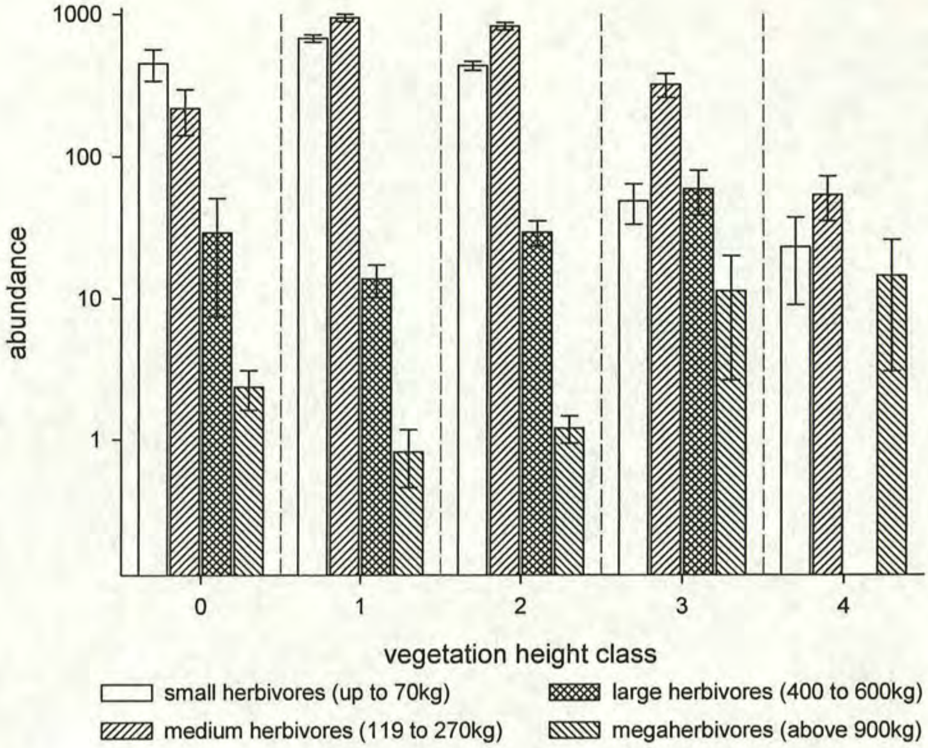


Figure 5.11a. Abundance of herbivores in four body size classes in quadrants of varying vegetation height. Error bars represent +/- 1 s.e.

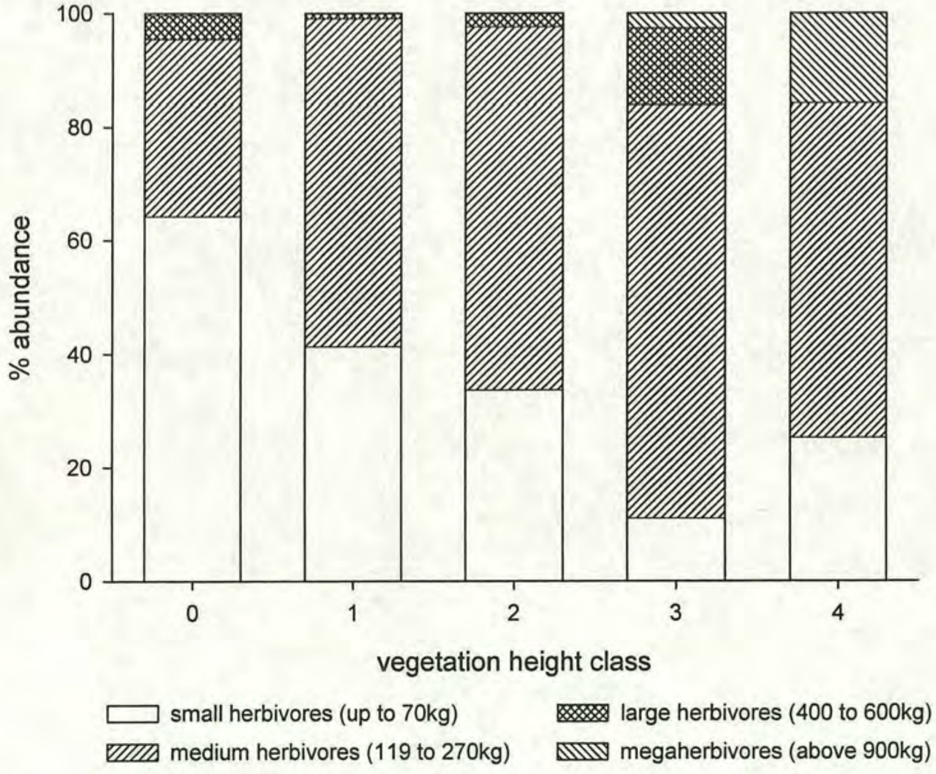


Figure 5.11b. Proportion of the total abundance of herbivores in four body size classes in quadrants of varying vegetation height.

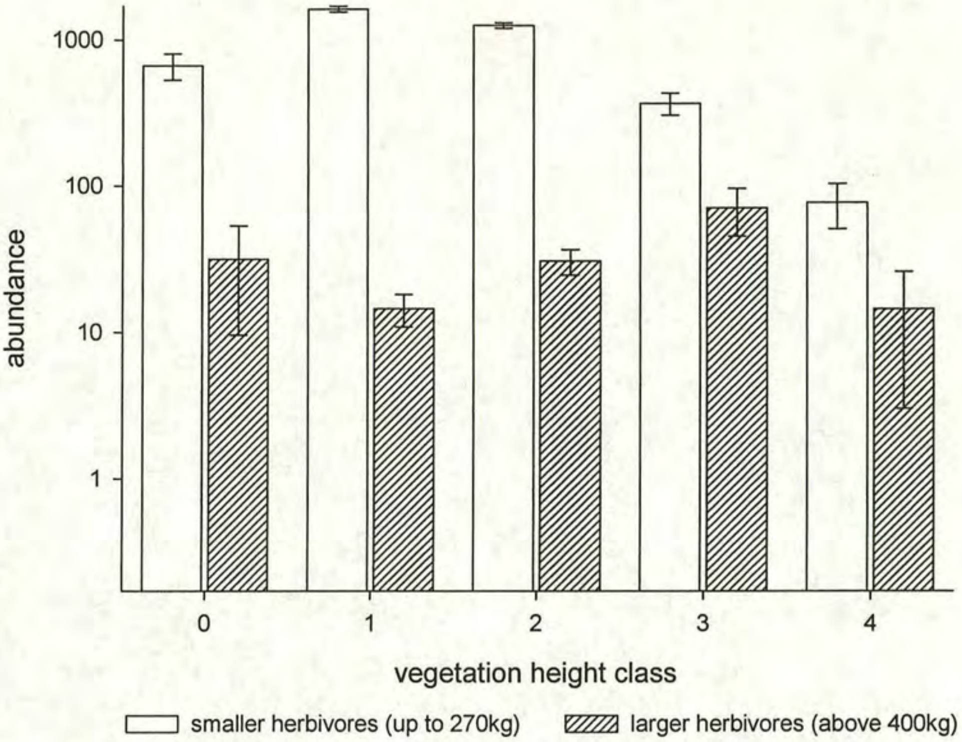


Figure 5.12a. Abundance of herbivores in two body size classes in quadrants of varying vegetation height. Error bars represent +/- 1 s.e.

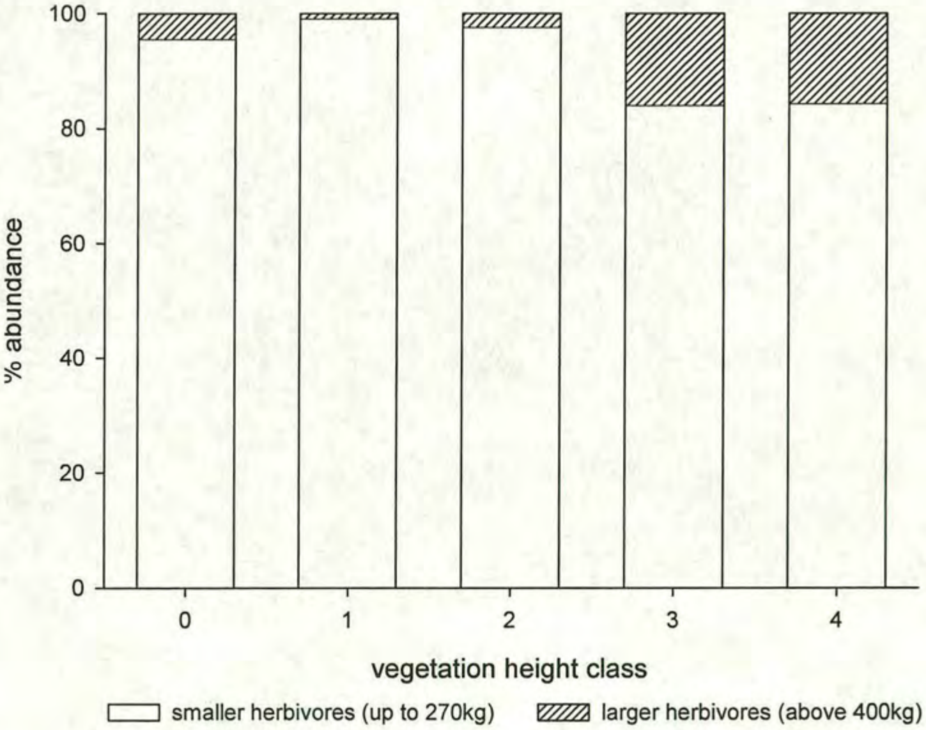


Figure 5.12b. Proportion of the total abundance of herbivores in two body size classes in quadrants of varying vegetation height.

H5. Species richness falls in productive, low quality swards

A weak test of Tilman's resource-ratio hypothesis is provided by plotting species richness against resource productivity. Reduced species richness at very low and at moderate to high productivity is consistent with the hypothesis. The test is weak because there are various alternative hypotheses that can potentially explain the pattern (see chapter 2, also chapter 7). Figure 5.13 supports this expectation, with lower species richness in vegetation height classes 0, 3 and 4, conforming to the expected longer rightward tail. Species richness increases rapidly from very low to low resource productivity, and then falls again more slowly from moderate to high levels of resource productivity.

Figure 5.14 shows that the mechanism underlying this pattern may be variation in abundance. Abundance first rises rapidly to a peak in vegetation height class 1, then falls more slowly through height classes 2, 3 and 4.

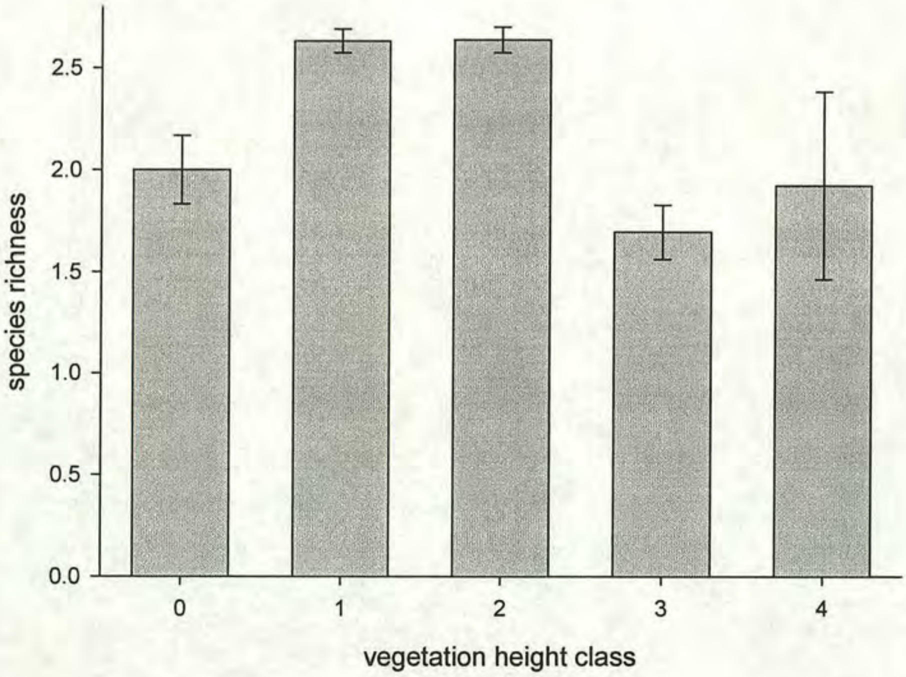


Figure 5.13. Variation in total species richness with vegetation height class. Variation is significant (one-way ANOVA: F = 16.19, d.f. = 4, *n* = 1444, P << 0.001). Species richness in vegetation height classes 1 and 2 is significantly higher than in vegetation height classes 0 and 3 (Tukey pairwise unplanned comparisons, family error rate = 0.05, individual error rate = 0.00642). Error bars represent +/- 1 s.e.

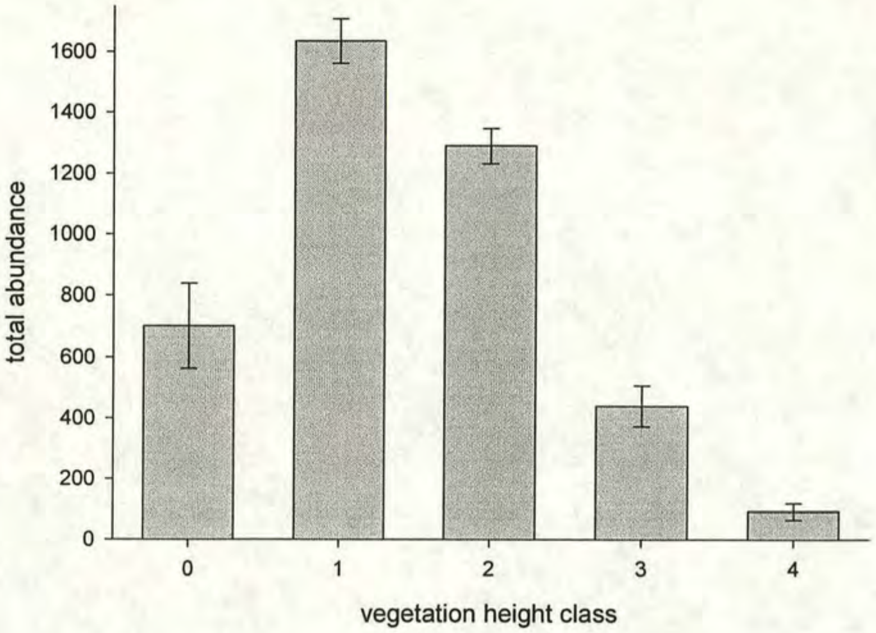


Figure 5.14. Variation in total abundance with vegetation height class. Variation is significant (one-way ANOVA: F = 24.76, d.f. = 4, *n* = 1444, P << 0.001). All differences in abundance are significant, except between classes 0 & 3, 0 & 4 and 3 & 4 (Tukey pairwise unplanned comparisons, family error rate = 0.05, individual error rate = 0.00642). Error bars represent +/- 1 s.e.

H6. On tall swards, the presence and abundance of smaller species depends on habitat modifications carried out by larger species

Unbalanced ANCOVA was used to test whether the species richness of smaller herbivores is affected by the species richness of larger herbivores, and whether these effects differ according to vegetation height. Facilitation is supported if species richness of smaller size classes is correlated to that of larger size classes, with a more positive slope in taller vegetation height classes than in shorter. This would indicate that the presence of smaller species in taller swards is a positive function of the presence of larger species.

There are six combinations of smaller and larger body size from within the four size classes, and a 7th compares 'smaller' to 'larger', so there are seven ANCOVA analyses. Full statistical test results from these analyses are given in table 5.9 a to g.

The test can only be carried out if there is significant variation among slopes in the ANCOVA. In one case, there was no significant heterogeneity among regressions (table 5.9 f), and in another there was no significant heterogeneity among slopes (table 5.9 g), leaving five cases where the facilitation hypothesis can be tested.

The regression lines from these analyses are illustrated in figure 5.15 (a to e, corresponding to the layout of table 5.9). In all five tests, ignoring the VH0 class (barren ground), facilitation is supported. Species richness of the smaller body size class is higher in taller vegetation height classes where species richness of the larger body size class is higher - the presence of larger species facilitates the presence of smaller species, in tall swards, but not in short swards.

Table 5.9. Statistical test results for facilitation analyses. See figure 5.15. ANCOVA was carried out using the equations of Zar (1996, table 17.1) and Sokal & Rohlf (1995, box 14.9) for unbalanced designs. If heterogeneity among regressions is not significant, then tests for heterogeneity among slopes and elevations, and *post-hoc* tests, are not carried out, and the best estimate of the single underlying regression is the *pooled within* regression. Heterogeneity among elevations tests are only carried out if heterogeneity among slopes is not significant. Post-hoc tests are only carried out if the respective heterogeneity test is significant. Slopes and intercepts of regressions are only given where the regression is significant. The 'large' body size class does not occur in vegetation height class = 4, and therefore has all records = 0. For these cases (b, d and f), the ANCOVA is calculated without the VH4 data (*i.e.* for four groups instead of five).
* = P < 0.05; ** = P < 0.01; *** = P < 0.001. a = numerator d.f.; b = denominator d.f.

a) X = small, Y = medium (figure 5.15 a)

ANCOVA	F	a	b	P
Initial ANOVA	9.008	4	1439	***
Heterogeneity among regressions	6.111	8	1434	***
Heterogeneity among slopes	4.656	4	1434	***
Heterogeneity among elevations (if among slopes is n.s.)	--	4	1438	--

Regressions	F	a	b	P	slope	intercept
VH0	0.792	1	62	n.s.		
VH1	3.561	1	580	n.s.		
VH2	34.228	1	623	***	0.270	1.152
VH3	19.432	1	158	***	0.558	0.787
VH4	10.471	1	11	**	1.472	0.778
pooled within (single underlying regression)	45.518	1	1438	***	0.223	1.052

Multiple pairwise comparisons (post hoc) - Tukey test

slopes	VH0	VH1	VH2	VH3	VH4
VH0					
VH1	n.s.				
VH2	n.s.	sig.			
VH3	n.s.	sig.	sig.		
VH4	n.s.	n.s.	n.s.	n.s.	

b) X = small, Y = large (figure 5.15 b)

ANCOVA	F	a	b	P
Initial ANOVA	2.082	3	1427	n.s.
Heterogeneity among regressions	3.851	6	1423	***
Heterogeneity among slopes	4.909	3	1423	**
Heterogeneity among elevations (if among slopes is n.s.)	--	3	1426	--

Regressions	F	a	b	P	slope	intercept
VH0	2.213	1	62	n.s.		
VH1	0.0100	1	580	n.s.		
VH2	4.435	1	623	*	0.0475	0.213
VH3	17.672	1	158	***	0.232	0.147
pooled within (single underlying regression)	8.949	1	1426	**	0.0447	0.184

Multiple pairwise comparisons (post hoc) - Tukey test

slopes	VH0	VH1	VH2	VH3
VH0				
VH1				
VH2				
VH3				

c) X = small, Y = mega (figure 5.15 c)

ANCOVA	F	a	b	P
Initial ANOVA	13.508	4	1439	***
Heterogeneity among regressions	7.075	8	1434	***
Heterogeneity among slopes	3.386	4	1434	**
Heterogeneity among elevations (if among slopes is n.s.)	--	4	1438	--

Regressions	F	a	b	P	slope	intercept
VH0	2.573	1	62	n.s.		
VH1	3.210	1	580	n.s.		
VH2	3.621	1	623	n.s.		
VH3	2.419	1	158	n.s.		
VH4	0.169	1	11	n.s.		
pooled within (single underlying regression)	4.107	1	1438	*	-0.0195	0.0944

Multiple pairwise comparisons (post hoc) - Tukey test

slopes	VH0	VH1	VH2	VH3	VH4
VH0					
VH1	n.s.				
VH2	n.s.	n.s.			
VH3	n.s.	n.s.	sig.		
VH4	n.s.	n.s.	sig.	n.s.	

d) X = large, Y = mega (figure 5.15 d)

ANCOVA	F	a	b	P
Initial ANOVA	13.215	3	1427	***
Heterogeneity among regressions	9.688	6	1423	***
Heterogeneity among slopes	5.977	3	1423	***
Heterogeneity among elevations (if among slopes is n.s.)	--	3	1426	--

Regressions	F	a	b	P	slope	intercept
VH0	5.699	1	62	*	0.370	0.130
VH1	1.721	1	580	n.s.		
VH2	3.429	1	623	n.s.		
VH3	6.449	1	158	*	0.168	0.118
pooled within (single underlying regression)	14.244	1	1426	***	0.0628	0.0592

Multiple pairwise comparisons (post hoc) - Tukey test

slopes	VH0	VH1	VH2	VH3
VH0				
VH1				
VH2				
VH3				

e) X = 'smaller', Y = 'larger' (figure 5.15 e)

ANCOVA	F	a	b	P
Initial ANOVA	3.986	4	1439	**
Heterogeneity among regressions	4.168	8	1434	***
Heterogeneity among slopes	2.769	4	1434	*
Heterogeneity among elevations (if among slopes is n.s.)	--	4	1438	--

Regressions	F	a	b	P	slope	intercept
VH0	0.00817	1	62	n.s.		
VH1	3.908	1	580	*	0.0290	0.164
VH2	4.348	1	623	*	0.0333	0.259
VH3	14.868	1	158	***	0.138	0.200
VH4	0.520	1	11	n.s.		
pooled within (single underlying regression)	17.024	1	1438	***	0.0433	0.205

Multiple pairwise comparisons (post hoc) - Tukey test

slopes	VH0	VH1	VH2	VH3	VH4
VH0					
VH1	n.s.				
VH2	n.s.	n.s.			
VH3	n.s.	sig.	sig.		
VH4	n.s.	n.s.	sig.	sig.	

f) X = medium, Y = large: no facilitation test possible (among regressions n.s.)

ANCOVA	F	a	b	P
Initial ANOVA	2.082	3	1427	n.s.
Heterogeneity among regressions	1.593	6	1423	n.s.
Heterogeneity among slopes	--	3	1423	--
Heterogeneity among elevations (if among slopes is n.s.)	--	3	1426	--

Regressions	F	a	b	P	slope	intercept
VH0	1.953	1	62	n.s.		
VH1	6.906	1	580	**	0.0448	0.147
VH2	2.973	1	623	n.s.		
VH3	12.455	1	158	***	0.117	0.111
pooled within (single underlying regression)	17.929	1	1426	***	0.0497	0.164

g) X = medium, Y = mega: no facilitation test possible (among slopes n.s.)

ANCOVA	F	a	b	P
Initial ANOVA	13.508	4	1439	***
Heterogeneity among regressions	7.625	8	1434	***
Heterogeneity among slopes	1.138	4	1434	n.s.
Heterogeneity among elevations (if among slopes is n.s.)	14.106	4	1438	***

Regressions	F	a	b	P	slope	intercept
VH0	0.248	1	62	n.s.		
VH1	3.212	1	580	n.s.		
VH2	3.515	1	623	n.s.		
VH3	0.278	1	158	n.s.		
VH4	0.635	1	11	n.s.		
pooled within (single underlying regression)	5.269	1	1438	*	0.0173	0.0543

Multiple pairwise comparisons (post hoc) - Tukey test

elevations	VH0	VH1	VH2	VH3	VH4
VH0					
VH1	n.s.				
VH2	n.s.	n.s.			
VH3	n.s.	n.s.	n.s.		
VH4	n.s.	n.s.	n.s.	n.s.	

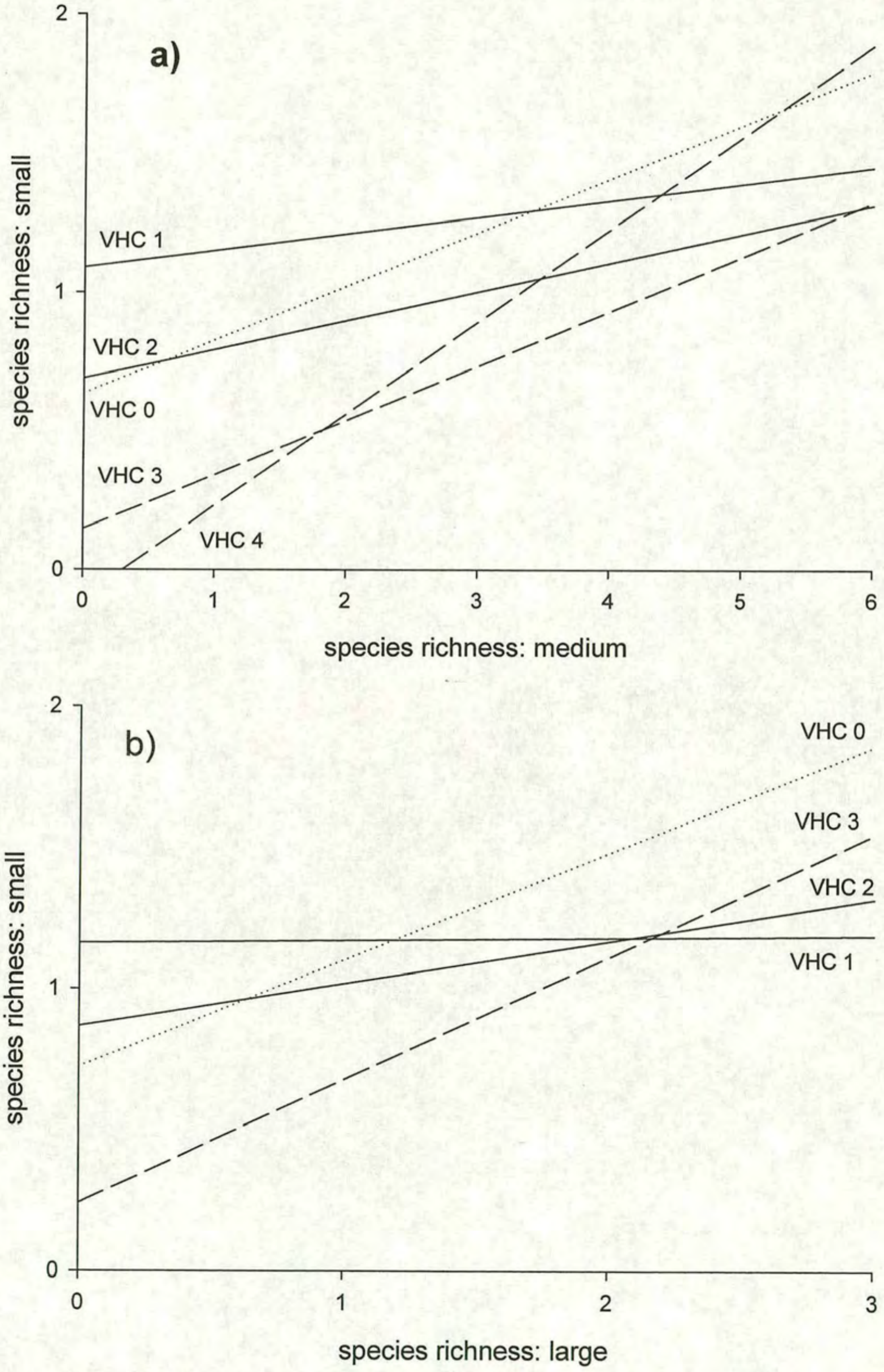


Figure 5.15a, b. Facilitation of small species richness (Y axes) by medium and large species richness (X axis) according to vegetation height class (VHC).

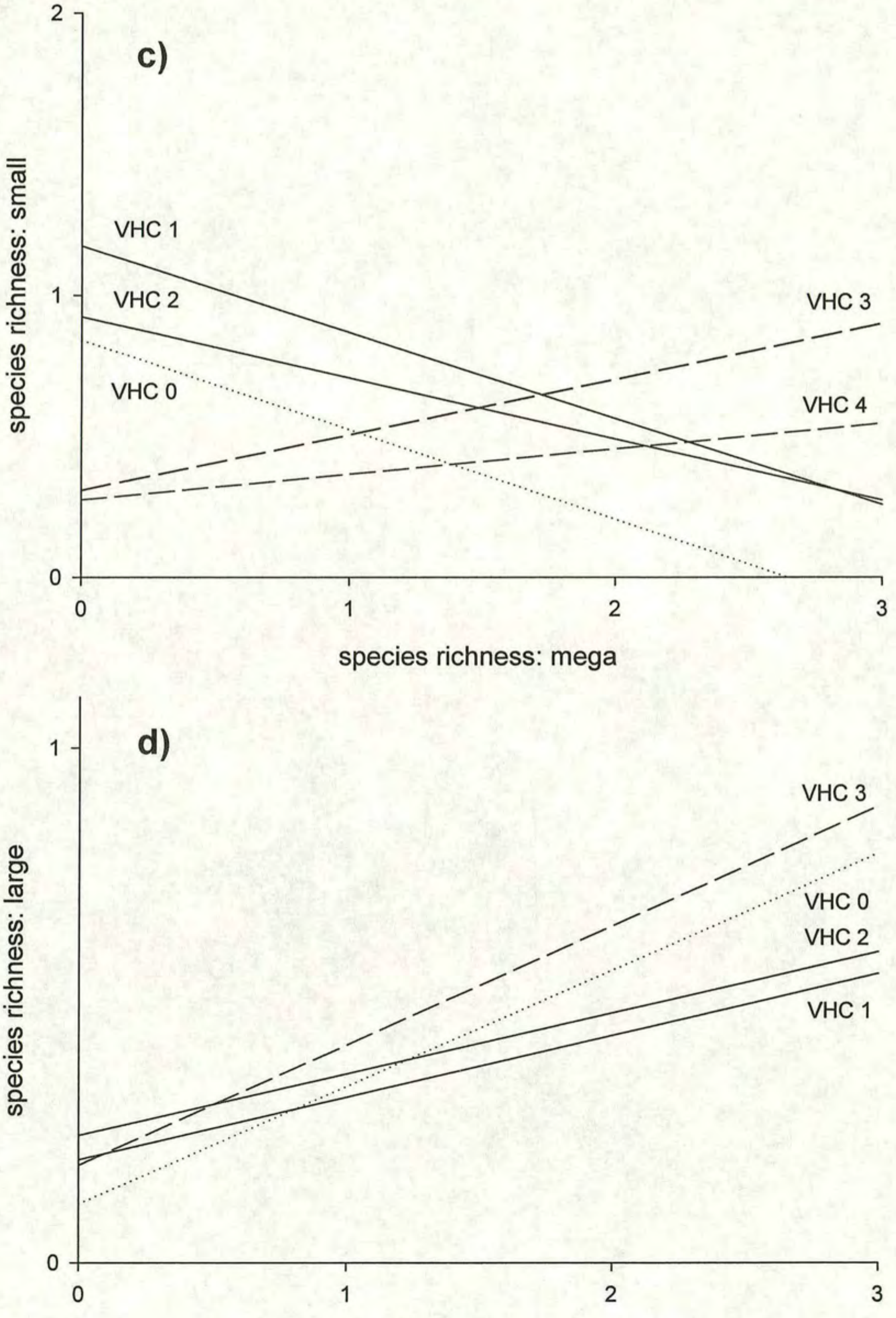


Figure 5.15c, d. Facilitation of small and large species richness (Y axes) by mega species richness (X axis) according to vegetation height class (VHC).

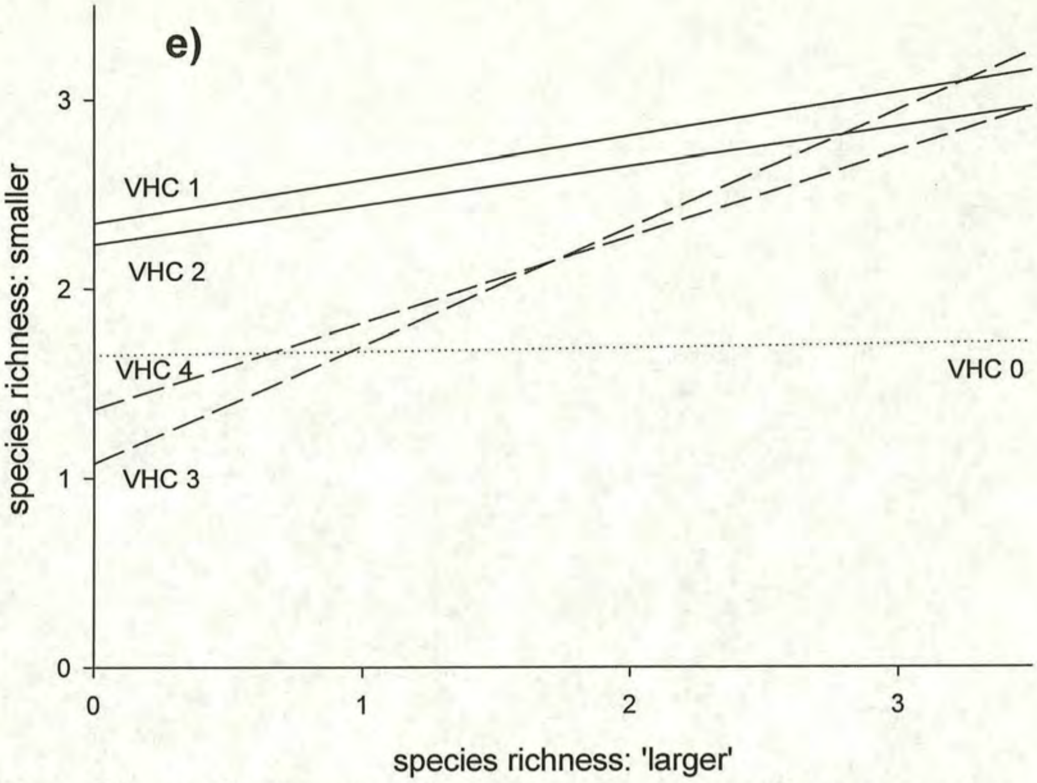


Figure 5.15e. Facilitation of smaller species richness (Y axes) by larger species richness (X axis) according to vegetation height class (VHC).

DISCUSSION

The dataset used in this chapter provides a uniquely detailed and extended description of an entire ecosystem. The analyses presented here, focussing on a small part of the ecosystem that is occupied for just a few months each year, are just the tip of a potential iceberg of ecological investigations. It seems strange that these data have not been subjected to detailed analyses before. It may simply be that computer manipulation of databases of this size was very unusual and difficult in the years immediately following the acquisition of these data. Today however, restructuring large databases, extracting data, and performing analyses are much more straightforward. This database provides truly unique opportunities for testing all sorts of hypotheses about community and ecosystem level dynamics.

Plant and herbivore biomass

The fact that herbivore biomass does not increase in taller swards is perhaps unexpected (figure 5.3). However, this supports the Bell-Jarman hypothesis that abundant resources, with their reduced quality, are in fact unavailable to most of the ungulate community. It also suggests that most of the plant biomass in tall swards is also unavailable as food even to the larger animals. Enough is available as food to maintain overall herbivore biomass, but tall swards do not represent super-abundant resources. This fits with Sinclair's (1975) argument that most plant biomass is unavailable as food, and therefore that suggestions that the herbivore guild is not food limited (Hairston, Smith & Slobodkin 1960, Slobodkin, Smith & Hairston 1967) are wrong.

The Bell-Jarman hypothesis and its application to community structure

The Bell-Jarman hypothesis (Bell 1970, Jarman 1974) provides a fundamental theorem for understanding herbivore community ecology (Murray 1989). Larger animals have a lower specific metabolic rate (energy requirement per *kg* body weight) than smaller animals, but they have a greater digestive capacity. This pre-adapts them for the lower quality forages that are most abundant, while smaller animals depend on rarer, high quality forage (chapter 2).

Bell (1982, 1984) applied this to ungulate communities, and predicted that in habitats where food is abundant but of poor quality, larger species would dominate the herbivore fauna. This hypothesis was tested using comparative data from ecosystems in regions that differed in soil nutrient availability (SNA) and rainfall (Bell 1982, East 1984). Where rainfall was high, SNA tended to be low, especially over ancient bedrocks. In these regions, the herbivore community tended to be dominated by larger species.

The results of testing H2, H3 and H4 support this hypothesis within a single ecosystem. On tall, low quality swards, the proportion of total ungulate biomass concentrated in the larger size classes increases (H2). Typical body size also increases (H3). Abundance within the larger size classes increases, and this is the likely proximate explanation for the greater species richness of larger body size classes in taller swards (H4). Bell's (1982) mechanism explains variation in abundance between size classes, and the strong correlation of species richness to abundance (figure 5.5) explains how this feeds through to diversity patterns.

Facilitation

Facilitation has most often been applied to temporal sequences of patch occupancy by a series of grazers. The sequence starts with large animals that graze and trample a tall, poor quality sward, stimulating re-growth that is palatable to smaller species (Vesey-Fitzgerald 1960, 1965, Bell 1970, 1971, Pennycuick 1975, Maddock 1979, see chapter 1). Often, the smaller species will be able to 'capture' the patch by keeping the sward too short to support larger species (chapter 2).

In this chapter, sequential data were not used. Instead, the association between smaller species and larger species was measured in swards of different heights. In all five variations of the test (comparing different pairs of body size classes), more smaller species were found on a taller sward if there were more larger species present. When large species diversity was low on a tall sward, few small species were found.

The converse pattern was also found in one case (mega *vs.* small species richness, figure 5.15c). As well as showing facilitation, in this comparison there was evidence of competitive exclusion of the mega species by the small species on short swards. Mega species richness on short swards was lower if small species richness was high.

Unimodal productivity-diversity relationship

Resource competition theory predicts that diversity should first rise steeply as productivity increases from very low levels, before reaching a peak and then falling again when productivity reaches relatively higher levels (Tilman 1982, see chapter 2). Observations of this pattern in animal communities have been used to argue that RCT describes interspecific interactions in these groups (Abramsky & Rosenzweig 1984, Owen 1988, 1990). However, simply observing this pattern provides only weak support for the theory (Abrams 1988, 1995, chapter 2), because there are many alternative explanations (Rosenzweig & Abramsky 1993, Rosenzweig 1995).

The analysis here provides similarly weak support of RCT. Ungulate diversity is significantly higher in short swards (VHC 1 and VHC 2) than in barren swards (VHC 0) or tall swards (VHC 3) (figure 5.13).

There are very many fewer individuals in tall swards than in short swards (figure 5.14), and the positive correlation between abundance and diversity (figure 5.5) may explain reduced diversity in tall swards. It is not possible to separate causation from correlation - diversity may fall in tall swards as a direct result of fewer individuals, or diversity may fall because of the RCT mechanism and the drop in abundance is an unrelated phenomenon. Of course, as in all things ecological, a combination of both explanations is entirely possible.

RCT predicts the fall in species richness when productivity is high because of an assumption that spatial variability in resource supply rates falls as productivity increases (see chapter 2, figures 2.1a and 2.1b). Hypothesis 8 was designed to directly test this mechanism. It would provide the first direct test of the RCT explanation of unimodal productivity-diversity curves in an animal community at the ecosystem scale (chapter 7 provides such a test at the continental scale). The test requires a measurement of spatial heterogeneity within each quadrant. This could be provided by records of burning. In the south-east plains, very few quadrants burn during the wet season, but data could be extracted for other regions to carry out this test.

Utilisation efficiency and intake efficiency

Murray (unpub. MS) contrasts the consequences for community dynamics of a competitive interaction based upon resource intake *vs*. utilisation efficiency (of similar sized species) with an interaction based upon the digestive and intake constraints of body size differences. In the former case, if consumption efficiency of primary production (CEPP) is high (a high proportion of the primary production is consumed by the herbivore community) then competition will be strong, and species will be excluded relatively quickly, reducing species richness in areas of high CEPP. In the latter case, coexistence of competing species can be stable, depending upon the resource ratio. A small amount of spatial heterogeneity leads to a range of different resource ratios, and different sets of species are able to coexist stably. This can lead to increased diversity under high CEPP because the standing biomass is reduced, and therefore any spatial heterogeneity will generate a large range of resource ratios.

Murray (*ibid.*) suggests a second, experimental test. In plant communities it has often been observed that fertilisation leads to higher productivity but lower species richness. Tilman (1980, 1982, Tilman & Pacala 1993) explains this as a consequence of reduced spatial heterogeneity. Adding a fixed amount of fertiliser to all locations within a habitat reduces the variance in the ratios of different resource supply rates (Abrams 1995). This may explain the general pattern in plant communities of reduced diversity at high productivity (Rosenzweig & Abramsky 1993, Tilman & Pacala 1993). Murray (*ibid.*) argues that for the herbivore community feeding on the fertilised vegetation, the increased quality of plant growth will lead to an increase in the CEPP, since a larger proportion of the growth is of sufficient quality to be profitably consumed. The increased CEPP will lead to an increase in herbivore diversity if the species are interacting via body size differences (because the range of resource ratios is increased). If, however, the community is composed of similar sized species interacting via differences in intake and utilisation efficiency, increased CEPP will decrease herbivore diversity because the reduced standing biomass of vegetation leads to an increase in the intensity of competitive interactions.

These ideas could be developed using ZNGI models similar to those used in chapter 2. The data contained within the SEMP database analysed in this chapter could then be used to carry out a test of the hypothesis.

APPENDIX 5.1. PUBLISHED ACCOUNTS OF THE SERENGETI SURVEYS

Very few papers refer to these surveys. Pennycuick (1975) used wildebeest data from the surveys as part of her data describing wildebeest movements through the park between 1960 and 1973. She refers to a paper in preparation by M. Norton-Griffiths describing the surveys. Maddock (1979) used data from the surveys to characterise the migratory patterns of wildebeest, zebra and Thomson's gazelle.

Information in the SRI annual reports

The Serengeti Research Institute Annual Reports also mention the flights. The 1969 report apparently describes the flights in detail.

The 1970 report (p.6) refers to the 1969 report for a description of the surveys. On p.35, the survey data for Thomson's gazelle is briefly described, and also an exercise comparing the recce flight estimates of Thomson's gazelle numbers to 101 ground transects. In 53% of the 101 25km squares used for this exercise, the density classes agreed fully. In a further 25%, density classes were one class different. On p.46, M. Norton-Griffiths describes progress in writing computer programs to analyse the survey data, including one that produces distribution maps. On p.49, references to

Lamprey, H.F. (1969). The range of possible observations. E. Afr. Agr. For. J. 34. Special issue. Proceedings of the Workshop on the use of light aircraft in wildlife management in East Africa, 64-69.

Lamprey, H.F. (1970). Serengeti Research Institute: the objectives and work of a field research station. I.B.P International Symposium on "The ecological bases for environmental management". Rome, 28th and 29th September.

In the 1971-2 Annual report, on p.7 M. Norton-Griffiths briefly describes the initial analyses of the recce data, concentrating on the correlations between different species. On p.9 there is a suggestion that the format of the flights will be modified in the future, mainly to become quarterly rather than monthly. On p.34, Kreulen and Kreulen state that their weekly aerial surveys of wildebeest used the same methods as the monthly recces, and that they were planning to analyse the data in collaboration with M. Norton-Griffiths. On p.58, a reference to

Lamprey, H.F., H. Kruuk & M. Norton-Griffiths (1971). Research in the Serengeti. Nature 230: 497-500.

6. SPATIAL AND TEMPORAL VARIABILITY IN A 17 YEAR NDVI TIME SERIES DATASET FOR AFRICA

INTRODUCTION

The aim of this chapter is to introduce satellite data that can be used to study resource supply conditions throughout continental Africa. The satellite data will be analysed to reveal patterns of spatial and temporal variability in primary productivity at the continental scale. The results of these analyses will then be used in chapter 7 to study continental scale variation in ungulate species richness.

Estimating primary productivity from satellite imagery

Terrestrial levels of primary productivity are often estimated indirectly from rainfall records, especially so in semi-arid regions (*e.g.* Abramsky & Rosenzweig 1984, Western 1991). For continental scale studies, spatial variability in rainfall must be interpolated from data at a limited number of weather stations. Satellite imagery offers a more direct method for measuring primary productivity, with much more detailed spatial coverage than is available from traditional meteorological databases.

Plants use the energy of sunlight to carry out photochemical reactions that synthesise carbohydrate molecules from water and atmospheric carbon dioxide. The four basic limitations on primary productivity are therefore the availability of energy, soil nutrients, carbon dioxide and water. Atmospheric CO_2 rarely limits plant growth (Fitter & Hay 1987, Kaufman 1989). Water does strongly affect plant growth, especially in seasonal semi-arid regions such as East Africa, as does soil fertility (Scholes & Walker 1993). However, plants that cannot grow because of lack of water or nutrients also cease photosynthesising, and stop absorbing light. The accumulation of biomass (*i.e.* productivity) can therefore be predicted if the amount of energy absorbed by the vegetation canopy can be measured (Curran 1980, Tucker & Sellers 1986).

The relevant energy to measure is the part of the spectrum that vegetation absorbs, photosynthetically active radiation (PAR), from 0.4 to 0.7 μm. In particular, actively photosynthesising vegetation absorbs a very high proportion of light in the visible part of the spectrum, but reflects most light in the near infrared (Knipling

1970, Curran 1980, Tucker & Sellers 1986). Absorbed PAR (APAR) is the energy fixed by photosynthesis, and plant growth rate is a near-linear function of APAR (Tucker & Sellers 1986, Kumar 1988).

APAR can be directly estimated from satellite imagery, in particular using the Normalised Difference Vegetation Index, or NDVI (Tucker & Sellers 1986, Kumar 1988, Wiegand *et al.* 1991). NDVI is a normalised ratio of the reflectance of near-infrared to red radiation from a surface:

$$\mathrm{NDVI} = \frac{\text{near IR - R}}{\text{near IR + R}} \qquad (1)$$

Vegetation reflects a high proportion of the incident near-infrared light, but absorbs most of the visible red light. A dense, actively growing canopy reflects almost no red light, and NDVI is high (close to 1). A thin, dormant canopy or open ground reflects more red light and absorbs less near infra-red, and NDVI is reduced. In fact, NDVI is a linear function of the proportion of PAR that a canopy absorbs, APAR/PAR (Tucker & Sellers 1986, Kumar 1988, Wiegand *et al.* 1991). PAR is essentially constant, at least during the growing season, and especially in tropical latitudes (Wiegand *et al.* 1991, Prince 1991), so plant growth can be modelled as

$$\begin{aligned} P_t &= \varepsilon \sum\nolimits_t APAR \\ &= \varepsilon \sum\nolimits_t a\left(NDVI_t\right) PAR \qquad (2) \\ &= a\varepsilon.PAR \sum\nolimits_t \left(NDVI_t\right) \end{aligned}$$

P_t = net primary production ($kg.ha^{-1}$) during time interval t

ε = efficiency of converting $APAR$ into biomass

$NDVI_t$ = $NDVI$ at vegetation surface during time interval t

PAR = incoming PAR during time interval t (essentially constant)

$APAR$ = amount of PAR absorbed by the canopy during time interval t

a = constant factor such that $a.NDVI_t$ = the proportion of PAR absorbed by the canopy

(Prince 1991).

NDVI, integrated over a time series, therefore provides a direct measurement of primary productivity. NDVI is in fact more directly related to biophysical rates such as primary production or actual evapotranspiration, than to states such as standing biomass or leaf area index (Tucker & Sellers 1986).

The NDVI satellite imagery used in this chapter and in chapter 7 comes from the NOAA (National Oceanographic and Atmospheric Administration) series of meteorological satellites carrying the AVHRR sensor (Advanced Very High Resolution Radiometer), collected in a database published on the Internet by the United States Geological Survey (see *Methods*). AVHRR NDVI data has been extensively used in Africa both for mapping vegetation (Townshend & Tucker 1984, Townshend & Justice 1986, Lloyd 1990, Townshend *et al.* 1991) and for assessing primary productivity, especially throughout the Sahel (Tucker *et al.* 1985, Justice & Hiernaux 1986) and in East Africa (Justice, Holben & Gwynne 1986), but also in other regions (Du Plessis 1999).

Temporal and spatial variability in primary productivity

Temporal variability was assessed using two methods. Principal components analysis of the time series (Eastman & Fulk 1993) extracts a set of uncorrelated images, each representing a different component of temporal variability in the data. Coefficients of variation were also used to index specific aspects of temporal variability - seasonal variability and variability between years.

The major pattern of spatial variability was assessed by calculating a mean NDVI image over the 17 year time series. Local variability was measured using the coefficient of variation in NDVI within sample grid cells.

Alternative indicators of primary productivity

Primary productivity is the rate at which biomass is accumulated by growing vegetation, per unit area. The best estimate is therefore obtained by directly measuring dry weights of standing vegetation throughout a growing season. Surrogate estimators have been developed to allow productivity estimates to be made with less work and over broader geographic extents than would otherwise be possible. Traditional indicators are annual rainfall (*e.g.* Abramsky & Rosenzweig

1984) and potential and actual evapotranspiration (*e.g.* Wright 1983, Currie & Paquin 1987, Currie 1991, Currie & Fritz 1993, Wright, Currie & Maurer 1993), but more recently methods using satellite imagery (as discussed above) have been developed.

No data on actual evapotranspiration were available for continental Africa, but the FAO CLIMWAT (Smith 1993) database contains potential evapotranspiration (ET_o) calculations for every weather station in the database. The formula used to calculate ET_o (Smith 1990, 1993) uses data on daily sunshine hours, temperature measurements, and windspeed. Potential evapotranspiration does not take water supply into account, but instead has been taken to measure the available energy in the environment (Wright 1983, Currie & Paquin 1987, Currie 1991, Currie & Fritz 1993, Wright, Currie & Maurer 1993).

METHODS

Source data

Normalised Difference Vegetation Index (NDVI) satellite imagery was downloaded from the African Data Dissemination Service (ADDS) website at http://edcintl.cr.usgs.gov/adds/adds.html. The ADDS is run by the United States Geological Service (USGS) Earth Resources Information System (EROS) Data Centre to provide a data resource for the US Agency for International Development (US-AID) Famine Early Warning System (FEWS). The NDVI imagery on this site was supplied by the National Aeronautics and Space Administration (NASA). The NDVI archive used was the 17 year, monthly time series produced by the NASA Global Inventory Monitoring and Modelling Studies (GIMMS) group (Los, Justice & Tucker 1994, Los *et al.* 2000).

The original data were collected by the National Oceanic and Atmospheric Administration (NOAA) meteorological satellites. These data were then processed by NOAA and by the GIMMS group to remove biases caused by sensor degradation over time, satellite orbital drift, and by the successive replacement of satellites and sensors during the data acquisition period (Kidwell 1998, Los 1993). Although the sensor captured the original data at a ground resolution of about 1.1 *km*, on-board generalisation of this data reduced the resolution to about 4 *km* (Townshend 1994, Campbell 1996). During processing of the database this resolution was further reduced to about 7.6 *km* (Townshend 1994, Townshend & Skole 1995).

Imagery of the entire continent is captured every day, but much of this data is degraded due to cloud cover and other atmospheric and orbit conditions. The daily data are therefore combined into a series of ten-day maximum value composites (dekads), so that each image in the published database is actually formed from the maximum NDVI recorded at each pixel during ten days. This pre-processing is very successful at removing biases in the data, since almost all such biases act to reduce the NDVI recorded at the satellite (Holben 1986). However, a proportion of the coverage of almost all dekad images remains obscured by clouds, and data for these pixels is set to zero in the USGS database. Los, Justice & Tucker (1994) and Los *et al.* (2000) provide reviews of the GIMMS dataset. Figure 6.1 summarises the pre-processing of the NDVI data.

Principal components analysis

Principal components analysis has been shown to be a very sensitive method of extracting signals from a time series of NDVI satellite imagery (Eastman & Fulk 1993). Each monthly image is treated as a separate variable in the PCA. There are 204 images in the 17 year time series, each image being the mean of the three dekadal images for that month. The PCA procedure extracts a small number of images that represent the most important sources of temporal variability in the time series.

The current work modifies the methods of Eastman & Fulk (*ibid.*) in two main ways. Firstly, unstandardised PCA was used, whereas Eastman & Fulk (*ibid.*) used standardised PCA. Standardised PCA ensures that each image in the original time series has the same mean and variance, and therefore potentially contributes an equal amount to the PCA output. Unstandardised PCA does not view this variation in variance as a bias, but as part of the pattern in the data. If some images have higher variances, then they rightly should contribute more to the PCA output.

Secondly, and more importantly, Eastman & Fulk (*ibid.*) did not mask out ocean areas from their analysis. Although oceans were masked to have a constant value (zero), and therefore could not contribute to any change components, nevertheless these regions distort the output components. This occurs because PCA extracts orthogonal components from the whole image area, whereas the area of interest (the African continent) is considerably smaller. By definition, orthogonal components are uncorrelated. However, PCA component images sampled from within the restricted area of interest (continental Africa) may exhibit significant correlation, even though samples taken from throughout the image area (*i.e.* including ocean pixels) are uncorrelated. This was the case in the current analysis, before the oceans were completely excluded from the analysis.

To exclude oceans (rather than simply mask them to be zero), the QUERY module of Idrisi for Windows (version 2.005, Eastman 1997) was used. This extracts data in one image from pixels under a region defined by a mask image. The resulting data consists of pseudo-image files one column wide by 323,173 rows long, one file for each month of the 204 month time series. These files were then imported to the MultiSpec (Landgrebe & Biehl 1999) image analysis software (in fact they had to be converted to 23 columns by 14,051 rows so that the software would accept the files as images), as if they were true images, and unstandardised PCA was carried out. This method works because although georeferencing of pixels was removed by the QUERY process, locational referencing still exists in that the n^{th} pixel in one file corresponds to the n^{th} pixel in all the other files.

A further difference in the current study is that deserts, as well as oceans, were excluded. This was because the study these data were extracted for relates to the distribution of ungulate species in sub-Saharan Africa, and deserts are specifically excluded from the terms of reference. The study region, sub-Saharan Africa, was defined using habitat maps produced by the International Geosphere-Biosphere Program Data and Information System (IGBP-DIS). The IGBP-DISCover Global 1 *km* Land Cover Data Set was derived from satellite imagery (Belward 1996, Loveland *et al.* 2000). DISCover maps and methodology can be downloaded from the Earth Resources Observation Systems (EROS) Data Center, Land Processes Distributed Active Archive Center (DAAC) web page at http://edcdaac.usgs.gov/glcc/glcc.html. This data was used to exclude deserts, large water bodies, and agricultural and urban areas from the sampling strategy. Figure 6.2 shows the IGBP DISCover map of Africa.

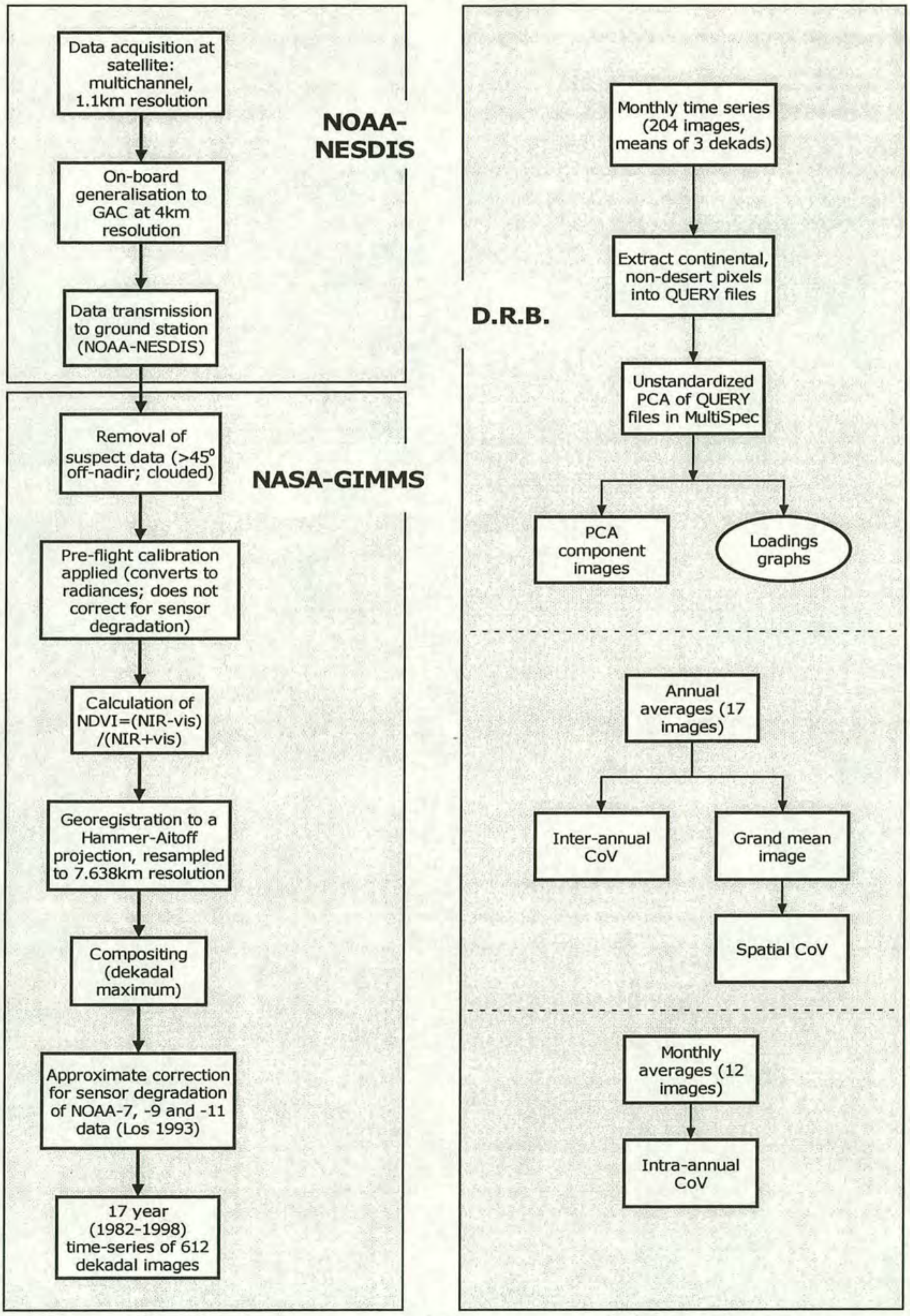


Figure 6.1. Pre-processing and analysis of the 17 year NDVI satellite imagery dataset. NOAA: National Oceanographic and Atmospheric Administration; NESDIS: National Environmental Satellite, Data, and Information Service; NASA: National Aeronautics and Space Administration; GIMMS: Global Inventory Monitoring and Modelling Studies; DRB: current author.

Alternative indices of temporal variability

The PCA method described above extracts temporal signals according to how much variance they account for in the time series. The output components must then be interpreted to characterise the signal contained within each image. An alternative approach is to specify *a priori* which time signals are of interest, and then to design an index that captures that signal. Coefficients of variation (CoV) were used as indexes. The CoV is the variance divided by the mean value of a data series (in this case, the time series of 204 NDVI values at each pixel location), giving a dimensionless measure of variability that is relative to the mean. This allows direct comparison among data sets having different mean values (Sokal & Rohlf 1995).

For this study, two signals are particularly interesting - seasonal (intra-annual) variability and year-to-year (inter-annual) variability. For inter-annual variability, 17 mean annual NDVI images were generated. These were then used to calculate the (CoV) among annual means (inter-annual CoV, or IECV). For intra-annual variability, 12 mean monthly images were generated. These were then used to calculate the CoV among monthly means (intra-annual CoV, or IACV).

Measuring spatial variability in primary productivity

Coefficients of variation (CoV) in NDVI were used to measure spatial variability in primary productivity to allow comparisons of variability at different locations. Data were sampled by superimposing a grid over the study region (see below) and calculating the CoV in NDVI within each grid cell. CoV is also the measure of spatial variability in productivity discussed by Tilman (1980, 1982, 1986) and Abrams (1988, 1995).

Sampling and analysis

A stratified random distribution of 301 points was generated using the Idrisi SAMPLE module. These point locations were assigned ID numbers. PCA component images, mean NDVI, and the intra- and inter-annual CoV images were sampled using this set of points with the Idrisi EXTRACT module. This module extracts the value of pixels in a data image, using a sample image to determine which pixels to record. This ensures that the same locations are sampled in different data images. Figure 6.2 shows the distribution of sample points superimposed on the IGBP habitat classification map.

Mean NDVI, inter- and intra-annual CoV were also sampled by superimposing a grid over the study region. This was the same grid used to calculate the spatial CoV, and was used to enable comparison of these variables with the spatial CoV. Grid cells smaller than 80,000 km^2 were excluded (for example, cells that partly fell over water bodies or deserts would be reduced in size and therefore excluded). This left a sample grid of 161 cells, varying in size from 80,617 to 132,809 km^2 (figure 6.3). The mean value of pixels in the data image under each grid cell was calculated.

Mean annual precipitation and mean temperature were taken from the database published on CD-ROM by Hutchinson *et al.* (1996). This provides GIS maps of climate variables which were imported to Idrisi and sampled using the grid scheme. Potential evapotranspiration (ET_o) was extracted from the FAO CLIMWAT database (Smith 1993), which provides climatic data averages for 1680 weather stations throughout Africa. ET_o values for each weather station were then assigned to a Thiessen tesselation of the continent. This simply means that all points closer to a given station than to any other station were assigned the same value as the station - no other interpolation routine was used. The grid sample image was then used to extract the mean value of ET_o under each grid cell.

Statistical analyses were carried out using Minitab 12.1 (Minitab Inc. 1998) and SigmaPlot for Windows version 4.00 (SPSS Inc. 1997).

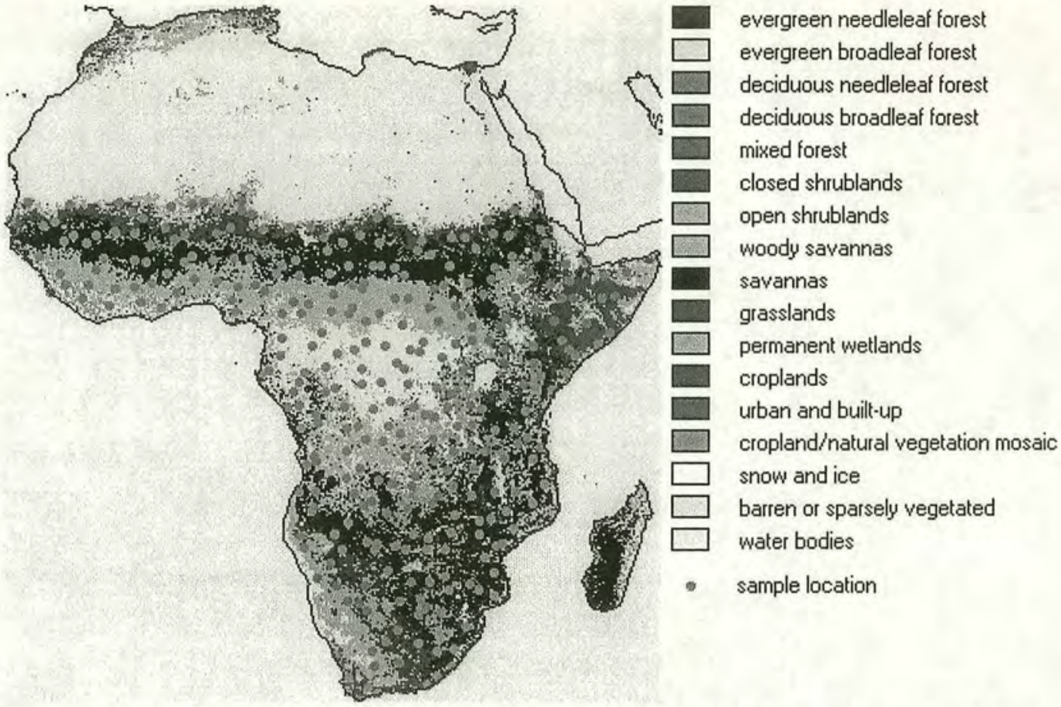


Figure 6.2. IGBP DISCover habitat classification of Africa, with the 301 point locations used to sample PCA and other images. Sample points were excluded from barren habitats, water bodies, urban locations, croplands, and from north of the Sahara.

Figure 6.3. Sub-Saharan Africa, as defined using a mask developed from the IGBP DISCover GIS database. The mask removes barren lands, large water bodies, and agricultural and urban areas from the data sampling procedure. The pattern of coloured grid cells illustrates the sample scheme of 161 cells, varying in size from 80,617 to 132,809 km^2.

RESULTS

Primary productivity

Figure 6.4 shows the mean NDVI image. Each pixel is the mean of NDVI values at that location in the 204 images of the time series. Figure 6.5 shows the relationship between mean annual NDVI and mean annual rainfall for the continent of Africa. NDVI is closely related to rainfall, and both measures provide estimates of primary productivity. However, the NDVI data is available at a far finer spatial resolution at the continental scale.

Evapotranspiration is a measure of the amount of water lost from a soil surface by evaporation and transpiration, and is more closely allied to plant growth than direct rainfall measurements. Actual evapotranspiration is difficult to measure, and data are not available for continental Africa. Potential evapotranspiration can however be estimated from basic meteorological data (Smith 1990, 1993), and its relationship to NDVI is shown in figure 6.6. Rather than providing another index of primary productivity, ET_0 has been interpreted as a measure of the amount of energy available in the environment. This explains why ET_0 is negatively related to productivity in Africa (figure 6.6), because high levels of available energy occur where temperatures and insolation are greatest. In Africa, productivity is more likely to be limited by water availability, which falls with increasing temperature and insolation.

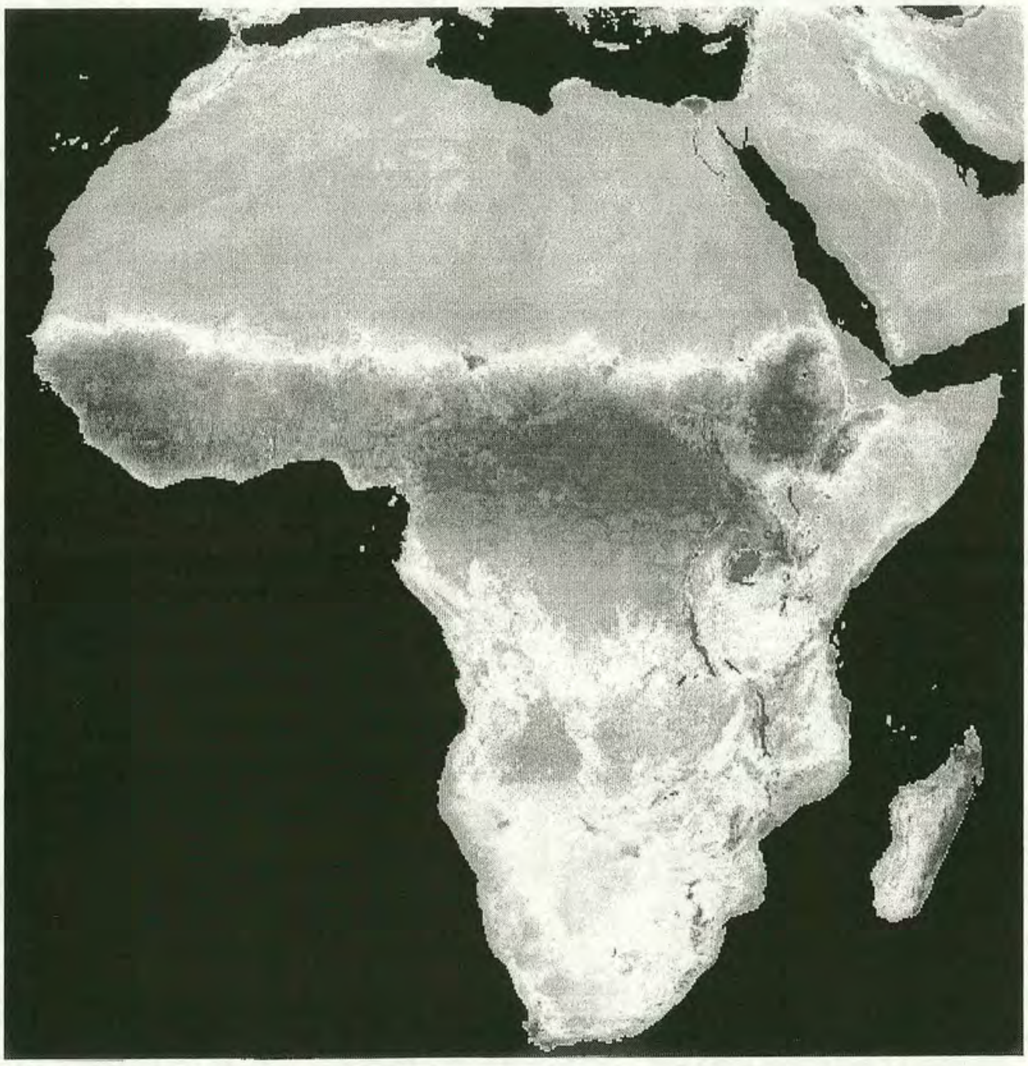


Figure 6.4. Mean NDVI from the 17 year dataset. Green pixels indicate high NDVI and primary productivity. Yellow and orange pixels indicate low and very low NDVI and primary productivity. NDVI is closely related to primary productivity.

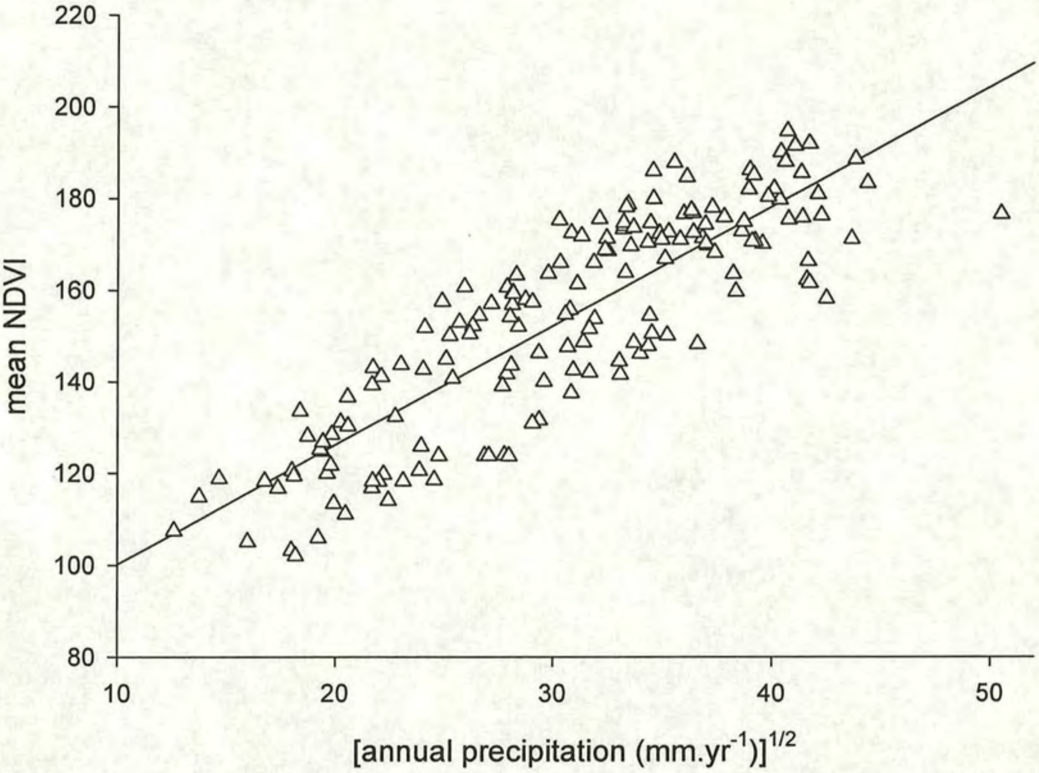


Figure 6.5. The relationship between mean annual NDVI, measured by satellite, and the square root of mean annual precipitation spatially interpolated from weather station records. NDVI is a unitless normalised ratio of reflectances in visible and infra-red wavebands, which has been re-scaled from its original range of -1 to +1 onto an integer scale 1-255. NDVI = 74.1 + 2.60 $[\text{rainfall}]^{1/2}$, $R^2_{adj} = 73.4\%$, $F = 441.85$, $n = 161$, $P << 0.001$.

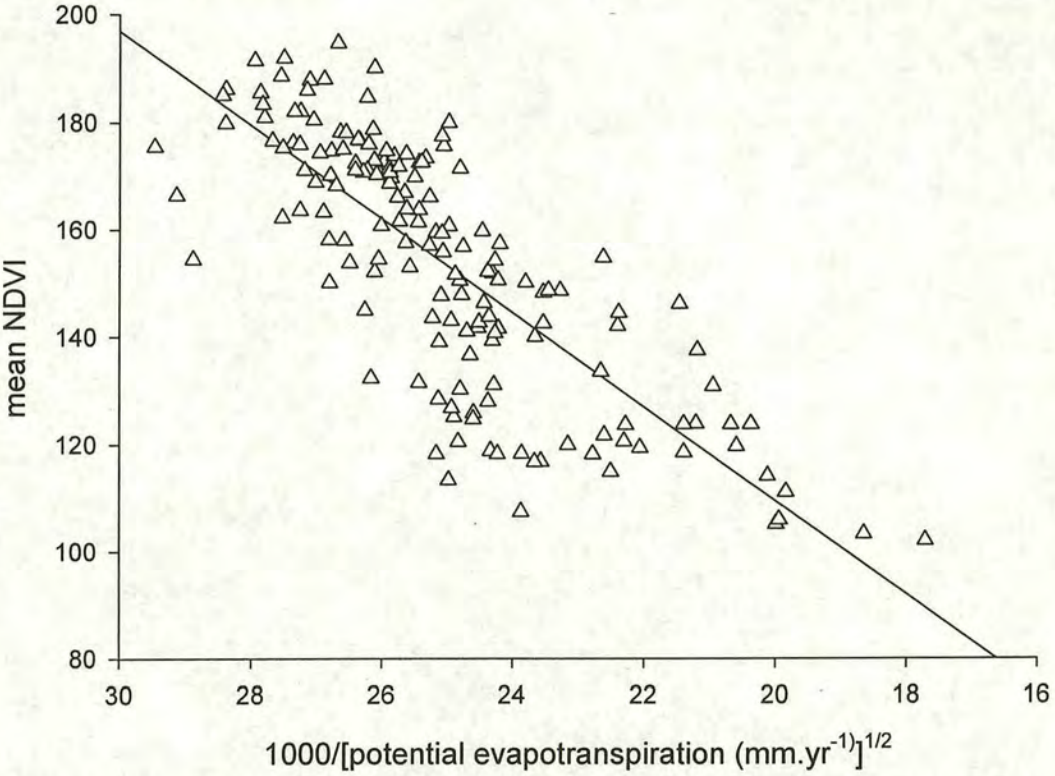


Figure 6.6. An alternative measure of the energy supply, potential evapotranspiration (ET_0). ET_0 was inverse square root transformed to normalise the data. The transformed ET_0 axis has been reversed so that evapotranspiration increases from left to right. ET_0 is negatively related to NDVI because it does not take water supply into account, and therefore is highest where temperatures are highest and insolation greatest. ET_0 has been used as an index of available energy in the environment rather than as a direct measure of energy flow through an ecosystem. The relationship is given by $NDVI = -65.3 + 8743[ET_0]^{-1/2}$, $R^2_{adj} = 62.1\%$, $F = 262.75$, $n = 161$, $P << 0.001$. The relationship of ET_0 with rainfall (not shown) is similar, though less strong, with $[rainfall]^{1/2} = -28.0 + 2338[ET_0]^{-1/2}$, $R^2_{adj} = 40.6\%$, $F = 110.53$, $n = 161$, $P << 0.001$.

Temporal variability in productivity: interpreting PCA output

The first 12 component images are illustrated in figure 6.7. Loadings graphs for the first 12 components are shown in figure 6.8. These represent the correlation (*y* axis) of each image in the monthly time series (*x* axis) to the PCA component image. Figure 6.9 shows the eigenvalues and % variance explained for the first 12 components. The eigenvalue of a component is proportional to the variance explained.

The first component is very strongly correlated to the mean NDVI image ($r = 0.9916$, $R^2_{adj} = 98.31\%$, $n = 301$, $P \ll 0.0001$) and explains most of the variance in the time series (54.3%, see figure 6.9). The loadings are positive throughout the year, with seasonal variation (figure 6.8 a). All other components vary around zero. The seasonal cycling agrees with previous work (Baird 1996) that showed that the correlation of monthly NDVI images to a mean image in East Africa varied cyclically with the seasons.

Components 2 and 3 are seasonal signals, out of phase with one another, with a single maximum and minimum per annum (figure 6.8a). Component 2 peaks in the second half of the year, and component 3 a little earlier, in mid-year. Component 3 exhibits more variability, with a tendency for the amplitude to increase during the period each satellite was in operation. In several years, the build-up in component 3 starts early, causing a 'shoulder' effect (*e.g.* 1983, 1984, 1986, 1990-1994, 1998). The cycling in component 2 is in contrast extremely regular.

The spatial distributions of components 2 and 3 (figures 6.7b and c) show that they are also somewhat complementary in geographical location. Component 2 represents the main annual seasonality pattern in Africa. A flush of growth in the second half of the year, in the region between the equator and the southern edge of the Sahara, is indicated by positive component values in that region of the image and peak loadings for that component in the second half of the year. The negative values in the image in southern Africa, together with the negative loadings in the first half of the year, indicate a growth season in southern Africa during the first half of the year.

Component 3 is a weaker event, with a much smaller eigenvalue than component 2 (see figure 6.9). The peak loadings occur in the middle of the year, a little ahead of those in component 2. Positive component values in the image (figure 6.7c) occur throughout eastern and southern Africa (which have negative component 2 values), as well as across a band to the south of the Sahel. The Sahel itself, the Ethiopian highlands, and a band to the south of central Africa have negative component 3 values. Component 3 indicates that the development of the growing season follows different patterns in different regions. In the Sahel, Ethiopian highlands, and to the south of central Africa, the beginning of the main growing season is a weaker event, whereas through eastern and southern Africa, the main growing season starts with very strong growth.

Components 4 and 5 loadings are uncorrelated ($r = 0.0047$, $n = 204$, $P = 0.946$), as are the component images themselves ($r = 0.0317$, $n = 301$, $P = 0.584$). However, the similar nature of the loadings graphs is illustrated by plotting the correlation coefficient between component 5 loadings, and lagged component 4 loadings (figure 6.10). The figure illustrates that component 5 lags behind component 4 by about one or two months.

Both components cycle twice annually, with two maxima and minima. The spatial distributions of the two components (figures 6.7 d and e) are somewhat complementary. Component 4 has positive values in the Horn of Africa, in central Africa, and in a band to the south of the Sahel, with negative values in the Sahel, southern Africa and the south of East Africa. Component 5 has negative values in central Africa, and positive values in the Sahel, southern Africa, and Kenya and southern Somalia.

Component 5 loadings (figure 6.8a) show some evidence of artefactual trends (see below) associated with satellites and/or sensors, with upwards trending scores in the latter half of the NOAA-11 flight, and through much of NOAA-14's flight. There is a sharp discontinuity between NOAA-11 and NOAA-14, even allowing for the brief interlude when NOAA-11 failed, and NOAA-9 and -12 were briefly reactivated (Kidwell 1998). However, compared to other artefactual components (see below), component 5 is primarily not artefactual.

Figure 6.7a. PCA component 1. High scores are indicated by lighter tones.

Figure 6.7b. PCA component 2. High scores are indicated by lighter tones.

Figure 6.7c. PCA component 3. High scores are indicated by lighter tones.

Figure 6.7d. PCA component 4. High scores are indicated by lighter tones.

Figure 6.7e. PCA component 5. High scores are indicated by lighter tones.

Figure 6.7f. PCA component 6. High scores are indicated by lighter tones.

Figure 6.7g. PCA component 7. High scores are indicated by lighter tones.

Figure 6.7h. PCA component 8. High scores are indicated by lighter tones.

Figure 6.7i. PCA component 9. High scores are indicated by lighter tones.

Figure 6.7j. PCA component 10. High scores are indicated by lighter tones.

Figure 6.7k. PCA component 11. High scores are indicated by lighter tones.

Figure 6.7*l*. PCA component 12. High scores are indicated by lighter tones.

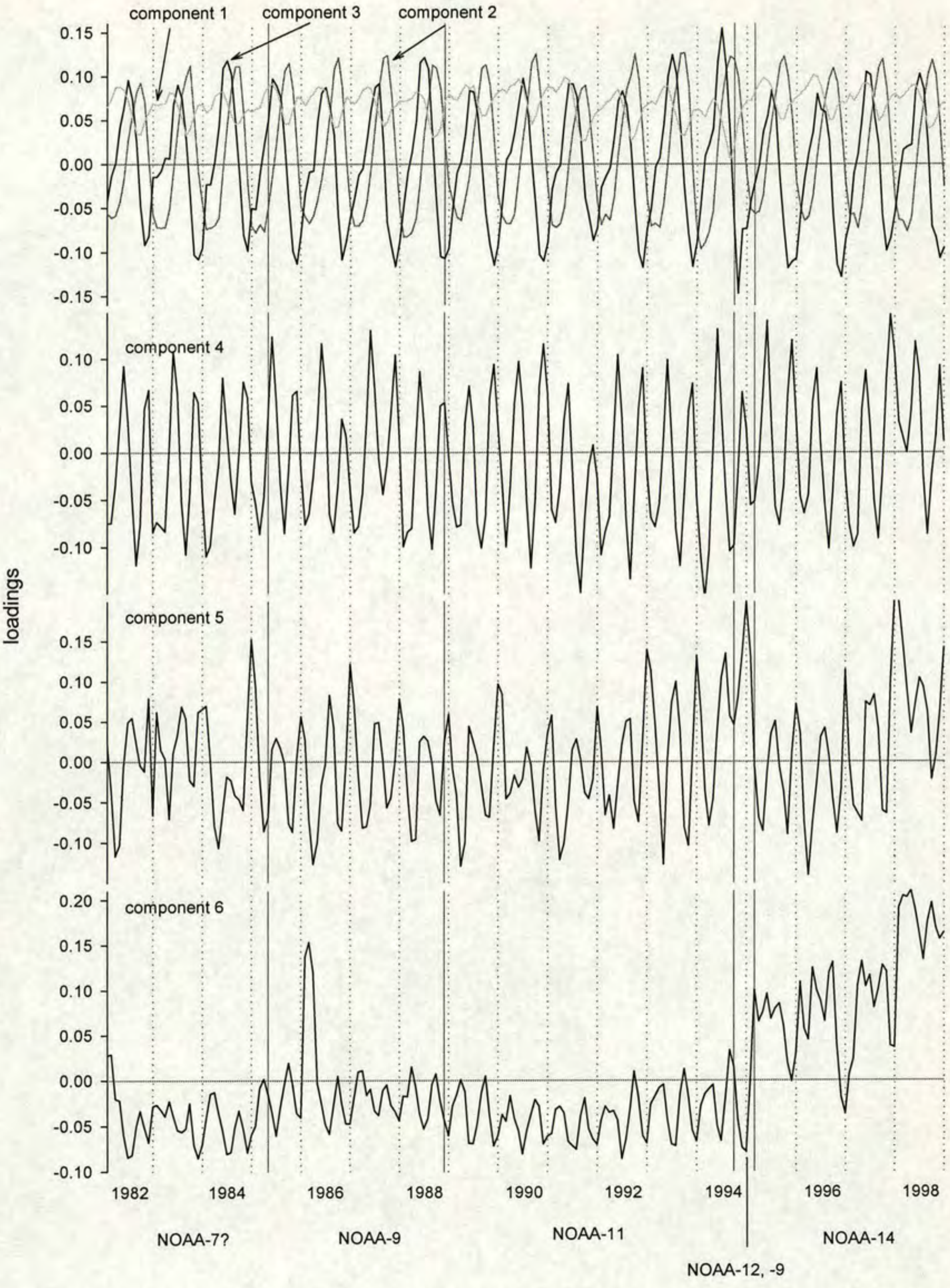


Figure 6.8a. Loadings graphs for PCA components 1 to 6. See legend to figure 6.8c for details. Component 1 is very highly correlated to the mean image of the time series. Components 2 and 3 are signals with a single cycle each year. Components 4 and 5 cycle twice each year. Component 6 is artefactual. See text for details of interpretation.

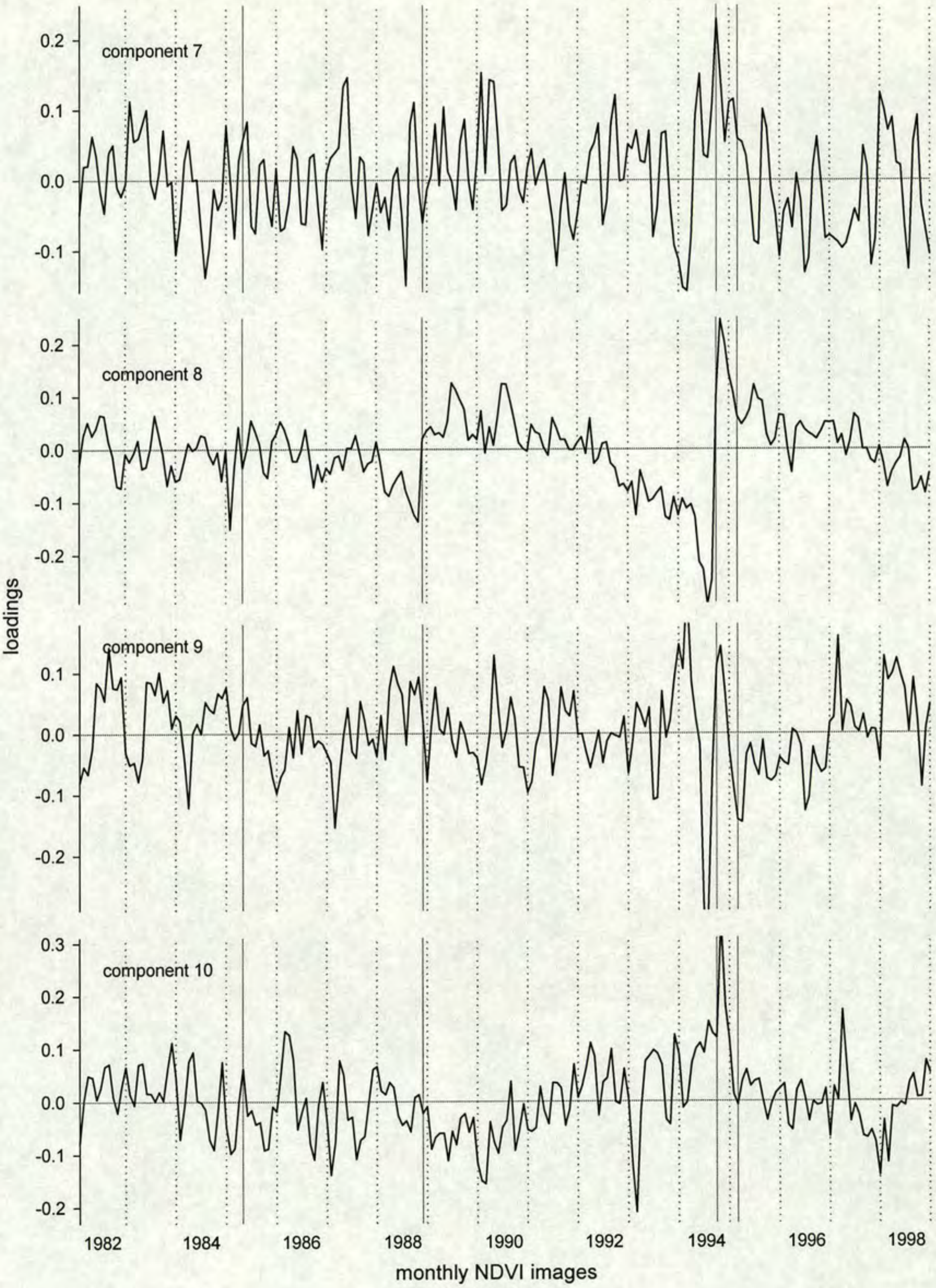


Figure 6.8b. Loadings graphs for PCA components 7, 8, 9 and 10. See legend to figure 6.8c for details. Component 7 does not appear to be artefactual, but has no clear interpretation. Components 8, 9 and 10 are artefactual. See text for details of interpretation.

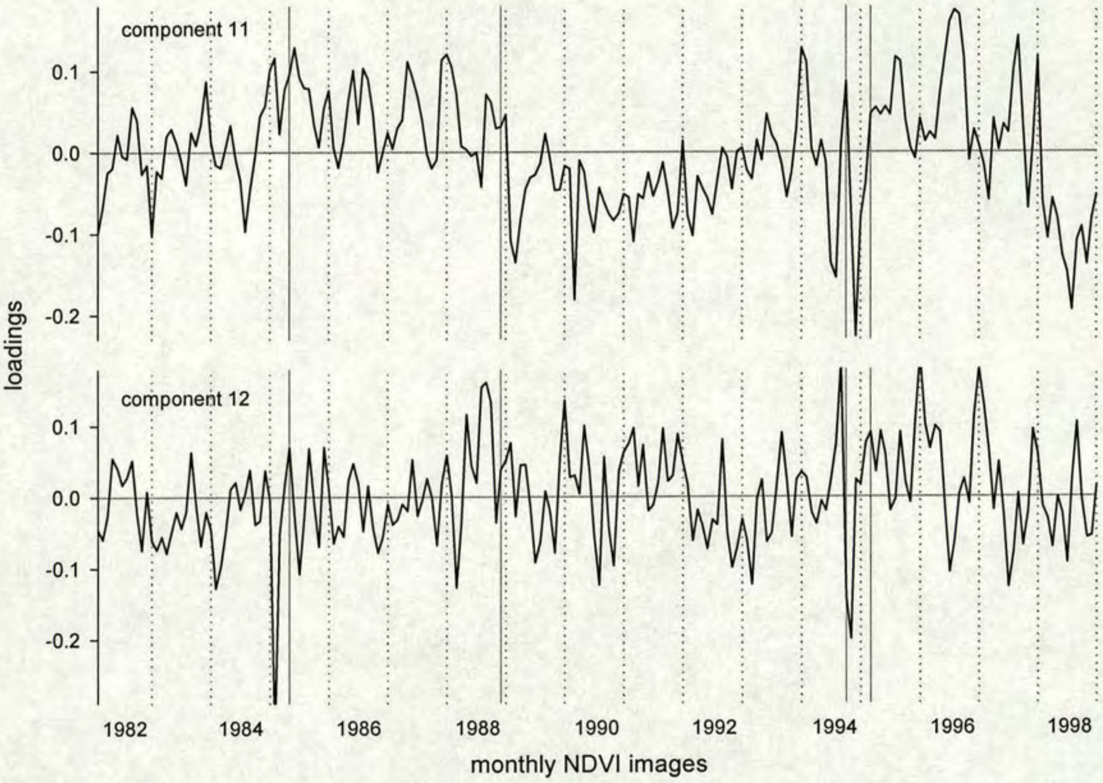


Figure 6.8c. Loadings graphs for PCA components 11 and 12. Component 11 is artefactual, and component 12 appears to be largely random noise. See text for details of interpretation.

The loadings for a component show the correlation (*y* axis) of each NDVI image in the time series (*x* axis) to that component. The time period of each satellite flight is indicated on the graphs. In late 1994, NOAA-11 failed, and for a few months older satellites were brought back into service until NOAA-14 began operation. Data collected during this period are unreliable (Kidwell 1998).

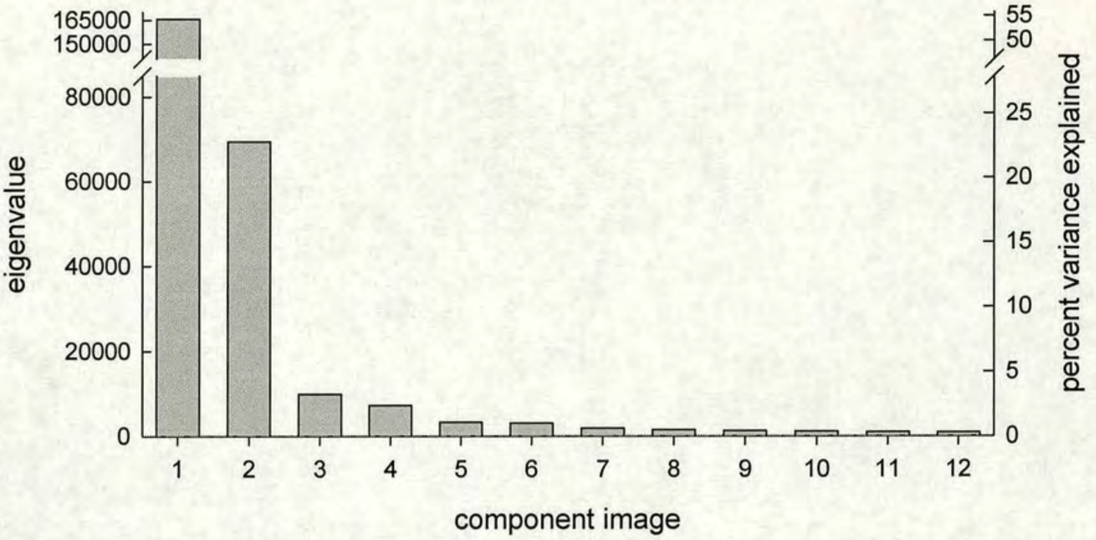


Figure 6.9. Eigenvalues and percent variance explained for the first 12 components. The first component, highly correlated to the mean image of the time series (see text), explains most of the variance (54.3%). The second component explains 22.8% of the variance, and the other components each explain less than 3.3%.

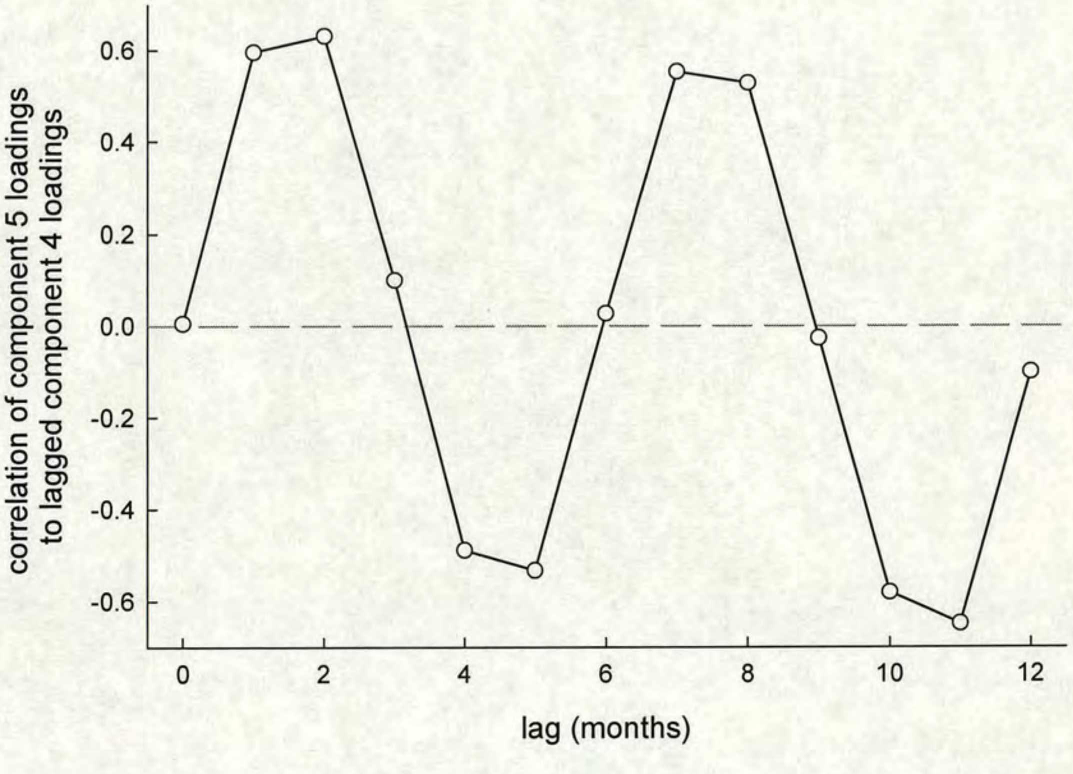


Figure 6.10. Components 4 and 5 loadings are uncorrelated, but component 5 is quite strongly correlated to component 4 loadings one and two months later. The lagged time series were created by moving component 4 loadings ahead by the indicated number of months (*e.g.* loadings for January are moved ahead to February for a lag of 1, March for a lag of 2 *etc.*).

Artefactual signals

Eastman & Fulk (1993) pointed out that a characteristic of components associated with sensor artefacts (in particular, degradation in sensor response over time, and orbital drift of the platform resulting in later equatorial crossing times) is that the image of the component should have very low variance because the same artefact occurs throughout the image. With the much longer time series available for the current analysis, further strong evidence of artefactual signals can be seen in the loadings graphs (figure 6.8). Trends in component loadings associated with specific satellite flights, and synchronisation of discontinuities in a component loading graph with replacement of satellites, each provide strong evidence of sensor bias. The loadings graphs have been marked to show the time during which each NOAA satellite was used for the collection of data used in the GIMMS dataset (Kidwell 1998).

These indicators easily identify components 6, 8, 9, 10 and 11 as being primarily or entirely artefactual. Component 6 loadings identify a strong upwards trend during NOAA-14, with the rest of the time series having negative loadings. Component 8 loadings trend downwards during every flight, with major discontinuities between flights. Component 11 loadings exhibit a strong downwards trend during NOAA-14, and discontinuities between most satellite transitions. The loadings graphs of components 9 and 10 show trends apparently associated with individual satellites. In component 9, there is a sharp discontinuity between NOAA-11 and -14, and a clear upwards trend during NOAA-14. In component 10, there is an upwards trend throughout the flight of NOAA-11, and a discontinuity at the -11 to -14 transition. The images of all of these components show very low spatial variability (figures 6.7 f, h, i, j and k).

The component 12 image (figure 6 *l*) also has very low variance, indicating that the component is unlikely to be a natural phenomenon. The loadings graph (figure 6.8c) is very spiky, but with no trends or discontinuities synchronised with satellite replacement. Component 12 therefore appears to be largely a random noise remnant.

Temporal and spatial coefficients of variation

Figures 6.11 and 6.12 show the images of intra- and inter-annual coefficients of variation. Seasonality (figure 6.11) is high across 2 broad west-to-east bands to the north and south of the central African forests. Inter-annual variability (figure 6.12), which may be thought of as an index of unpredictability, is high in the Sahel, East Africa, and to the south of the central African forests. These regions include the major savanna and grassland biomes of Africa (see figure 6.2).

Figure 6.13 shows the spatial coefficient of variation image. This image was generated using the FILTER module of Idrisi to calculate the CoV at each pixel of a 9x9 grid of pixels centred on that pixel. The image therefore does not show the data that were sampled for analysis, but provides a visual indication of variability in spatial heterogeneity. Again, highest variability occurs across the two bands to the north and south of central Africa, and in East Africa.

The relationship between mean NDVI and its spatial variability is shown in figure 6.14. At low and at high primary productivity, spatial variability is very low. At intermediate levels of productivity, the range (and therefore also the mean) of variability increases, resulting in a unimodal relationship between primary productivity and its spatial variability.

The relationships between mean NDVI and the 2 temporal coefficients of variation are shown in figures 6.15 a and b. There is a strong unimodal relationship with intra-annual variability ($R^2_{adj} = 40.0\%$). Seasonality is low wherever productivity is either low or high. Intermediate levels of productivity are associated with higher seasonality. Productivity and inter-annual variability are only very weakly correlated ($R^2_{adj} = 2.64\%$, $n = 161$, $P = 0.0222$).

The most important PCA temporal change components are components 2 and 3. In figure 6.16, these components are plotted against the two CoV indexes. The seasonality index (IACV) is related to both components 2 and 3 in a complex and complementary manner. In particular, the seasonality index first falls as component 2 increases, but then seasonality rises again. With component 3, seasonality is constrained to high values when PCA component 3 is either low or high, but seasonality varies in an unconstrained fashion over intermediate values of component 3. There is also a negative linear relationship between the unpredictability index

(IECV) and PCA component 3 ($R^2_{adj} = 10.2\%$, $n = 301$, $P < 0.0001$). There is no systematic relationship between the unpredictability index and component 3, nor between unpredictability and seasonality (figure 6.17, $R^2_{adj} = 0.02\%$, $n = 301$, $P = 0.3057$).

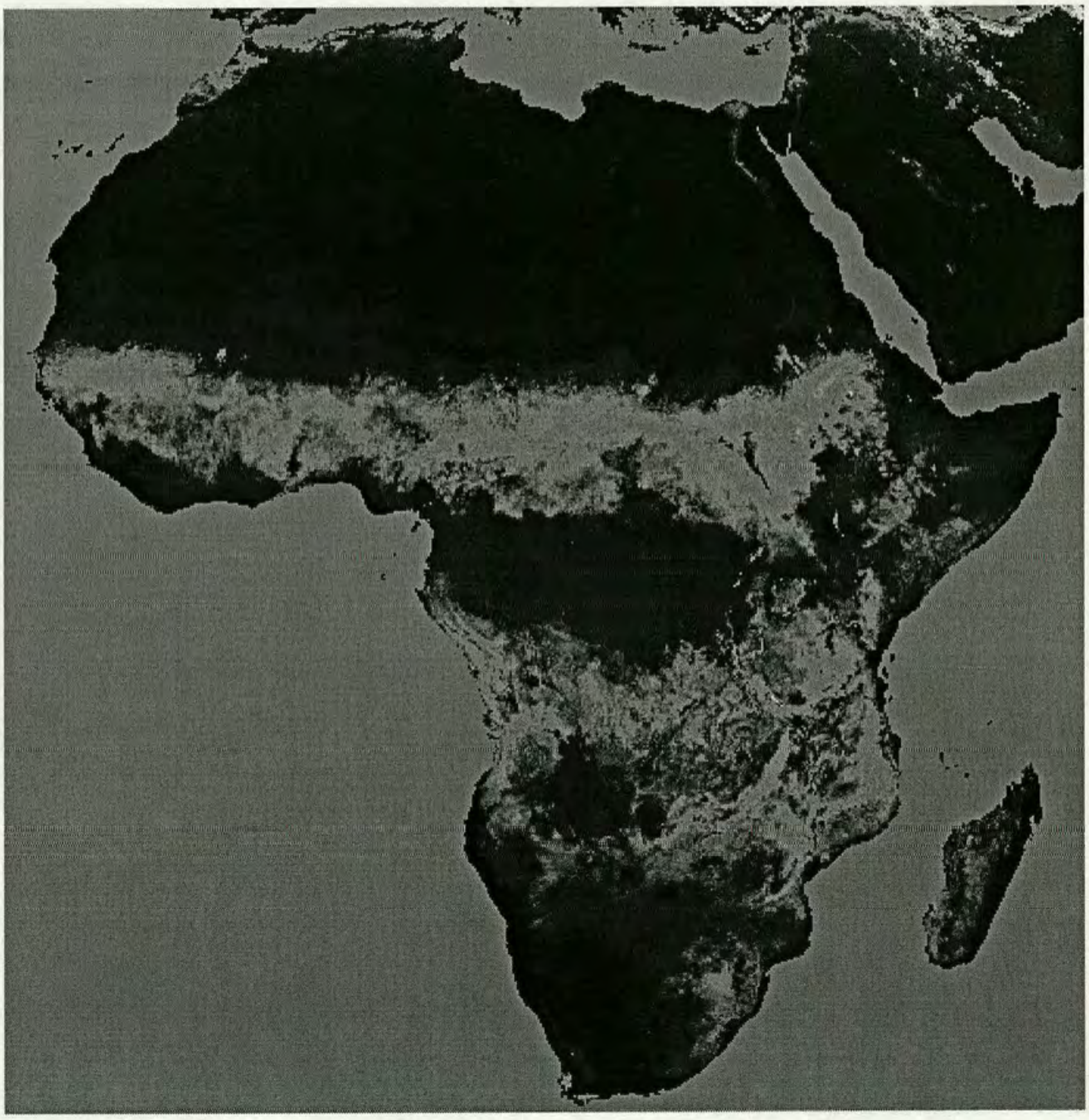


Figure 6.11. Seasonality index: intra-annual coefficient of variation (IACV).

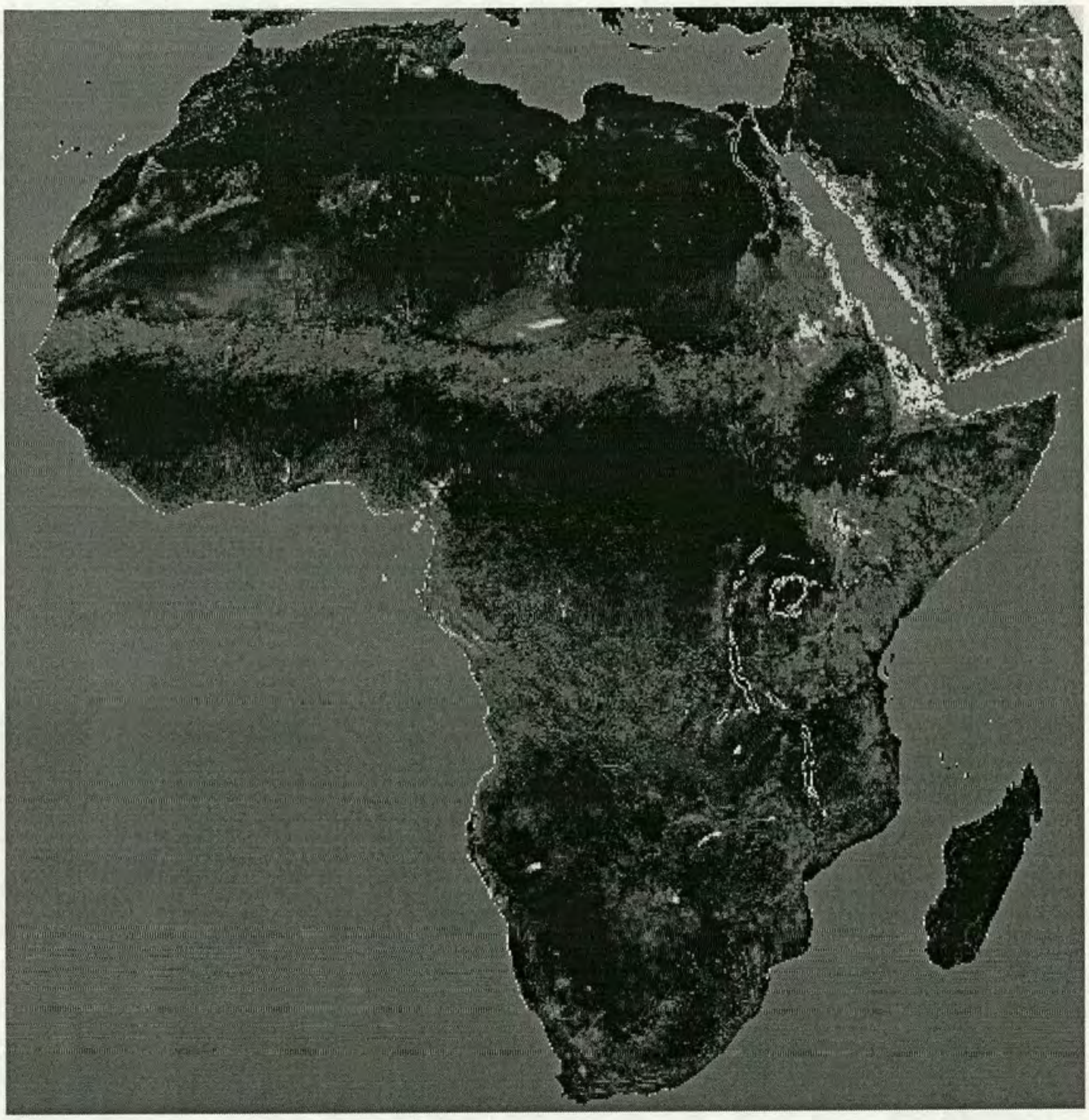


Figure 6.12. Unpredictability index: inter-annual coefficient of variation (IECV).

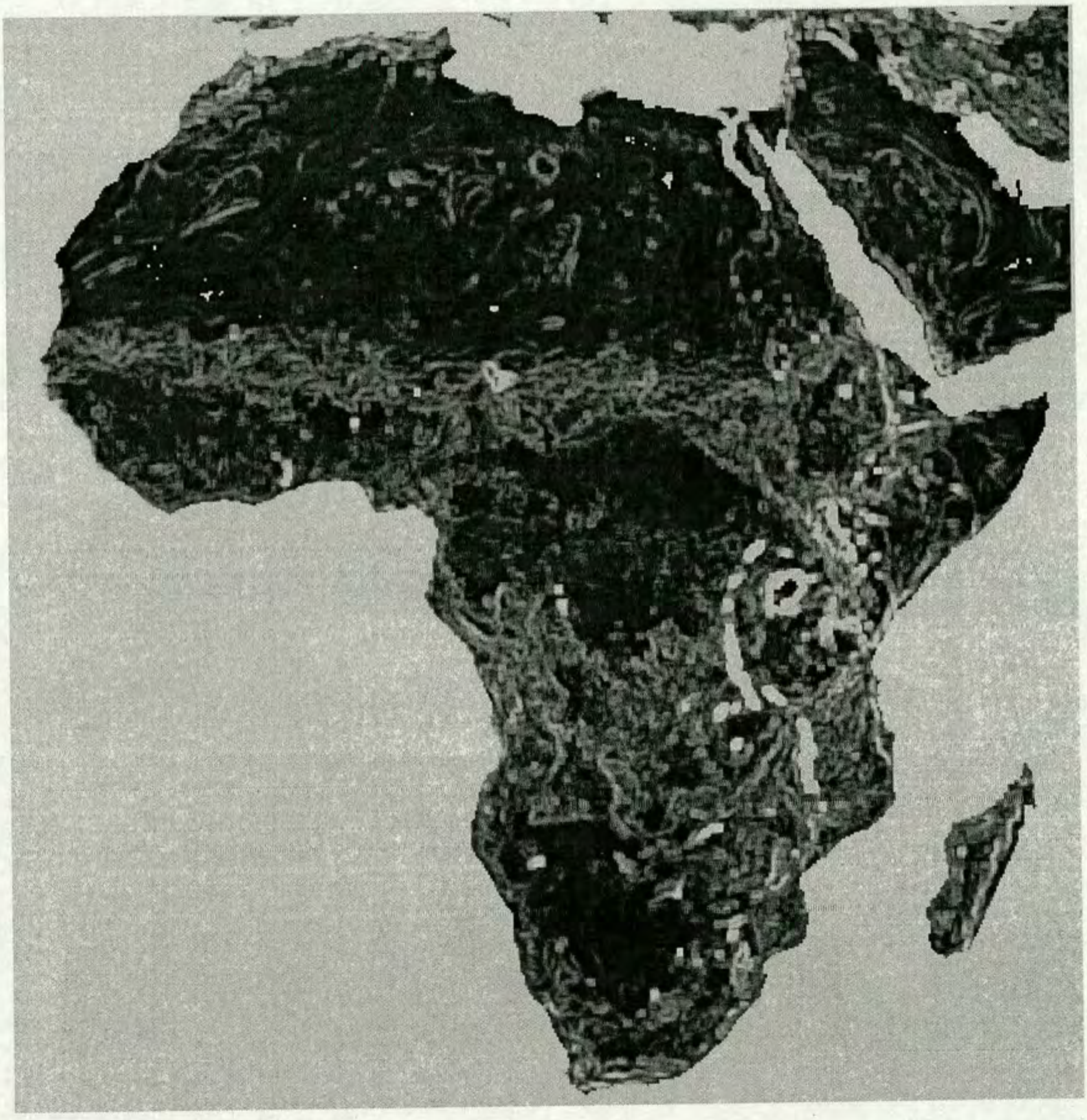


Figure 6.13. Spatial coefficient of variation, calculated from the mean NDVI image.

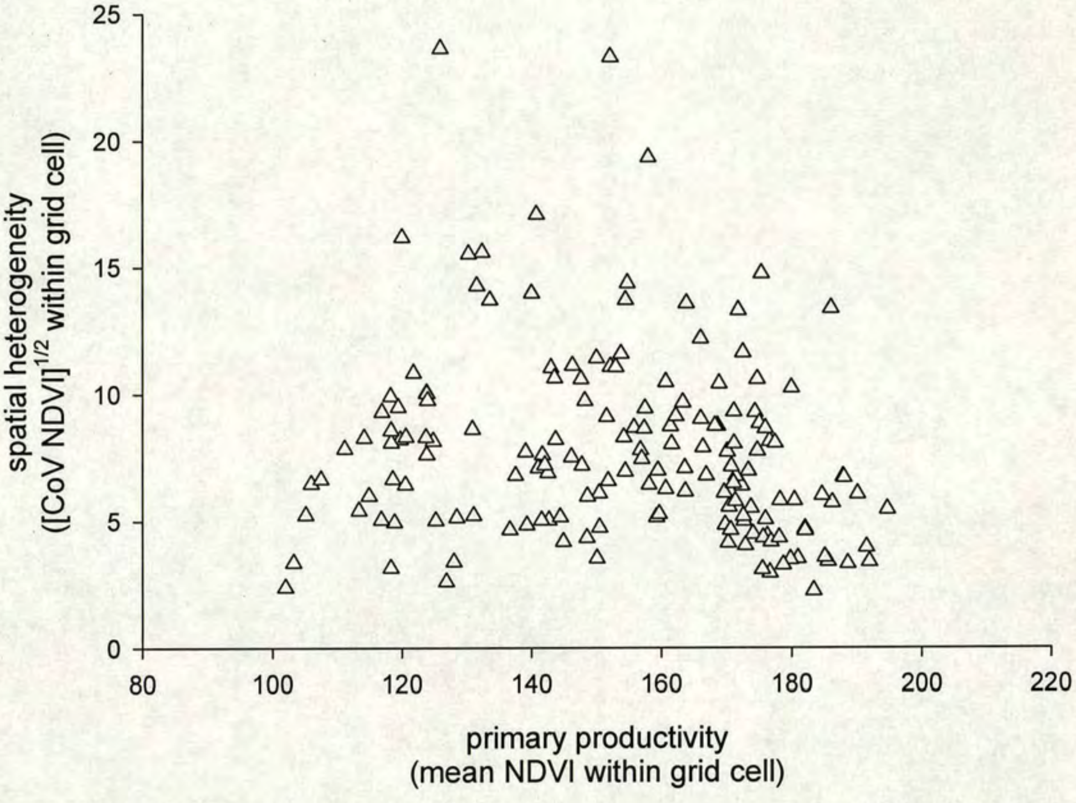


Figure 6.14. Variation in spatial heterogeneity with primary productivity. Spatial heterogeneity is defined as the coefficient of variation in NDVI within a grid cell. There is a slight, negative linear relationship ($[\text{CoV NDVI}]^{1/2} = 11.8 - 0.0264$ NDVI, $R^2_{adj} = 2.2\%$, $F = 4.61$, $n = 161$, $P = 0.033$), but the unimodal relationship is much stronger: $[\text{CoV NDVI}]^{1/2} = -37.0 + 0.645 \text{ NDVI} - 0.00225 \text{ NDVI}^2$, $R^2_{adj} = 11.9\%$, $F = 11.83$, $n = 161$, $P < 0.0001$. The quadratic function reflects the restriction of spatial heterogeneity to low values at either end of the productivity gradient, with unconstrained variability in heterogeneity over the intermediate part of the productivity gradient.

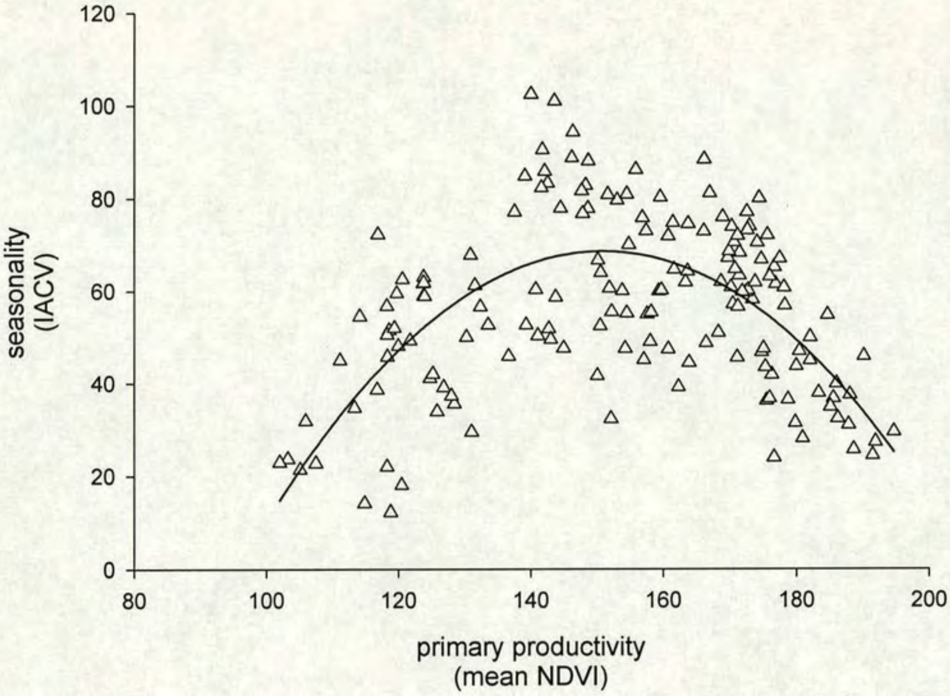


Figure 6.15a. The unimodal relationship between productivity and seasonality. IACV = -445.6936 + 6.8208 (mean NDVI) - 0.0226 (mean NDVI)^2, $R^2_{adj} = 0.400$, F = 54.431, n = 161, P < 0.0001.

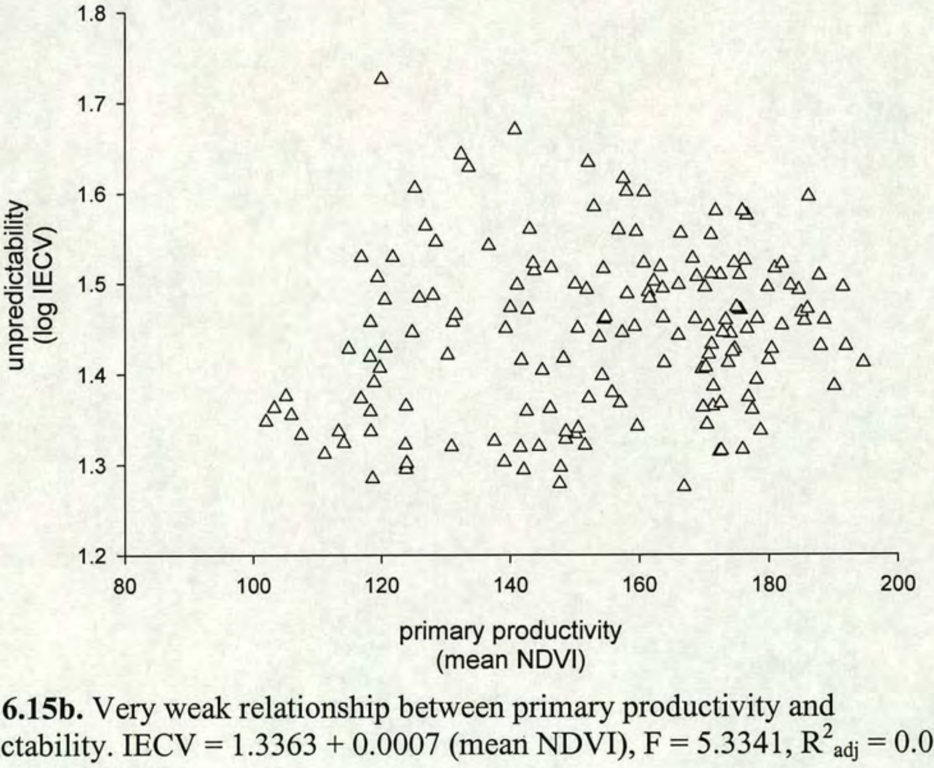


Figure 6.15b. Very weak relationship between primary productivity and unpredictability. IECV = 1.3363 + 0.0007 (mean NDVI), F = 5.3341, $R^2_{adj} = 0.0264$, n = 161, P = 0.0222.

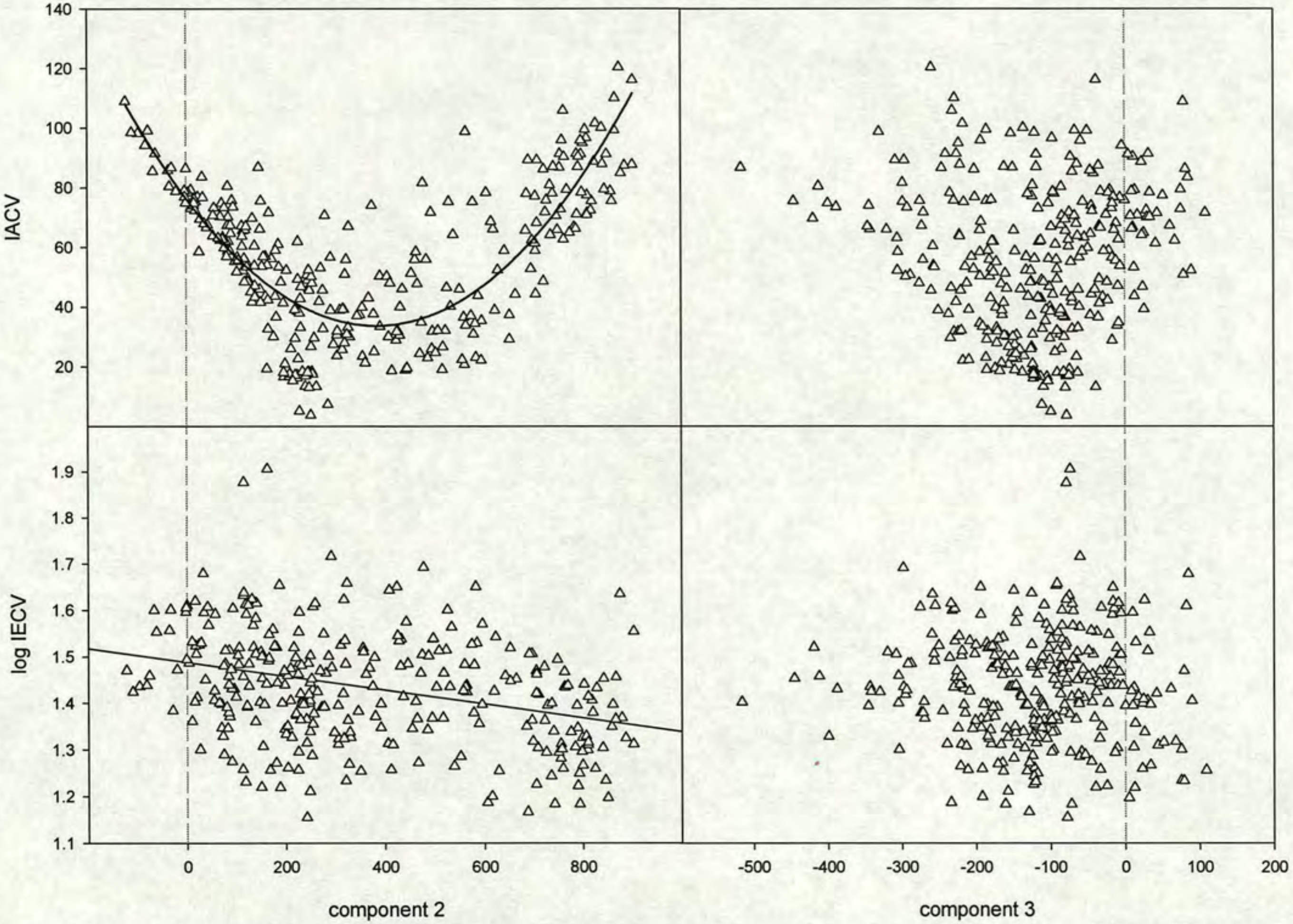


Figure 6.16. Relationships between PCA components of temporal change, and intra- and inter-annual coefficients of variation. PCA component 2 and IACV are closely linked: IACV = 76.4103 - 0.2224 cpt2 + 0.0003 $(cpt2)^2$; $R^2_{adj} = 0.636$, n = 301, F = 262.974, $P < 0.0001$. IECV and PCA component 2 are also related: log(IECV) = 1.4880 - 0.0001 log(IECV); $R^2_{adj} = 0.102$, n = 301, F = 34.965, $P < 0.0001$. IACV is constrained to have high values when PCA component 3 is low or high, with unconstrained variation in IACV when PCA component 3 has intermediate values. There is no relationship between PCA component 3 and IECV: $R^2_{adj} = - 0.003$, n = 301, F = 0.1708, P = 0.6797.

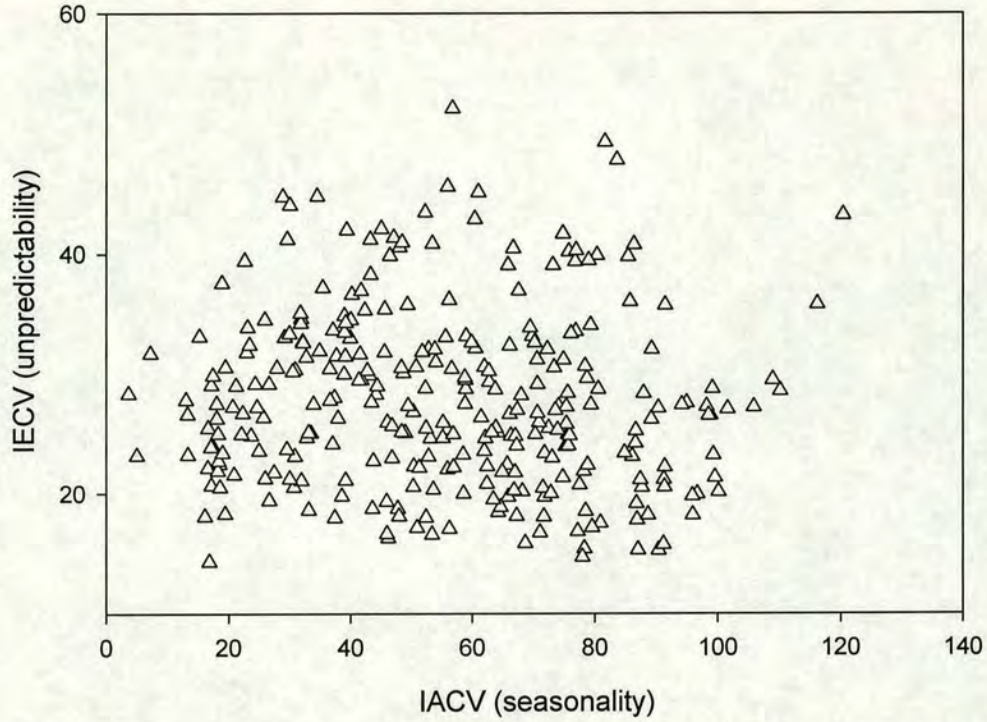


Figure 6.17. Seasonality and unpredictability are independent ($R^2_{adj} = 0.00018$, $F = 1.0529$, $n = 301$, $P = 0.3057$).

DISCUSSION

Satellite data provide a powerful means of describing spatial patterns of variation in environmental conditions across very broad geographic scales. The NDVI data collected by the NOAA series of polar orbiting satellites are unique because they have been collected over a long time period, allowing temporal variability to be assessed in great detail as well.

The NDVI data used in this chapter are highly correlated to primary productivity, as reviewed in the *Introduction* and as illustrated by the close relationship of NDVI to both rainfall and potential evapotranspiration. The NDVI data provide a better measure of primary productivity than the climatic variables, firstly because of the much more detailed geographical and temporal coverage available, but also because NDVI measures a biophysical parameter - absorbed PAR - that is directly dependant on primary productivity. Rainfall and ET_o are less directly correlated to primary productivity.

Principal components analysis of the time series of satellite images revealed several different patterns of temporal variability, and also identified the regions that experience those patterns. There were two single-cycle annual patterns, one lagging the other by a few months, and two double-cycle annual patterns, again with a lag of a few months.

The eigenvalue of each component provides a measure of its relative importance or contribution to overall variability. Only the first two components had large eigenvalues, and since the first component is essentially the mean, component 2 is the most important component of temporal variability. This component shows the geographic regions affected by the main annual wet/dry season cycle - two broad bands from west to east, above and below the central forests, and meeting in East Africa. The northern band, with positive values on the component image, has peak productivity in the second half of the year, as shown by the maxima on its loadings graph. The southern band, with negative values on the image, has peak productivity in the first half of the year, as shown by the minima on the loadings graph.

The low eigenvalues of the other components do not automatically mean they are unimportant. Instead, for non-artefactual components, low eigenvalues can result either because the pattern is of low amplitude, or else because it is restricted to a small set of geographical regions. Component 3 for example, is largely restricted to narrow bands and patches in comparison to component 2. Component 3 identifies areas whose component 2 cycle is modified above or below the productivity predicted by component 2. This illustrates the sensitivity of the PCA method, with its ability to dissect temporal variability and its geographic distribution.

As is typical of principal components analyses, interpretation is not simple and *a priori* patterns cannot be easily introduced to the method (although see below - *Some further analyses*). The inter- and intra-annual CoV's were used in an attempt to examine temporal patterns that were of particular interest - seasonality, and variation between years (which can be thought of as unpredictability). The unimodal relationship between primary productivity (mean NDVI) and seasonality may be explained because the lowest productivity habitats must have constantly low productivity, and the highest productivity habitats have constantly high productivity. Perhaps as may have been expected, unpredictability has no systematic relationship to mean productivity. The unpredictability image represents one-off perturbations, and long term trends such as el Niño phenomena.

Primary productivity also has a unimodal relationship with its spatial CoV. Again, this pattern may be explained if the lowest productivity regions (sample grid cells) have uniformly low productivity, and the highest productivity cells have uniformly high productivity. This pattern has implications for explanations of the relationship between ungulate species richness and primary productivity. These were discussed in chapter 2, and will be examined in chapter 7.

Sensor bias and degradation

Despite the fact that the data were intensively pre-processed by NOAA and NASA to remove calibration errors and other biases, the PCA has revealed that systematic errors associated with satellite flights still remain. The PCA has identified these signals, and has isolated them, so that we can be confident that the other signals represent true patterns, and are not artefactual.

Eastman & Fulk (1993) did not have such a long time series of imagery available to them. Furthermore, the Idrisi GIS system (designed by Eastman) was and is not capable of handling such a large number of images, and Multispec had not been developed at that time. Multispec was designed to analyse the data produced by a more modern generation of sensors, which record imagery in dozens of very narrow wave bands rather than a few broad bands. In fact, the PCA facility of Multispec was originally designed to reduce these multispectral data sets to a small number of channels. The application to a temporal sequence of images is new. The ability to analyse such a long time series provided the opportunity of plotting loadings graphs across the flights of several satellites, providing further strong evidence of the artefactual nature of some components

Some further analyses

A major methodological difference from Eastman & Fulk (1993) was to use a habitat map to restrict the analysis to specific regions, and to exclude ocean regions from the PCA. This method could be extended much further, by using the DISCover map to extract specific habitats from each image and restrict the PCA to a single habitat. For instance, an analysis restricted to desert regions might be particularly sensitive to signals caused by sensor degradation, orbital drift and satellite replacement, since natural variation in NDVI is minimised in these habitats. PCA restricted to habitat types as identified in the DISCover maps would reveal temporal patterns exclusive to those habitats that may be undetectable when data from all habitats are analysed together.

The length of the time series would also allow an amalgamation of PCA with *a priori* definition of time scales of particular interest. A PCA of 17 mean annual images would generate components associated with inter-annual variation, and would very likely identify el Niño effects. A PCA of 12 mean monthly images would provide in depth analysis of seasonal variability.

ACKNOWLEDGEMENT

Data used by the author in this study include data produced through funding from the Earth Observing System Pathfinder Program of NASA's Mission to Planet Earth in co-operation with the National Oceanic and Atmospheric Administration. The data were provided by the Earth Observing System Data and Information System (EOSDIS), Distributed Active Archive Center at Goddard Space Flight Center which archives, manages, and distributes this data set.

7. RESOURCE COMPETITION AT THE CONTINENTAL SCALE: PRIMARY PRODUCTIVITY AND UNGULATE DIVERSITY IN SUB-SAHARAN AFRICA

INTRODUCTION

Species richness in virtually all groups that have been studied increases as primary productivity increases from very low levels (Rosenzweig 1995). This basic pattern may be understood as a straightforward consequence of the species abundance distribution. If species abundances are approximately log-normally distributed, then there will be a lower limit to abundance below which populations of rare species are not viable (Preston 1962a, b). Preston (*ibid.*) called this minimum viable population size the 'veil line'. In unproductive regions, all species abundances are low and many species will be 'veiled' - their potential abundance is too low for populations to persist, and diversity is low.

This mechanism explains why diversity is positively correlated to primary productivity at low to intermediate productivity, and is not controversial (Rosenzweig 1995). Rarity increases extinction risk. However, the Prestonian mechanism does not explain the very common observation that species richness falls as primary productivity exceeds some threshold value. Unimodal productivity-diversity relationships have been reviewed by Tilman & Pacala (1993), Rosenzweig & Abramsky (1993), Rosenzweig (1995), and Begon, Harper & Townsend (1996). Various hypotheses have been advanced to explain the decrease phase (reviewed by Rosenzweig & Abramsky 1993, Rosenzweig 1995). Most are either flawed, or only apply to a few situations. One model that does provide a general mechanism is resource competition theory (RCT).

The theoretical relationship between resource supply rate and species richness was described in chapter 2. Briefly, if species are competing for limited resources, then each species will be a superior competitor to all others for a specific range of resource supply ratios. A habitat that supplies a broad range of resource ratios can support a larger number of species. In order to supply a broad range of resource supply ratios, productive habitats must be very heterogeneous - resource supply rates must vary widely. In less productive habitats, a smaller range of variability can supply sufficient heterogeneity to support a large number of species. Figure 2.1a illustrates the basic theory.

This mechanism was described by Tilman (1980, 1982, 1986). An important assumption was that heterogeneity does not increase with productivity (figure 2.1a). This assumption has not been tested, and if violated could lead to monotonic increases in diversity (probably to an asymptote) throughout the entire productivity gradient (Abrams 1988, 1995, see figure 2.1b).

The amount of data required to provide estimates of spatial variability in productivity, alongside estimates of mean productivity and species richness, is prodigious, but satellite data are now available to do the job. This chapter will assess spatial variability in productivity in order to test between Tilman's (1980, 1982, 1986) and Abrams' (1988, 1995) hypotheses.

First, however, the relationship between productivity and ungulate species richness must be assessed. Previous studies at the regional scale have shown that ungulate species richness varies unimodally with primary productivity (Western 1991, Rosenzweig 1995, Baird 1996, Ritchie & Olff 1999). In chapter 5 (figure 5.13), a unimodal productivity-diversity relationship was observed within a single ecosystem. This chapter extends the analysis to the continental scale.

An alternative (or complementary) explanation of the unimodal pattern is that species richness and productivity both vary unimodally with disturbance rates and magnitudes, and that the species richness-productivity unimodal co-variation is caused by this (Rosenzweig & Abramsky 1993, Rosenzweig 1995). The long time series of satellite imagery analysed in chapter 6 will allow this hypothesis to be tested.

Hypotheses

1. **The pattern**: ungulate species richness is unimodally related to primary productivity.
2. **Tilman's assumption**: the spatial CoV of primary productivity is negatively correlated to productivity.
3. **The RCT mechanism**: species richness is positively correlated to the spatial CoV of primary productivity (*i.e.* to heterogeneity [standard deviation] corrected for varying productivity).
4. **The underlying RCT mechanism**: beta diversity (species turnover) is positively correlated to spatial CoV (because turnover should increase if habitats are more variable).
5. **The disturbance hypothesis:** species richness and primary productivity are both independently, unimodally related to disturbance.

METHODS

Data and sampling strategy

Normalised Difference Vegetation Index (NDVI) satellite imagery was downloaded from the African Data Dissemination Service (ADDS) website. Chapter 6 provides a full description of this dataset, describes how NDVI is directly related to primary productivity, and explains the procedures used to characterise spatial and temporal variability in primary productivity. Spatial variability was characterised using a mean NDVI image calculated over the entire time series, and a spatial coefficient of variation calculated from the mean NDVI image. Temporal variability in the NDVI dataset was characterised in chapter 6 using principal components analysis, and coefficients of variation (CoV).

The entire dataset is composed of 204 monthly images of mean NDVI, throughout Africa, for 17 years between January 1982 and December 1998 inclusive. Principal components analysis revealed four components of temporal variability, composed of two single annual cycle components, out of phase with one another, and two double annual cycle components, again out of phase. Two CoV indices were also generated - an intra-annual coefficient of variation characterised seasonality, and an inter-annual coefficient of variation characterised unpredictability.

Extent of occurrence (Gaston 1991) distribution maps for 89 species of African ungulates (table 7.1) were extracted from the African Mammals Database (Boitani *et al.* 1998). These maps were then overlaid to create a map of ungulate species richness throughout Africa (figure 7.1). 24 species were not included - reasons for their exclusion are given in table 7.1. In particular, species whose ranges are entirely restricted to the Sahara were excluded because the study region for this thesis is sub-Saharan Africa.

All data were manipulated and sampled using the geographic information system (GIS) Idrisi (Eastman 1997). Data were sampled by superimposing a grid over the study region, as described in chapter 6 (see figure 6.3). Within each cell, the total number of ungulate species occurring anywhere in the cell were counted, and average species richness within the cell was calculated. Satellite imagery and the various derivatives quantifying spatial and temporal variation in primary productivity that were generated in chapter 6 were also sampled using the grid scheme. The area in square kilometers of each cell was recorded. Comparisons between mean NDVI and PCA change components were carried out using the point sample scheme described in chapter 6. Statistical analyses were carried out using Minitab 12.1 (Minitab Inc. 1998).

Table 7.1. Classification of African ungulates, with number of species (bracketed) occurring in Africa. The taxonomic treatment followed here is based on Boitani *et al*. (1998), who generally follow Wilson & Reeder (1993), except where IUCN SSC Specialist Groups have recommended modifications. 89 of the 113 species were used in this study.

- Hyracoidea (11)
- Perissodactyla (6)
    - Equidae (4)
    - Rhinocerotidae (2)
- Proboscidea (1)
- Artiodactyla (95)
    - Non-Ruminantia (9)
        - Camelidae (1)
        - Hippopotamidae (2)
        - Suidae (6)
    - Ruminantia (86)
        - Bovidae (82)
            - Aepycerotinae (1)
            - Alcelaphinae (7)
            - Antilopinae (25)
            - Bovinae (10)
            - Caprinae (3)
            - Cephalophinae (19)
            - Hippotraginae (8)
            - Peleinae (1)
            - Reduncinae (8)
        - Cervidae (1)
        - Giraffidae (2)
        - Tragulidae (1)

Total = 113

Species not used in this study:

Hyracoidea	11 species
Perissodactyla	
Rhinocerotidae	2 species (black and white rhino)
Proboscidea	1 species (elephant)
Artiodactyla	
Suidae	1 species (feral pig)
Bovidae	
Caprinae	3 species
Hippotraginae	5 species
Cervidae	1 species (red deer)
	Total = 24

Reasons for exclusions:

Hyracoidea: taxonomically and ecologically distinct group.

Rhinocerotidae: current distributions are distorted and reduced by poaching, and distribution maps are kept confidential.

Feral pig: introduced species, only found on Mediterranean coast of north west Africa.

Caprinae: all occur north of study area (Sahara, Nile Valley, northern Ethiopia).

Hippotraginae: Scimitar-horned oryx and addax only occur in the Sahara, north of the study region, and *Oryx leucoryx*, the Arabian oryx, is also found outside the study area. *Hippotragus leucophaeus*, the blue buck, went extinct at the beginning of this century (Skinner & Smithers 1990). *Oryx beisa* is classed as a sub-species of *Oryx gazella* in the AMD database.

Red deer: only found on the Mediterranean coast of north west Africa.

Biodiversity components

Diversity was measured using GIS maps of the distribution of each ungulate species in Africa, obtained from the African Mammals Databank (Boitani *et al.* 1998). Biodiversity can be divided into three spatial components (Peet 1974, Magurran 1996). Species richness, or *alpha diversity*, is the number of species occurring within a habitat. In this study, alpha diversity is estimated as the mean number of species occurring throughout a sample grid cell, and therefore is a measure of the average alpha diversity within the cell. *Gamma diversity* is the species richness of an entire landscape, and here is estimated as the total number of species found within the cell.

Beta diversity, or differentiation diversity, represents the change in diversity associated with the change from one habitat to another, or along an environmental gradient. Here, beta diversity is estimated as the residual from the regression of alpha *vs.* gamma diversity (figure 7.2). In this scheme, beta diversity can be positive (more species occur within the area of the cell than predicted by the regression) or negative (fewer species than predicted). Beta diversity is also known as *turnover*, which refers to the fragmentation of species distributions, or the rate at which new species are encountered when travelling along a transect or through a region. Positive deviations from the regression indicate higher than average turnover, and negative deviations identify lower than average turnover.

Beta diversity has traditionally been measured using a variety of indices using sites-by-species data derived from sampling transects (reviewed in Magurran 1996). These indices measure beta diversity between pairs of sampling locations. The measure of beta diversity used here was developed to estimate beta diversity within a region (grid cell) rather than between point localities.

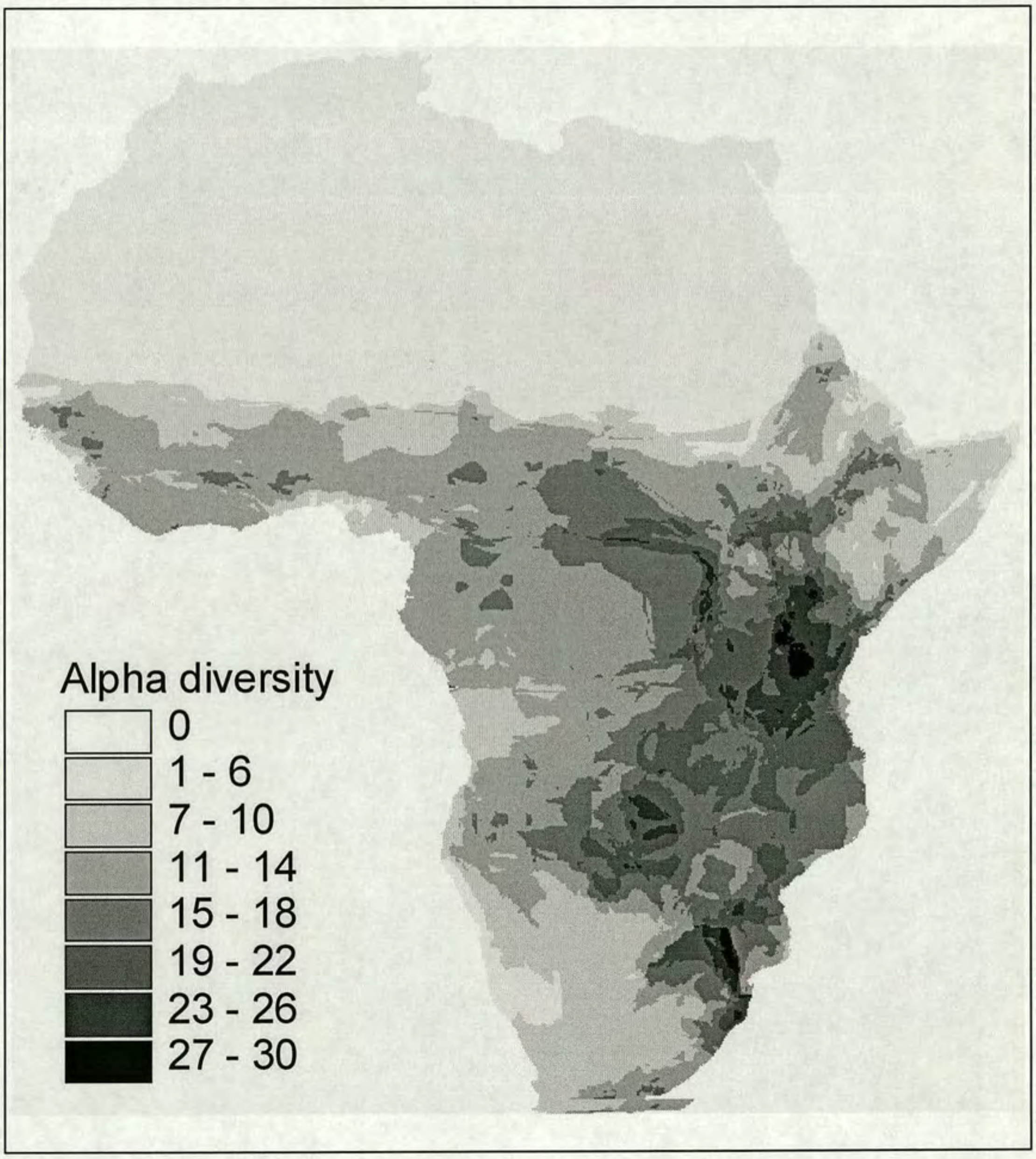


Figure 7.1. Ungulate species richness in sub-Saharan Africa. See table 7.1 for a list of the 89 species included in this figure. In particular, note that species with ranges restricted to the Sahara were excluded.

RESULTS

Biodiversity components

Mean or alpha diversity is closely, linearly related to total or gamma diversity ($R^2_{adj} = 70.8\%$, $P << 0.001$, figure 7.2). This relationship is further illustrated in the similarity of the species-area curves for each component (figure 7.3). In fact, probably because the range in area of the grid cells is small (from 80,617 km^2 to 132,809 km^2), none of the three components has a species-area relationship that differs from random (figure 7.3). Beta diversity is defined here as the residual deviation from the regression of gamma diversity as a function of alpha diversity (figure 7.2).

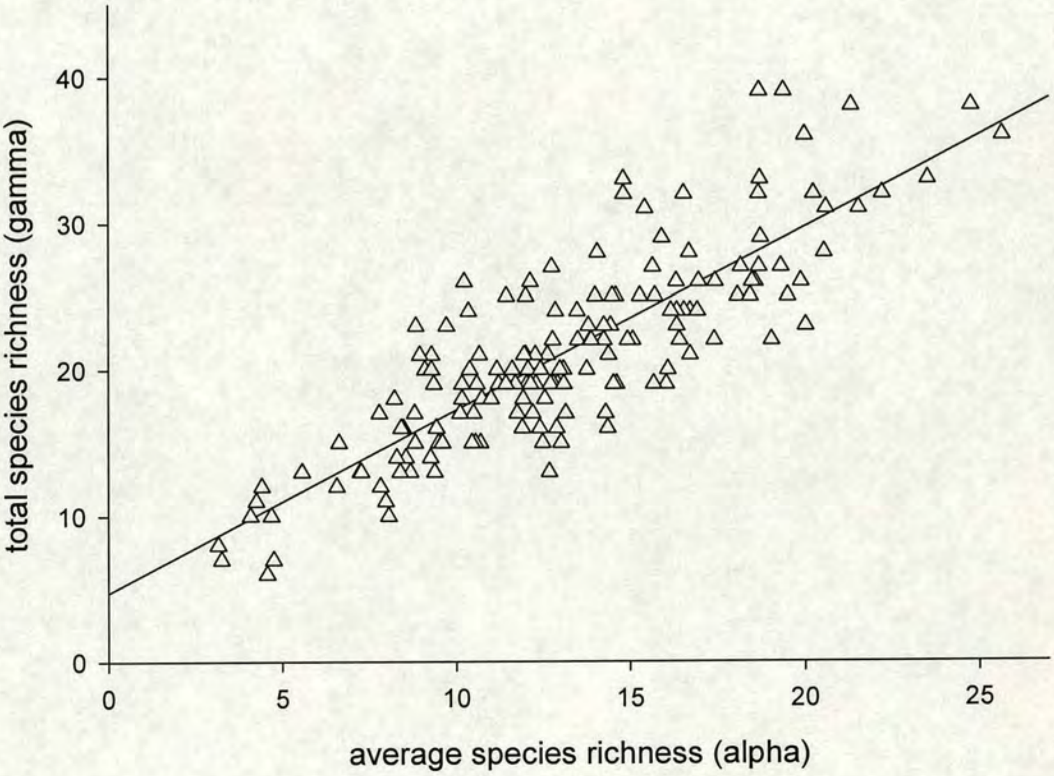


Figure 7.2. Alpha, beta and gamma diversity. Total species richness within a sample cell is closely, linearly related to mean species richness (gamma = 4.729 + 1.250 alpha, $R^2_{adj} = 70.8\%$, $F = 389.29$, $n = 161$, $P < 0.0001$). Beta diversity (or turnover) is defined here as the deviation from this regression line. Beta is positive where more species occur within the cell than predicted, and negative when fewer species occur than expected.

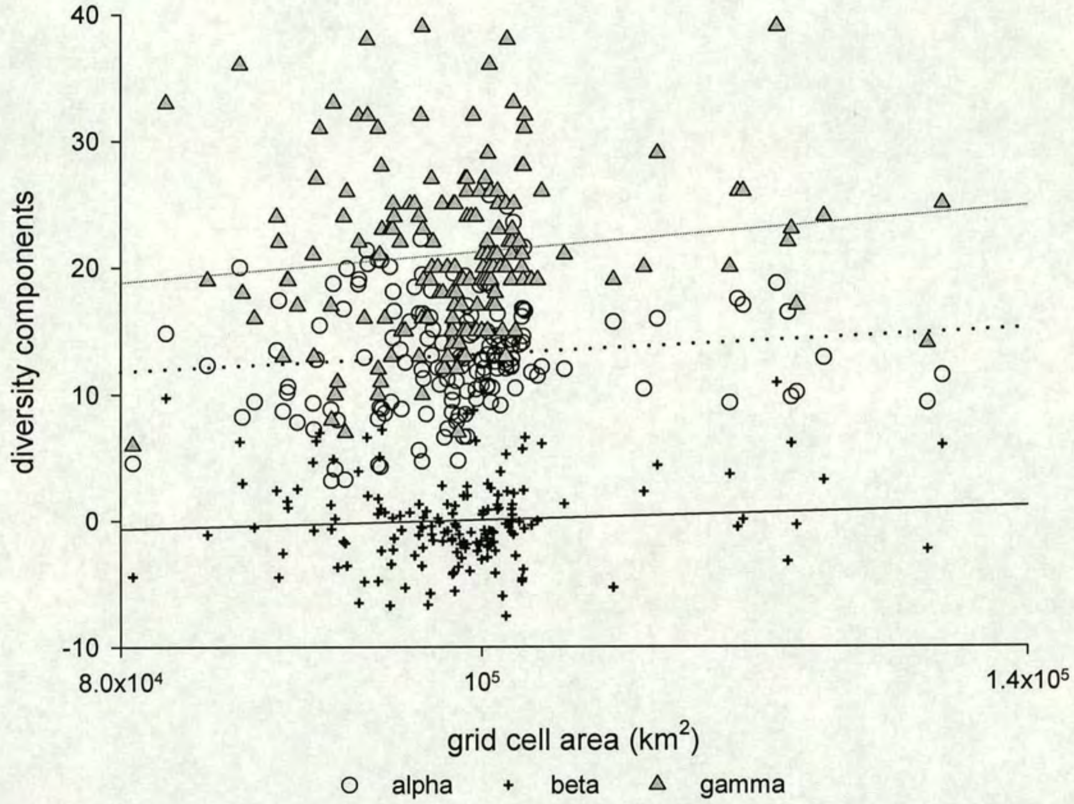


Figure 7.3. The three biodiversity components are not related to variation in the area of the sample cells.

alpha = $-57.2 + 14.1 \log(\text{area})$, $R^2_{adj} = 0.5\%$, $F = 1.75$, $n = 161$, $P = 0.188$.
beta = $-37.0 + 7.41 \log(\text{area})$, $R^2_{adj} = 0.0\%$, $F = 0.75$, $n = 161$, $P = 0.386$.
gamma = $-104 + 25.0 \log(\text{area})$, $R^2_{adj} = 0.9\%$, $F = 2.52$, $n = 161$, $P = 0.115$.

Biodiversity components and productivity

Figure 7.4 shows the relationships between the three measures of productivity or energy availability (rainfall, NDVI and ET_o) and the three biodiversity components (alpha, beta and gamma diversity). Alpha and gamma (mean and total) diversity respond similarly to the productivity and energy gradients. On NDVI and rainfall (the productivity gradients), both components show a general positive correlation to productivity, but with a pronounced peak. Maximum biodiversity occurs at intermediate levels of primary productivity. This unimodal pattern (for alpha diversity) has been observed in many taxa (see reviews for example in Rosenzweig & Abramsky 1993, Rosenzweig 1995, Begon, Harper & Townsend 1996, and in chapter 2), and also in other data sets on African ungulate communities (Western 1991, Ritchie & Olff 1999).

All three biodiversity components have a unimodal relationship to available energy (ET_o), but the general trend this time for alpha and gamma diversity is negative. Table 7.2 summarises the functional relationships illustrated in figure 7.4.

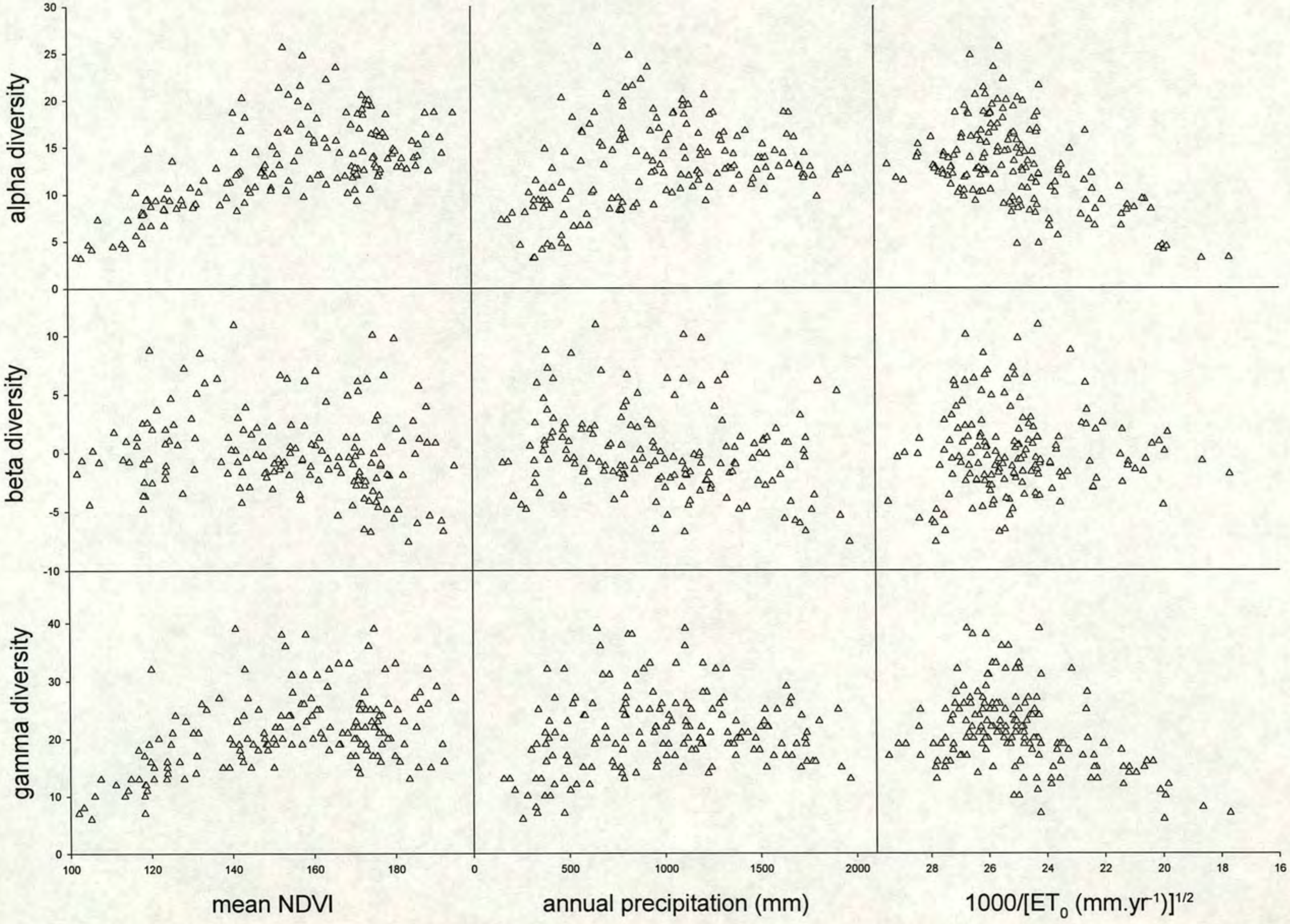

alpha diversity
beta diversity
gamma diversity
mean NDVI
annual precipitation (mm)
1000/[ET$_0$ (mm.yr^{-1})]$^{1/2}$
30
25
20
15
10
5
0
10
5
0
-5
-10
40
30
20
10
0
100
120
140
160
180
0
500
1000
1500
2000
28
26
24
22
20
18
16

Figure 7.4. (page above). Responses of three ungulate biodiversity components (alpha, beta and gamma diversity) to different measures of the energy supply gradient in sub-Saharan Africa. Variables were sampled using a grid pattern superimposed over the continent in a GIS (see figure 6.3). Alpha diversity is the mean number of species occurring within the grid cell. Gamma diversity is the total number of species occurring within the cell. Beta diversity is the residual from a regression of gamma diversity as a function of alpha diversity (see figure 7.2). Primary productivity is estimated either from a ratio of reflectances in the visible and infra-red wavebands measured by satellite (mean NDVI, see chapter 6), or from a database of mean annual rainfall interpolated from records collected from meteorological stations throughout the continent (Hutchinson *et al.* 1996, see chapter 6). Potential evapotranspiration (ET_o) was extracted from a FAO meteorological database (Smith 1993, see chapter 6), and provides an estimate of the available energy in the environment, rather than a measure of energy flow through the ecosystem. Statistics for these relationships are summarised in table 7.2.

Table 7.2. Functional relationships of biodiversity components to indicators of energy flow (primary productivity: mean NDVI and annual rainfall) and energy availability (ET_o) - see figure 7.4. Quadratic models include the energetic variable and its square as independent variables in a multiple regression. For all significance tests, $n = 161$.

			Energetic variable					
			Mean NDVI		**$[\text{rainfall}]^{1/2}$**		**$1000/[ET_o]^{1/2}$**	
		Function	R^2_{adj} (%)	P	R^2_{adj} (%)	P	R^2_{adj} (%)	P
Biodiversity components	**Alpha**	Linear	41.2	<0.001	12.0	<0.001	23.2	<0.001
		Quadratic	49.6	<0.001	25.1	<0.001	30.0	<0.001
	Beta	Linear	1.5	0.067	3.4	0.011	0.0	0.692
		Quadratic	3.4	0.025	4.0	0.014	0.8	0.197
	Gamma	Linear	21.1	<0.001	3.0	0.015	14.9	<0.001
		Quadratic	31.9	<0.001	16.2	<0.001	23.6	<0.001

Tilman's assumption - spatial variability in productivity

Figure 6.13 shows the spatial coefficient of variation image. Figure 6.14 illustrates how spatial variability in productivity varies with productivity. Rainfall and evapotranspiration data could not be used to measure spatial variability, because the underlying data used to derive these variables had been interpolated to provide predicted values between the more or less widely scattered weather stations. The dense spatial coverage of satellite and other remotely sensed data provides the large volume of data needed to measure spatial coefficients of variation.

Figure 6.14 shows that at very high productivity, Tilman's assumption (Tilman 1980, 1982, 1986) that spatial variability is a negative function of productivity is justified. However, at low productivity, the relationship is reversed. In landscapes of very low productivity, habitats are uniformly barren. Similarly, in very productive landscapes, habitats are uniformly productive. Between these two extremes, productivity varies in an unconstrained way with respect to the landscape average.

The relationships of biodiversity to spatial heterogeneity are shown in figure 7.5. All three biodiversity components are positive functions of spatial heterogeneity in primary productivity. However, the dependency of alpha diversity on heterogeneity is very weak (R^2_{adj} = 3.20%). Beta diversity shows the strongest relationship, with R^2_{adj} = 23.7%. Beta diversity is by definition statistically independent of alpha diversity, since beta was defined as the residuals from the regression of alpha against gamma diversity. Gamma diversity also has a relatively strong dependence on spatial heterogeneity (R^2_{adj} = 17.9%), which reflects the relationship of gamma to beta diversity. This suggests that the dependency of biodiversity in African ungulates on spatial heterogeneity in primary productivity comes about through an increase in species turnover with spatial heterogeneity.

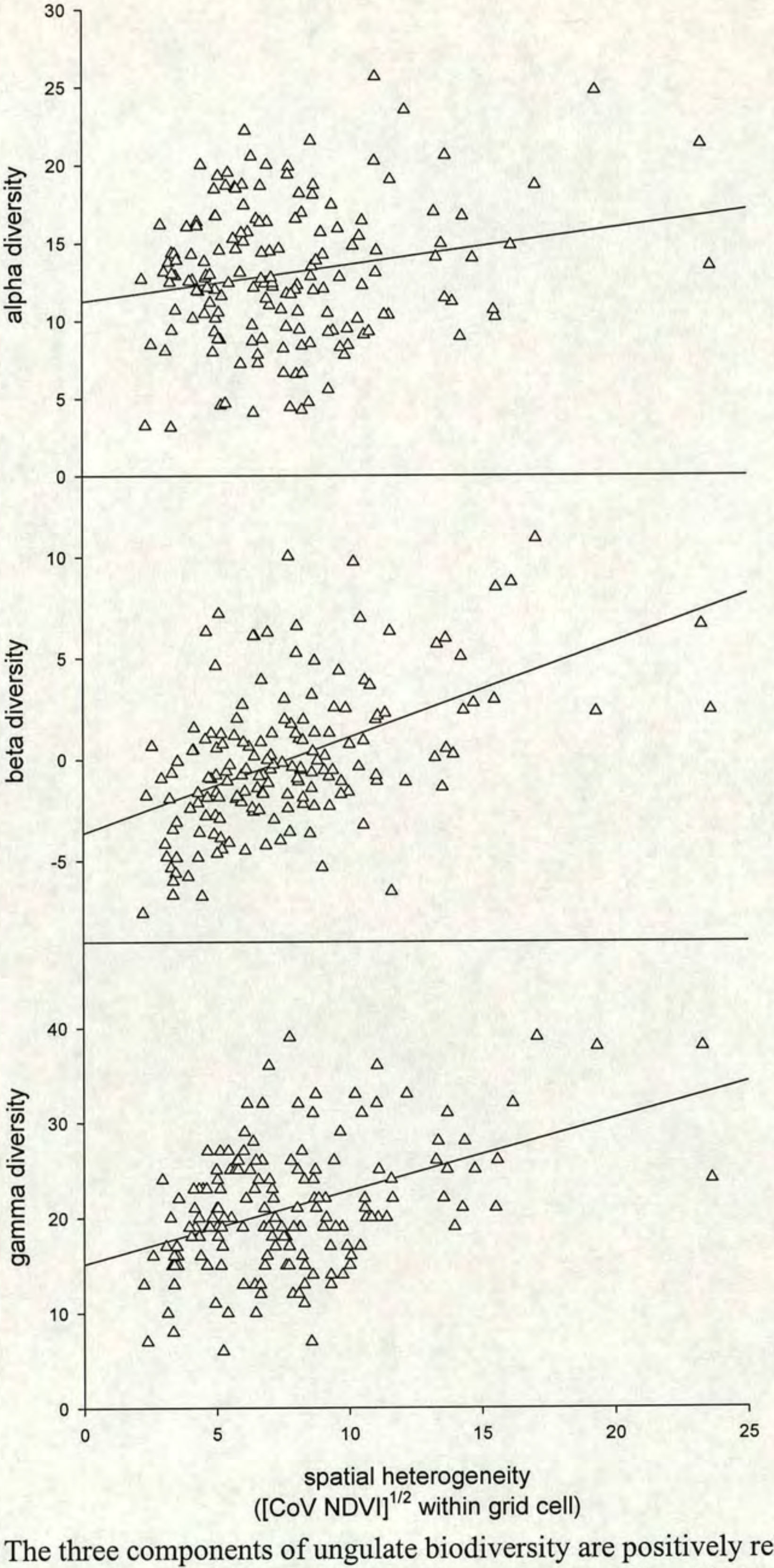


Figure 7.5. The three components of ungulate biodiversity are positively related to spatial heterogeneity in primary productivity. The strongest relationship is with beta diversity (see table 7.3 for regression statistics). Although gamma diversity closely varies with alpha diversity (figure 7.2), gamma diversity shows a much closer relationship to spatial heterogeneity than does alpha. This may suggest that observed relationships between measures of species richness and spatial heterogeneity occur via turnover or differentiation diversity, rather than alpha diversity.

Table 7.3. Regression statistics for biodiversity components as a function of spatial heterogeneity in NDVI. In all cases, n = 161. See figure 7.5.

		constant	**slope**	**R^2_{adj} (%)**	**F**	**P**
Biodiversity components	Alpha	11.3	0.235	3.20	6.29	0.0131
	Beta	-3.67	0.473	23.7	50.82	< 0.0001
	Gamma	15.1	0.767	17.9	35.95	< 0.0001

Biodiversity and components of temporal variability

There is a strong unimodal relationship between primary productivity and seasonality (figure 6.15a), but very little evidence of any relationship between productivity and inter-annual unpredictability (figure 6.15b). PCA change components are also unimodally related to productivity (figure 7.6). The PCA components vary above and below zero, so that unimodality operates in both the positive and negative directions. Most indicators of disturbance therefore have greatest magnitudes in the middle of the productivity gradient.

Figure 7.7 shows the linear correlation of species richness to the PCA components. Species richness is significantly correlated to change components 2, 3, 4 and 5. Figure 7.8 graphs these relationships. The strongest relationships are with the single annual cycle components 2 and 3. The double annual cycles 4 and 5 explain very little variation in species richness.

The *a priori* defined change components, IACV (seasonality) and IECV (unpredictability) are plotted against species richness in figure 7.9. The relationship with unpredictability depends on an outlier and explains very little variance in diversity. Species richness is however unimodally related to seasonality (quadratic regression: $R^2_{adj} = 12.9\%$, $P < 0.0001$).

In summary, disturbance varies unimodally along a productivity gradient. Ungulate species richness also varies unimodally with some indices of disturbance, mainly seasonality.

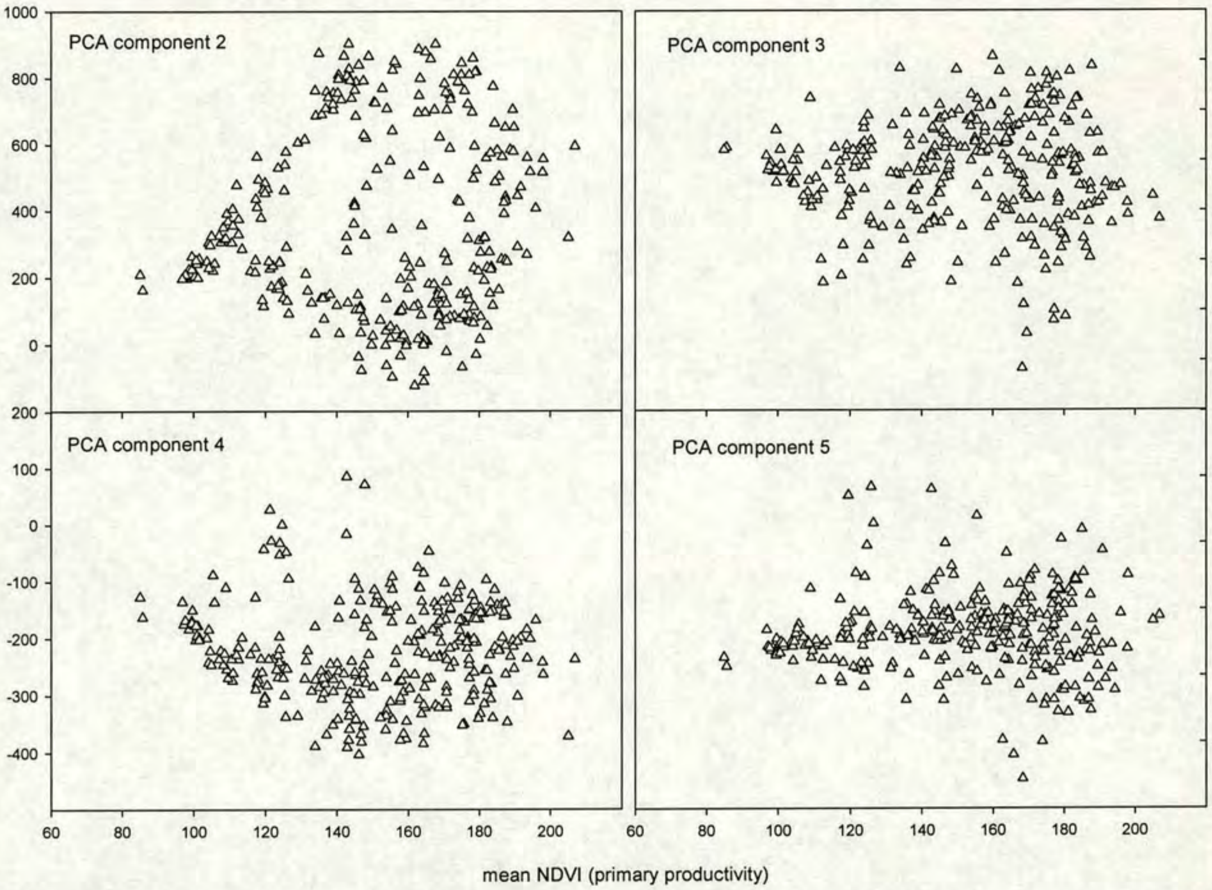


Figure 7.6. Unimodal covariation between primary productivity and PCA change components.

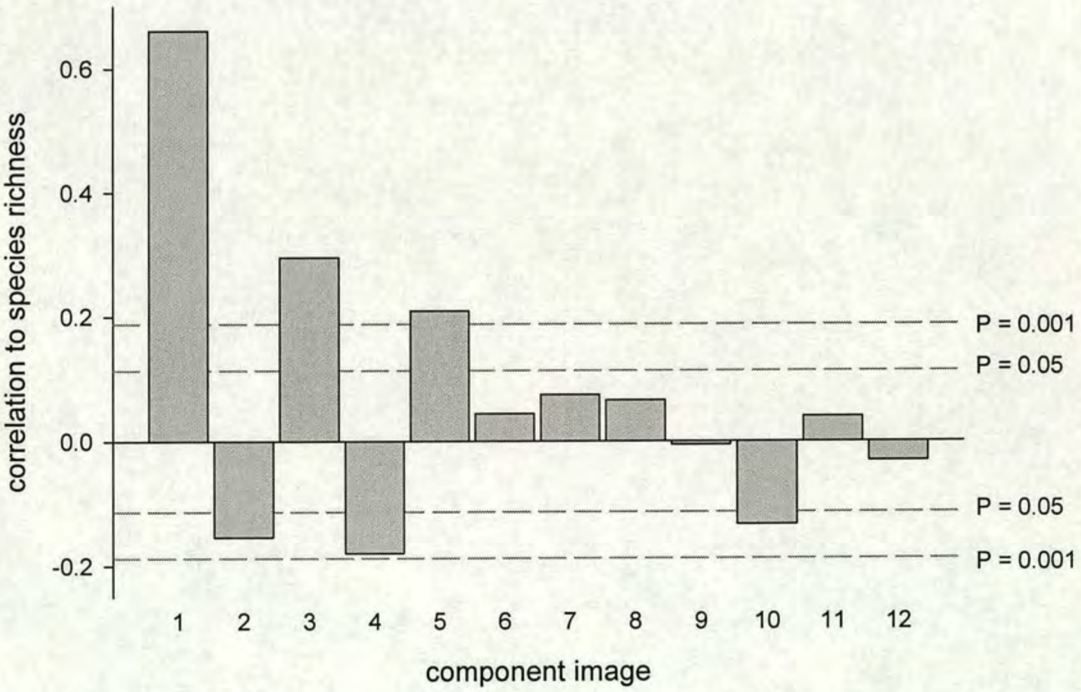


Figure 7.7. Correlation of ungulate species richness to PCA change components. Significance levels for values of the correlation coefficient are shown (n = 301).

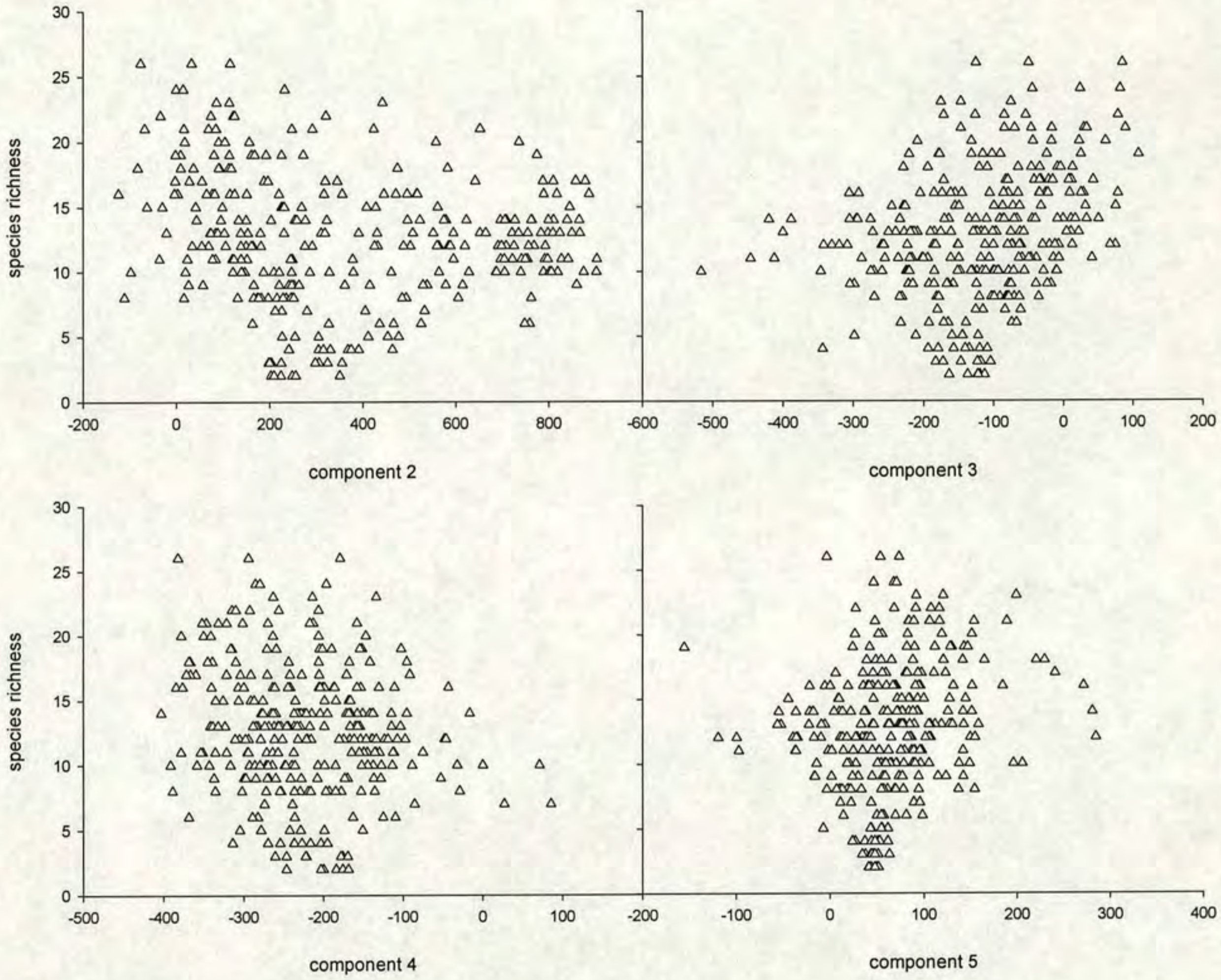


Figure 7.8. Species richness *vs.* PCA change components.

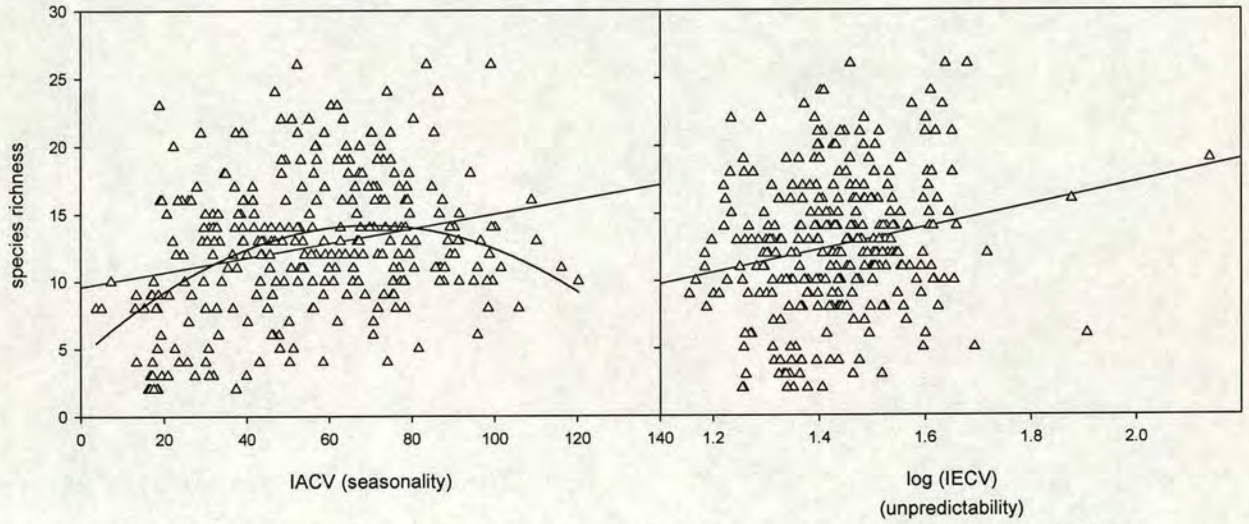


Figure 7.9. Variation in ungulate species richness with seasonality and unpredictability.

$SpR = 9.6013 + 0.0537\ IACV$

$R^2_{adj} = 0.0637, F = 21.4228, n = 301, P < 0.0001$

$SpR = 4.4312 + 0.2781\ IACV - 0.0020\ (IACV)^2$

$R^2_{adj} = 0.1288, F = 23.1761, d.f. = 2, 298; P < 0.0001$

$SpR = 0.6116 + 8.3415 \log (IECV)$

$R^2_{adj} = 0.0400, F = 13.5074, n = 301, P = 0.0003.$

DISCUSSION

Diversity-productivity relationships of African ungulate communities

Previously analysed diversity-productivity data for African ungulates have exhibited a unimodal pattern, with species richness first increasing but then decreasing again along productivity gradients (Western 1991, Baird 1996, Ritchie & Olff 1999). Western (1991, redrawn in Rosenzweig 1995) plotted species richness in a set of National Parks and other protected areas in East Africa against annual rainfall, and found a peak at about 600 $mm.yr^{-1}$. This curve was symmetrical around the peak, with no evidence of a skew. Baird (1996) used 32 distribution maps published in Kingdon (1989, 1992a, 1992b) to produce a map of ungulate species richness in East Africa. When plotted against the 10 year mean NDVI (a satellite-derived index of primary productivity), species richness again showed the unimodal response, but this time with a left skew. Against rainfall, the peak occurred at around 700 $mm.yr^{-1}$, with no skew. Ritchie & Olff (1999) surveyed species richness of grazers in 28 East African nature reserves, and found that species richness peaked again at about 600 $mm.yr^{-1}$, but this time with a strong right-skewed tail.

These analyses were all carried out for ungulate communities in East Africa. This thesis extends the spatial scale of analysis in both directions. Within a single ecosystem (the Serengeti), figure 5.13 shows diversity reaching a maximum in localities with low productivity (short swards), before falling again when sward length increases. In the current chapter, a unimodal pattern was again observed, this time at the continental scale (figure 7.4). Against rainfall, diversity peaks at about 675 $mm.yr^{-1}$, with a right skew. Against NDVI there is also a skew, but this time the tail is to the left.

The coefficients of determination in the plots of Baird (1996) for East Africa, and in the present study for the entire continent, are considerably lower than those observed by Ritchie & Olff (1999). This is probably because the latter authors used data from nature reserves which, because of management protection and re-introductions, probably support close to the maximum possible number of species. The maximum diversity constraint boundaries (rather than best fit curves) observed in the plots of Baird (1996) and in the present work more closely match the curve reported by Ritchie & Olff (1999).

Testing Tilman's assumption - spatial variability and community diversity

Tilman's (1980, 1982, 1986) explanation for unimodal diversity-productivity curves has two components: León & Tumpson's (1975) model of resource competition, and an assumption about how productivity and its spatial heterogeneity co-vary. That RCT can be used to describe and explain competitive interactions between ungulates was demonstrated in chapters 2, 3 and 5. Figure 6.14 allows a test of Tilman's assumption.

Tilman assumed that as productivity increases, the gross variability in productivity values within a habitat does not increase (figure 2.1a). This requires that the CoV of productivity should fall. In figure 6.14, beyond a threshold productivity, the CoV does indeed fall. For intermediate to high productivity, Tilman's assumption holds and the RCT model of community diversity is supported.

For low productivity however, the CoV in fact increases (figure 6.14), but this is not fatal to the theory. When P is low, rarity becomes much more important, and diversity is controlled by Preston's veil.

In pointing out that the RCT predictions depend on how productivity and its CoV co-vary, Abrams (1988, 1995) described several scenarios that would lead to different predictions. In particular, it was possible that diversity could increase monotonically, and he also showed that even if the relationship was unimodal, different patterns of co-variation between productivity and its CoV could place the peak anywhere on the productivity gradient. Tilman's (1980, 1982, 1986) expectation of long, right-skewed distributions was not axiomatic. A corollary of this is that right-skewed diversity-productivity plots do not in themselves support a hypothesis of RCT processes, as argued in the past (*e.g.* Abramsky & Rosenzweig 1984, Owen 1988, 1990).

In the current work, there is in fact a leftwards tail in the plot of alpha diversity against mean NDVI (figure 7.4). NDVI is linearly related to primary productivity (see chapter 6), so Abrams (1988, 1995) analysis may be supported.

However, the plot is right-skewed if productivity is indexed by rainfall (figure 7.4). Ungulate diversity is particularly low in high rainfall areas (Bell 1982, 1984, East 1984, see chapter 1) because of the particularly low quality of the vegetation. The evidence therefore for a right skew at the continental scale is equivocal.

Although the relationship between productivity and its spatial variability is unimodal in so far as there is a peak, in fact the distribution may be better described as constrained to low variability at either end of the productivity gradient. In the lowest productivity environments, productivity is low everywhere. Similarly, in the highest productivity environments, productivity is high everywhere. In intermediate productivity, environments, productivity may be uniform or may vary widely. This contradicts Rosenzweig's (1995) expectation that high productivity environments will have habitats with a broad range of productivities.

Most theories of community diversity, including RCT, predict a positive relationship between species richness and spatial heterogeneity. This pattern occurs in the current data for beta and gamma diversity, but is much less apparent for alpha diversity (figure 7.5 and table 7.3). Beta diversity (turnover) is most strongly related to spatial heterogeneity. This high turnover in species in more heterogeneous environments leads to higher overall (gamma) diversity, but is less strongly associated with higher average diversity (alpha).

Temporal variability

The relationship between primary productivity and its temporal variability is also unimodal, as seen in figure 6.15a for seasonality, much more weakly (if at all) for inter-annual unpredictability in figure 6.15b, and for PCA change components in figure 7.6. There is some evidence that ungulate diversity also varies unimodally with some temporal variability indices, especially seasonality (figure 7.9). However, co-variation of species richness and PCA change components is either linear, or random (figures 7.7 and 7.8).

This data cannot reject the hypothesis that part of the unimodal relationship between species richness and productivity is due to the relationships between productivity and disturbance, and disturbance and species richness. However, any such causation is weak, and cannot fully explain the species richness-productivity pattern.

Conclusions

The results presented in this chapter provide support for the RCT explanation of unimodal diversity-productivity curves in African ungulates. This is the first time the spatial heterogeneity RCT mechanism has been tested in an animal community. The lack of a strong right skew to the species richness-productivity curve argues that identifying such a skew does not in itself provide support for the RCT mechanism, as has been claimed for some animal communities (Abramsky & Rosenzweig 1984, Owen 1988, 1990).

Data presented in this chapter and in chapter 5, together with previous analyses, have shown that unimodal species richness-productivity curves are exhibited by African ungulates at all spatial scales, from within a single ecosystem (figure 5.13), through regional data sets (Western 1991, Rosenzweig 1995, Baird 1996, Ritchie & Olff 1999 for East Africa), to the entire continent (figure 7.4).

An alternative hypothesis, that the species richness-productivity curve is in fact a consequence of unimodal co-variation in productivity and its temporal variability, was also supported, although its influence is weak. Ecological communities are highly complex, and most phenomena are subject to multiple causation.

RCT has not been developed to make specific predictions about the different components of biodiversity. The model of variation in community diversity in response to variable resource supply conditions presented in chapter 2 (figures 2.1a and b) should probably be interpreted as a model of beta diversity responding to variability in resource supply ratios, and ultimately affecting gamma diversity, being the total number of species encountered within a habitat described by the circles in these figures.

CONCLUDING REMARKS

The importance of mechanism

Whereas the function of theory for individual scientists is to further their own understanding of how the world works, the justification for spending research grants on developing theory must ultimately be that good theory can generate accurate predictions (Peters 1991). If such a theory is built upon an explicit model of how the world works, then it becomes aesthetically satisfying as well as practically useful. More importantly, a mechanistic model generates more testable hypotheses (Tilman 1987), and in the long run is more amenable to further development. For competition theory, the advance from phenomenological theory that describes and predicts, but does not explain, to a well-developed model based on the real world mechanisms that underlie observed phenomena, has been especially prolonged and difficult.

As in many areas of modern biology, Darwin was the first to set forth a model of the mechanisms and outcomes of competition. From the premise of a Malthusian, resource-based mechanism acting to limit the populations of most species, Darwin developed his argument that organisms exist within a milieu of life or death struggle for the control of resources against their neighbours, both intra- and inter-specific.

The next major development in competition theory came with the mathematical formulations of Lotka and Volterra, and the laboratory experiments of Gause. However, it is important to recognise that the Lotka-Volterra equations do not embody any mechanism through which competition occurs (Tilman 1987, Grover 1997). In the single-species formulation, they describe (but do not explain) a density-dependent limitation of population growth. This density-dependence takes its inspiration from Malthusian resource limitation, but the equations do not explicitly model resources.

In the two-species case, the density dependence of each species on its own population size is extended to a density dependence of one species on the population size of the second. Calibration of this inter-specific density dependence is achieved through the competition coefficient. MacArthur & Levins (1967) linked the Lotka-

Volterra equations directly to resources by relating it to a function of the similarity of resources used by the two species, but again the mechanism of resource-mediated competition is not modelled by calibrating the competition coefficient. The Lotka-Volterra formulation states that competitors negatively influence one another, but does not describe how this negative influence comes about (Tilman 1987).

The Lotka-Volterra model was elaborated enormously during the 1960's and 1970's (Schoener 1982). The field studies of competition reviewed by Schoener (1983) and Connell (1983) were all based on the Lotka-Volterra approach, where competition is inferred from changes in the density of one species in response to negative or positive manipulations of the density of a potential competitor. But these experiments shed no light on the mechanisms underlying responsive changes in population densities, and the Holy Grail of a truly mechanistically based mathematical formulation remained elusive. RCT provides a mechanistic explanation of interactions, and from this it derives testable predictions. The development of RCT came out of a desire to understand what goes on under the hood. CCT is a black box theory, RCT gets at the nuts and bolts.

Resource competition theory and ungulate community dynamics

As demonstrated in chapters 2 and 3, RCT can be successfully applied to ungulate foraging scenarios. The description of ungulate resources within the RCT framework leads to models of ungulate foraging that accurately describe many aspects of their ecology. The Bell-Jarman relationship between body size and digestive ability is expressed in the different slopes of the ZNGI's of different sized animals. Selectivity is described by the slopes of the consumption vectors, and the ability of smaller animals to subsist on shorter swards is indicated by the proximity of their ZNGI to the origin. The inhibitory effect of low quality forage, and the ability of larger animals to tolerate this, is described by the upwards-sloping segment of the ZNGI's. This latter effect leads to a strong prediction of facilitative interactions.

The tests of theory presented in this thesis represent a first step towards fully validating the RCT description of ungulate ecology. The major handicaps that RCT suffers from are its requirement for detailed information about the foraging ecology of each species, and the necessity of running multiple field tests under varying resource supply conditions in order to test its predictions. Ungulates are an attractive group to study because so much is already known about their foraging ecology and physiological requirements - probably more than is known about any other vertebrate group. Ungulates are an unattractive group to study because of the difficulty of manipulating resource supply conditions and of studying population interactions for extended periods. This experimental difficulty however could be largely overcome by using simulation modelling techniques.

Multiple causation and spatial scale

Understanding the dynamics of community organisation is a considerable task. At a local scale, the ZNGI models developed in chapters 2 and 3 neatly encapsulate many aspects of ungulate foraging ecology. The mechanism of interaction in these models is resource modification. Ungulate distributions both respond to and affect resource abundance and quality. This feedback between population distributions and resource distributions, coupled with the mixture of strong positive and negative interactions between species, goes a long way towards explaining the complexity of ungulate community structure. Nothing is straightforward, and nothing operates in isolation.

When the spatial scale is increased first to ecosystem level, and then to the entire continent, external controls on resource supply become more important. Within an ecosystem, herbivores are capable of modifying local vegetation conditions, but rainfall and soil nutrient conditions can vary significantly and exert major influences on the vegetation and therefore on the ungulate community. This becomes apparent in the unimodal relationship between ungulate diversity, and in the changes in community composition in response to sward height within the Serengeti.

At the continental scale, ungulate diversity is influenced by a productivity gradient that is entirely outside the influence of these communities. At this scale, geomorphology, rainfall, and resulting variation in soil nutrient status are dominant. This however does not simplify the causation of ungulate diversity patterns, because new processes become apparent, such as the influence of disturbance both on primary productivity and on ungulate diversity. At such a broad scale, there are always more hypotheses to test, and no single factor controls community composition.

The great difficulty of doing community ecology derives from scale and multiple causation. Broad spatial scale makes experimentation difficult and multiple causation the norm, while multiple causation makes interpretation difficult. Again, hope must lie in the development of realistically complex simulation models that can be experimentally manipulated.

Macroecological perspective

Theoretical explanations of community structure are difficult to test because individual communities are influenced much more by the idiosyncrasies of historical events and the eccentricities of species characteristics than by the mechanistic processes suggested by theoretical ecologists (Maurer 1999). The macroecological research program developed in the last decade (Brown & Maurer 1989, Brown 1995, Maurer 1999) attempts to study large numbers of communities over broad spatial and temporal scales, in the expectation of finding statistical regularities in community structure. By averaging out the chance effects of history, regularities in community structure may be identified in a comparative statistical, rather than experimental reductionist, paradigm.

In this type of analysis, constraint boundaries can be as important as functional relationships. This means that we may expect ecosystems to exert limits on the properties of the communities that exist within the system. Within those limits, communities may exist that exhibit a broad range of properties (Lawton 1990, Maurer 1999). Whereas statistical methods for studying functional relationships (such as regression lines and best-fit curves) are well developed, methods for studying or even describing constraint boundaries are almost entirely lacking (Lawton 1990). However, visual inspection should suffice at least to identify likely constraints that require a theoretical explanation.

Future steps

The richness of the databases used in this thesis would provide almost endless opportunities for further analysis. Three of the most interesting possibilities (from the point of view of the work reported here) are mentioned.

In chapter 5, two hypotheses were stated but could not be tested using data from the south-east short-grass plains. These hypotheses referred to the relationship between spatial heterogeneity and species richness. CCT and RCT both predict a positive relationship between spatial heterogeneity and species richness. This was H7 in chapter 5. H8 provided a method of testing between CCT and RCT, because RCT predicts that species richness should be more strongly influenced by spatial heterogeneity in habitats of relatively low productivity. The test would involve identifying a part of the Serengeti where burning occurs quite frequently. Burning rarely occurs throughout an entire quadrant, and the extent of burning is recorded in the database, providing an excellent measure of heterogeneity.

Much more information could be extracted from the satellite data. In particular, it would be possible to extend a method described by (**ref**) to the entire continent, to estimate growing season length (GSL) at every location on the continent. This variable is likely to have a strong influence on both the diversity and the composition of ungulate communities. GSL and productivity could be separated by regression (comparing ungulate diversity to GSL and to the residuals of a regression of GSL on productivity).

Finally, as has been argued several times, a simulation modelling approach would provide excellent opportunities to test RCT in ungulate communities. The simulation model would describe ungulates foraging on variable resources. Manipulations of the resources and the species feeding on them could be monitored to observe the conditions under which species exclude one another or co-exist. These conditions would then be compared to predictions generated by a ZNGI model such as that described in chapter 3.

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