CHAPTER 11A

STRUCTURING HERBIVORE COMMUNITIES

The role of habitat and diet

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Abstract. This chapter tries to address the question "Why are there so many species?" with a focus on the diversity of herbivore species. We review several mechanisms of resource specialisation between herbivore species that allow coexistence, ranging from diet specialisation, habitat selection to spatial heterogeneity in resources. We use the ungulate community in Kruger National Park to illustrate approaches in niche differentiation. The habitat overlap of the ungulate species is analysed, continued with the overlap in diet and the spatial heterogeneity in resources. This focus on the constraints on species' exclusive resources is a useful tool for understanding how competitive interactions structure communities and limit species diversity. In explaining community structure of mobile animals, we argue that the existence of exclusive resources governed by spatial heterogeneity plays an important role. Trade-offs between food availability and quality, food availability and predation risk, or food and abiotic conditions (different habitat types) may constrain competitive interactions among mobile animals and allow the existence of exclusive resources. We propose that body mass of the animals considered is crucial here as animals with different body mass use different resources and perceive spatial heterogeneity in resources differently. A functional explanation of the role of body mass in the structuring of communities is still lacking while the study of how much dissimilarity is minimally needed to permit coexistence between strongly overlapping species is still in its infancy. Nevertheless, a theoretical framework is emerging from which testable hypotheses can be generated..
Keywords. assembly rules; body mass; coexistence; competition; diet selection; facilitation; habitat selection

INTRODUCTION

Why are there so many species? For many decades, various theoretical and empirical studies aim at understanding how species that utilise similar resources can coexist. Resource specialisation and competitive interactions between species lie at the foundation of our understanding of the structure and diversity of ecological

communities. These interactions are central in resource ecology. For many sedentary species, such as intertidal organisms and vascular plants, one species may completely eliminate another species when they occur together, i.e., competitive

This chapter reviews mechanisms of resource specialization between herbivore species that could allow coexistence

exclusion (Connell 1983; Schoener 1983). Coexistence is then only possible when there is some form of partitioning in resource or habitat, to allow exclusive use of resources. This competitive exclusion is, however, especially rare for mobile animal species (Ritchie 2002). Individuals of mobile species can sample many aspects of their environment and thus have the ability to go to certain locations and avoid others, or to select certain patches or types of resources and ignore others. Based on what cues do animals select locations and is this selection the result of competition? This chapter reviews several mechanisms of resource specialisation between herbivore species that could allow coexistence, ranging from diet specialisation, habitat selection to spatial heterogeneity in resources.

Why are there so many herbivores? In many parts of the world ungulates seem to dominate the green world, especially in the savannas of Africa. African mammalian herbivores are frequently used as a model system for the study of community structure and dynamics (e.g., Prins and Olff 1998; Ritchie and Olff 1999; Olff et al. 2002; Sinclair et al. 2003). A great variety in species can be found there, apparently living peacefully together, sometimes even operating in large mixed herds like the wildebeest, zebra and Thomson's gazelle on the Serengeti plains. Frequently they also seem to utilise the same resource, i.e., grass. The question arises then how all these species can live together, apparently showing no signs of interspecific competition. Or do they? Therefore, the fundamental question at stake here is: do all these species occupy a different niche such that coexistence is possible?

The classical approach to analyse niche differentiation is not without problems. From early on, the niche concept has known two approaches that have been used separately, combined and integrated to various degrees. The first is the niche as the

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place in an environment that a species occupies (Grinnell 1917). This includes all the necessary conditions for a species' existence. The second is the niche of a species as its functional role within the food cycle and its impact on the environment (Elton 1927). The vagueness of these approaches was greatly improved by the work of Hutchinson, MacArthur and others, who tried to quantify the concept. Hutchinson (1957) defined the niche as the sum of all environmental factors acting on the organism; the niche thus defined is a region of an n-dimensional hypervolume. For each species an explicit number (n) of limiting factors could be determined defining the range of conditions where a species could exist. Hutchinson also introduced the difference between the fundamental niche (all the aspects of the n-dimensional hypervolume in the absence of other species), and the realised niche as the part of the fundamental niche to

which the species is restricted due to interspecific interactions. MacArthur (1958), Levins (1968) and others greatly expanded Hutchinson's approach by emphasising the view that interspecific competition was of great importance in the structuring of natural communities (for review, see Chase and Leibold 2003). The new models were almost always based on the Lotka-Volterra equations. Later on, also these models were criticised for lack of statistical rigour and null models, rigorous testing (Chase and Leibold 2003) and for the strong focus on competitive interactions. In fact, the whole niche concept has been strongly criticised as being irrelevant (Hubbell 2001). Notwithstanding the debate about the relevance of this neutral theory (Chave 2004), a large body of theoretical literature exists nowadays that includes various aspects of species' niches: competitive interactions, effects of predation, and intrinsic and extrinsic spatial and temporal heterogeneity (Kotler and Brown 1999; Ritchie 2002; Chesson 2000a, 2000b). Recently, Chase and Leibold (2003) came with a new definition of the niche as the joint description of the environmental conditions that allow a species to satisfy its minimum requirements so that the birth rate of a local population is equal to or greater than its death rate along with the set of *per capita* effects of that species on these environmental conditions. This definition combines the location and the role of a species and makes rigorous quantitative testing possible.
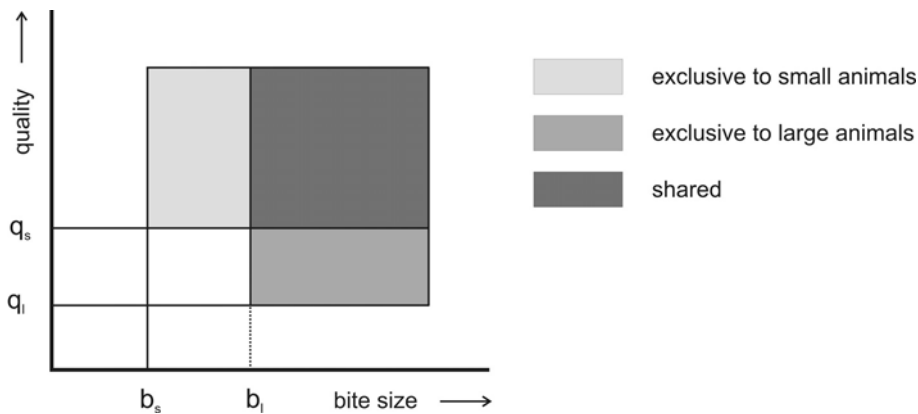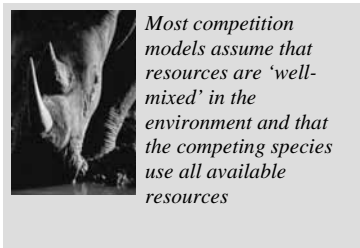
So far, the quantitative approach, as applied to real communities, is still in its infancy (but see, e.g., Ritchie and Olff 1999; Mendoza et al. 2002). It is still highly theoretical or confined to observational studies or small-scale experiments and it has yet not been applied to ungulate communities. Therefore, we still have to apply a more general approach in which we explore how species can be positioned along a few important resource axes and try to deduce what the likelihood is that species either are clearly separated or show potentially high overlap. First, we expand on the theory about competition among mobile animals. We then use a specific animal community to illustrate approaches in niche differentiation, i.e., the ungulate community in Kruger National Park, South Africa. The habitat overlap of the ungulate species is analysed, continued with the overlap in diet and the spatial heterogeneity in resources.

COMPETITION AMONG MOBILE ANIMALS

The choices for forage, rest, mate, drink, etc., of mobile animals may be constrained by particular physiological and morphological characteristics of the animals, so that differences among species in these characteristics can dictate differences in their choices (Ritchie 2002). Many of these choices are phenotypically or behaviourally plastic or 'adaptive' (Abrams 1988). See Owen-Smith (Chapter 8) for a review on adaptive behaviour. This plasticity allows individuals of a species to avoid competition with other species. Also, constraints of the resource distribution, such as large distances between necessary resources, may negatively affect the choices of animals (Prins and Van Langevelde, Chapter 7; Boone et al., Chapter 9). Extensive field-experimental studies suggest that, among species pairs of mobile animals that seem likely to compete, competition can be detected, such as in terrestrial and

aquatic insects (Belovsky 1986; Wissinger et al. 1996), lizards (Petren and Case 1996, 1998), birds (Wiens 1992; Loeb and Hooper 1997), small mammals (Rosenzweig and Abramsky 1997; Morris et al. 2000) and large mammals (Edwards et al. 1996). Competition resulted in competitive exclusion of a species appeared only in very few cases (Ritchie 2002).

Most competition models assume that resources are 'well-mixed' in the environment and that the competing species use all available resources, only at different rates. Tilman (1982) showed that if two species are competing for a single resource, then the species that can persist on the lowest availability of that resource will competitively exclude the other. However, if some resources used by each species do not overlap, then species would not use all available resources (Schoener 1976). Instead, some resources would be exclusively available to individuals of each species. Sufficiently abundant exclusive resources for each species could support at least a certain density of these species regardless of the intensity of competition for shared resources, and thus guarantee coexistence. Because of their ability to move and make choices, mobile species are therefore highly likely to 'find' exclusive resources and thus to coexist (Ritchie 2002).

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Figure 11.1. *Hypothetical diagram of minimum plant quality (Q_S, Q_L) and bite sizes (B_S, B_L) for small (S) and large (L) herbivores (Belovsky 1986, 1997). The indicated bite sizes are the minimum acceptable item size accepted by a herbivore species. Trade-offs in these minimum thresholds lead to exclusive resources for each species.*

Some of the evidence for exclusive resources comes from studies with herbivores. Among herbivores, species of different size may choose resource items of different size and quality because of a trade-off between greater retention and
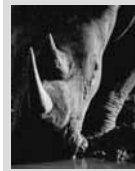
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digestion of low-quality food in the digestive tract versus higher metabolic rate, and thus resource requirements, for larger animals (Van Soest 1985; Belovsky 1986, 1997). Different-sized herbivore species, therefore, may partition plant parts (twigs, leaves or parts of leaves) by their relative size and quality (protein, soluble carbohydrate, and secondary chemical content) in a way that generates unique sets of plant parts that are exclusively available to each species (Figure 11.1). Examples for this trade-off generating exclusive resources and competitive coexistence are given by Belovsky (1984, 1986).

Segregation in habitat is another mechanism of avoiding competition that can generate exclusive resources and thus coexistence. Habitat selection is often density-dependent (Fretwell 1972). This means that when a population of a species is at sufficiently high densities, individuals may be forced to use less-preferred habitat. Then, they could face competition from other species. Exclusive habitat use among species can arise from trade-offs in their risk of predation, food patch size and quality or different abiotic conditions among different habitats (Kotler and Brown 1999; Olff and Ritchie 1999; Ritchie 2002; Olff et al. 2002).

Exclusive resources imply that trade-offs in species traits do more than just allow them to use resources at different rates as suggested by Tilman (1982). Instead, trade-offs generate access to resources that make coexistence probable (Ritchie 2002). If so, the detailed dynamics and full set of parameters governing competition may be largely irrelevant to understanding competitive outcomes. This implies that perhaps the most important aspect to know about two competing species is what determines their respective sets of exclusive resources (Ritchie 2002). If there are general patterns in these trade-offs, then coexistence models focusing on the constraints on species' exclusive resources may provide a powerful tool for understanding how competitive interactions structure communities and limit species diversity (Ritchie 2002). In Box 11.1, some general principles that structure communities are summarised.

Box 11.1. *Community assembly rules*

An important goal of community ecology is to find out how (local) communities are assembled from (regional) species pools. This goal is based on the idea that communities are characterised by some degree of order as the result of some ordering principle from which an assembly rule can be derived. Keddy and Weiher (1999) distinguish four parts in the procedure of finding assembly rules:
1. Defining and measuring the property of assemblages;
2. Describing patterns in the property;
3. Explicitly stating the rules that govern the expression of the property;
4. Determining the mechanism that causes the pattern.
    Species sorting should be based on some measurable property of populations. Various properties thought to play an essential role in the sorting process, have been used; among them are body size, morphological traits like incisor width, and functional group. So far, most work has been done on describing patterns in communities. Within local rodent communities, Dayan and Simberloff (1994) found a much more uniform average ratio of incisor width of succeeding species than expected from communities drawn by chance alone. Similar patterns have been found for body size (Brown and Bowers 1984). Many workers actually use pattern as a synonym for assembly rule (Kelt et al. 1999). Most patterns described are apparently interrelated and this strongly suggests that some common underlying mechanism is operating. The logical candidate for this is interspecific competition because it is strongest among similar species, and it has been demonstrated repeatedly to operate in and to affect local communities (for review see chapters in Keddy and Weiher 1999). It is well recognised that interspecific competition is not the only factor affecting communities, and the effects of historical and geographic processes are not easily to be dismissed (Ricklefs and Schluter 1993). These effects, together with the process of allopatric speciation, might especially affect the composition of regional species pools. Scale effects might also influence community structure, and it is not always easy to define the regional species pool or to make out if the locality of a local community is a representative subset of the region. Increasing the area for the study of local communities might lead to a more 'checkerboard' pattern, permitting more species to be present and leading to communities which are nested (M'Closkey 1978).
    Describing and explaining a pattern is not the same as formulating a rule with which communities can be assembled. Community assembly is ultimately driven by the invasion (e.g., immigration, speciation) and extinction of species played out against a complex background of environmental constraints. The environment acts as a filter, eliminating some species and promoting others. Assembly mechanisms are therefore the regulatory agents and processes, which define the suite of plausible system stages or transitions through which a system can proceed (Drake et al. 1999). Drake et al. (1999) define an assembly rule as: an operator, which exists as a function or consequence of some force, dynamic necessity, or context, which provides directionality to a trajectory. The nature of this direction includes movement toward a specific state, or some subset of all possible states. In ecological terms, assembly rules define reachable and unreachable community states, the community being some complete set of species exhibiting limited membership. Within this context, Weiher and Keddy (1999) point out that assembly rules are not so much about recipes for building communities, but, rather, that they are a set of limits that constrain how species can come together to form assemblages. Diamond (1975) is generally cited as the first who tried to formulate a principle with which he could predict bird communities on islands. He matched resource utilisation curves of species to availability of resources (resource production curves), and by subtracting individual resource utility curves from resource production curves till no resource space was left, could make estimates of which combinations of species were either 'forbidden' or 'allowed' on specific islands. This work led to much more research in this field and much discussion among ecologists (see chapters in Weiher and Keddy 1999).

(cont.)

Box 11.1. (cont.)

Despite all this work, surprisingly few assembly rules have been formulated to date. The best-known is the one of Fox (1987, 1989, 1999), who worked on desert rodents and other small-mammal communities. As property he used the functional group (or guild) and he stated a rule by which species belonging to different guilds should enter a developing local community. The rule was: there is a much higher probability that each species entering a (local) community will be drawn from a different functional group until each group is represented, before the cycle repeats (Fox 1999). If some functional group becomes disproportionally represented in a local community, competition lowers the probability that the next species to colonise will belong to that group and raises the probability that it will belong to one of the other groups. A local community is in a 'favoured state' whenever all pairs of functional groups have the same number of species or differ by at most one (if resource availabilities are equal). If the number of species differs by more than one, the local community is in an 'unfavoured' state. The prediction was tested against a null-model of random assembly, and Fox found indeed the rule to apply to the small-mammal communities he studied. The rule has also been found to operate in other communities, e.g., lemurs in Madagascar (Ganzhorn 1997), rodents in Chili (Kelt and Martinez 1991), and shrews in North America (Fox and Brown 1993). Despite this apparent success, Fox's rule has been heavily criticised on various grounds (Stone et al. 2000). The challenges related to both the existence (the rule was probably an 'artefact') and the interpretation of the assembly rule (no evidence that interspecific competition had shaped the local community). In their reactions, Brown et al. (2000) were able to counteract much of the criticism although the debate has most likely not yet fully come to an end. To find the right null-model, for example, is an important consideration before any test can be made. Fox (and many others) tested against communities that were randomly assembled from the regional species pool, but in reality many communities are biased, and then the null-model should reflect this bias and a distribution of the expected number of favoured states should be generated. Even applying randomness is not easy in tests. Empirical data can potentially be compared to multiple random distributions because different random distributions can be expected (e.g., normal, lognormal, broken stick) and different test statistics can be applied (parametrical versus non-parametrical tests, each with unique assumptions).

The fact that, after 30 years of work, still so few real assembly rules have been formulated while the existing ones have not yet been fully accepted either, makes clear that only limited progress has been made in our understanding of communities. Are, then, most (mammal) communities only random assemblages of a regional species pool? Do we need to incorporate many more field data on species and resources before we can make proper analyses? Have history and other stochastic events in many instances blurred regularity in patterns that, without these, would have been revealed? Are ecological communities too complex (Stone et al. 2000)? Surely many communities exhibit some pattern deviating from randomness or some other null-model, yet important properties have been identified and, maybe most important, interspecific competition has been demonstrated to be a key mechanism by which species are structured. This should be sufficient incentive for future ecologists to take up the challenge and pursue the quest for finding fundamental assembly rules governing mammal communities.

OVERLAP IN HABITAT

Although a niche may be composed of many dimensions, the focus in general is on only a few. In ungulate ecology, the most important ones are habitat and diet. If species are completely separated in these aspects, there is no niche overlap and they can coexist. Therefore, we will start with these before adding other dimensions. As a rather arbitrary example, we will focus for our analysis on a community of ungulates living together in a regional setting of ca 19,000 km^2 in South Africa, the Kruger National Park. Thirty species of ungulates can be found here (Table 11.1) which, in principle, have free access to the whole area. One of the conspicuous features of the

list in Table 11.1 is the wide range in body sizes that the community comprises: from the 5-kg suni to the 4000-kg African elephant. We cannot specifically analyse this particular system itself in great detail but merely will use this community to demonstrate some general principles which lie at the basis of understanding animal-community structure.

Table 11.1. *Ungulates of Kruger National Park*

Species	Common name	BW (kg)	Species	Common name	BW (kg)
Neotragus moschatus	suni	5	*Damaliscus lunatus*	tsessebe	130
Raphicerus sharpei	Sharpe's grijsbok	11	*Alcelaphus buselaphus*	hartebeest (Licht.)	175
Cephalophus grimmia	common duiker	12	*Kobus ellipsiprymnus*	waterbuck	190
Cephalophus natalensis	red duiker	12	*Hippotragus niger*	sable antelope	210
Oreotragus oreotragus	klipspringer	12	*Tragelaphus strepsiceros*	greater kudu	220
Raphicerus campestris	steenbok	13	*Connochaetes taurinus*	blue wildebeest	230
Ourebia ourebio	oribi	15	*Equus burchelli*	Burchell's zebra	259
Pelea caprealus	vaal rhebok	25	*Hippotragus equinus*	roan antelope	260
Redunca fulvorufula	mountain reedbuck	30	*Taurotragus oryx*	eland	650
Tragelaphus scriptus	bushbuck	45	*Syncerus caffer*	African buffalo	650
Aepyceros melampus	impala	55	*Giraffe camelopardalis*	giraffe	700
Redunca arundinum	common reedbuck	80	*Diceros bicornis*	black rhino	1200
Phacochoerus africanus	warthog	80	*Hippopotamus amphibius*	common hippo	1500
Potamochoerus porcus	bushpig	80	*Ceratotherium simum*	white rhino	1900
Tragelaphus angasi	nyala	90	*Loxodonta africana*	African elephant	4000

BW: body weigh
Licht. stands for Lichtensteins's
From http://www.ecoafrica.com/krugerpark/mammals.htm

In a large area like Kruger various habitats can be distinguished (Table 11.2) and from literature we can derive the habitat preference of the species involved (Table 11.3). The habitats are arranged along a 'cover-axis', going from an open landscape to dense thicket. Table 11.3 makes clear that no species exclusively can make use of its preferred habitat. The minimum number of species in any habitat is 5 while in the open savanna 16 species can be found. Many species can be found in more than one habitat. Nevertheless, with the dimension habitat some differentiation within the community can be made. So it is unlikely that species typical of open landscape

(oribi, vaal rhebok, mountain reedbuck, common reedbuck) will ever meet species closely related to habitats with dense cover (common duiker, klipspringer, bushbuck, kudu). So, it is unlikely that interspecific competition between these species occurs.

Table 11.2. *Habitat classification for Kruger National Park ungulates (based on Haltenorth and Diller 1994; Kingdom 1997)*

Code	Habitat	Description
LS	light savanna	open grassland, light savanna, savanna
WS	woodland savanna	woodland savanna, light woodland
Wo	woodland	woodland, dense woodland
Fo	forest	forest
SB	savanna with bush	grass savanna with bushveld, grassland with scattered bush, grassland with thick bush
BS	bush savanna	bush savanna, dense savanna
Bu	bush	bush, bushveld
Th	thicket	thicket, thick bush

With the dimension habitat, some separation can thus be made, but it certainly is not enough as all habitats share a number of species. It also has to be noted that it is not always easy to distinguish between habitats, especially when small, but important, habitat elements are laid out in a fine-grained mosaic with other habitat elements. The small steenbok can be found in rather open woodland savanna, but is nevertheless bound to low bush, which thus needs to be present.

OVERLAP IN DIET

Grass and browse

There is circumstantial evidence for exclusive resources among ungulate-species pairs in field data (Van Wieren 1996b). Food specialisation is likely the most important resource dimension for separating species within communities. While, when considering herbivores as predators, plants are easy to catch, they are much more difficult to process than prey for carnivores. Plants are rich in fibre that requires special adaptations to digest, and this is a slow and not very efficient process. Compared to carnivores, herbivores eat a low-quality diet. Therefore they have to consume large quantities and have to spend many hours a day to meet these requirements. It is thus highly relevant that they search well for the best food (Laca, Chapter 5; Fryxell, Chapter 6; Owen-Smith, Chapter 8).

Food specialisation is likely the most important resource dimension for separating species within communities

The plant world is highly variable in its morphology and chemical composition, but a major distinction in two forage types can be made to which ungulates have adapted themselves through a number of specialisations. There are a few fundamental differences between monocots (grasses and sedges) and dicots (herbaceous and woody plants); they are summarised in Table 11.4.

Grasses are more fibrous than browses, while the cell wall of grasses is thick. The cell wall of grasses is relatively low in lignin, and as lignin is the most important inhibitor for the digestion of the cellulose and the hemicelluloses that make up most of the cell wall (Van Soest 1994), the potential digestibility of the grass cell wall is quite high.

Table 11.3. *Habitat preference of Kruger ungulates (for legend see Table 11.2; based on Haltenorth and Diller 1994; Kingdom 1997)*

	Habitat preference							
	LS	WS	Wo	Fo	SB	BS	Bu	Th
suni			•	•				•
Sharpe's grijsbok		•			•	•		
common duiker							•	•
red duiker				•			•	•
klipspringer								•
steenbok		•			•	•	•	
oribi	•							
vaal rhebok	•							
mountain reedbuck	•							
bushbuck						•	•	•
impala	•	•						
common reedbuck	•							
warthog	•	•						
bushpig				•			•	•
nyala			•			•	•	•
tsessebe	•	•			•	•		
hartebeest (Licht.)	•	•	•				•	
waterbuck	•	•			•			
sable antelope			•			•		•
greater kudu							•	•
blue wildebeest	•	•				•		
Burchell's zebra	•	•						
roan antelope		•				•		
eland	•	•	•					
African buffalo	•	•	•	•				•
giraffe	•	•			•	•		
black rhino							•	•
common hippo	•							
white rhino					•	•		
African elephant	•	•	•	•	•	•	•	•

Box 11.2. *Polyphenolics and mammalian herbivores*

Plants can defend themselves against herbivory by means of structural adaptations like hairs and thorns and by certain chemicals that in some way or the other have a deterrent effect on the herbivore that eats them. Many of such secondary compounds are known with widely varying effects. As an example we highlight here the polyphenolic compounds and their effects because they are quantatively the most abundantly produced group of plant allelochemicals and they are widespread throughout the plant kingdom, although mostly found in woody plants like trees and shrubs. They also seem to be one of the earliest groups of allelochemicals (Swain 1978).

Polyphenolics are not a clearly defined group of molecules but they share a high molecular weight, numerous phenolic groups and a lack of other functional groups (Mole 1989). There are two major types of chemically distinct groups, one being the condensed tannins and the other the hydrolysable tannins. These differ in both their component subunits and the type of bonding between these. An important characteristic is that they can form complexes with natural polymers, such as proteins and polysaccharides (starch, cellulose, etc).

The most investigated effect of polyphenolics is their presumed ability to reduce the digestive process in herbivores. This might happen by direct inhibition of digestive enzymes, and by the binding of polyphenols to substances in the diet, thus depriving digestive enzymes of access to them. Robbins et al. (1987) found protein digestion in deer to become reduced (with associated elevated levels of nitrogen in the faeces), while others found that also cell wall digestion decreased with increasing tannin levels because of the inhibiting effect on cellulase functioning (Van Hoven and Furstenburg 1992; McSweeney et al. 2001).

Apart from effects on the digestion process, tannins can also depress voluntary intake (e.g., in goats, Provenza and Malechek 1984), while in snowshoe hares reduced food intake was in proportion to increased levels of polyphenols (Sinclair and Smith 1984). Monogastric herbivores seem to suffer more than polygastric ones, but especially pregastric species seem to be able to metabolise hydrolysable tannins (Mole 1989; McSweeney et al. 2001), while certain species of ruminants are much less affected than others because of the variation in effectiveness of microbial fermentation to deal with a range of dietary components. Grazing species like sheep and cattle seem to be more affected than more browsing species like deer (Barry and Manley 1986; Robbins et al. 1987). Clear evidence is also available that browsers and mixed feeders differ significantly in their ability to cope with tannins (reviewed by Owen-Smith et al. 1993). Production of special proteins that bind with tannins is one way in which animals can gain protection. Salivary proline-rich proteins (which bind strongly to tannins) are being produced in the parotid salivary glands of ruminants, and it has been found that these (per unit body mass) are three times larger in browsers than in grazers, the kudu, however, being a notable exception to this rule (Owen-Smith et al. 1993).

Probably the most widely known effect of tannins is that they cause an astringent sensation in the mouth. The physical basis for this may be that tannins bind to and perhaps precipitate salivary mucoproteins and that they also may bind to taste receptors (Mole 1989). A logical consequence of plants becoming unpalatable is that herbivores try to avoid these plants. Both in feeding trials and in the field, a strong selection against high levels of tannins has been found in numerous cases, e.g., leaf-eating black colobus monkey (Oates et al. 1980), arctic herbivores (Bryant and Kuropat 1980), African buffalo (Field 1976) and deer (Robbins et al. 1987). It is generally thought that herbivores try to limit the intake of tannins by broadening their diet and indeed, many large herbivores are generalist feeders (Freeland and Janzen 1974).

The effects of tannins might even work up to the population level. Freeland et al. (1985) suggested that, because of the sodium-depleting potentials of tannins, these latter might have a population-regulating effect through the limiting of this scarce mineral. Population regulation effects of secondary substances have also been hypothesised to explain microtine cycles (Jensen et al. 1999). During the increasing phase, microtine rodents deplete their resources of preferred foods through heavy grazing, forcing them to switch to plant species that would normally be avoided because of the plant chemicals they contain. Apart from the 'normal' deterrents present, crashes are especially thought to occur because of induced production of toxins as the result of heavy grazing.

(cont.)

Box 11.2. (cont.)

Although generally considered deterrents, tannins may also have positive effects on vertebrates. Complexes of proteins with hydrolysable tannins can hydrolyse in gastric acidity beyond the rumen, releasing protein and amino acids that can then be taken up by the host (Martin 1982; Makkar 2003). Maybe this is the reason that some species actually select for a low level of tannins in their diet (Duncan et al. 1998). In feeding trials, roe deer adjusted their food choice to obtain 4% tannins in their diet (Verheyden-Tixier and Duncan 2000). Tannins have also been found to reduce the detrimental effects of saponins (another secondary metabolite) (Freeland et al. 1985) and to reduce the physiological effects of alkaloids by preventing the absorption of alkaloids in the bloodstream (Freeland and Janzen 1974). Further they are effective anti-oxidants (Hagermann et al. 1998), and they have been found to control intestinal worms (Hodgson et al. 1996).

In contrast, browses have generally less cell wall but these cell walls are high in lignin and have therefore a low to very low digestibility. Only when in a very young stage, browse cell walls can be utilised, otherwise herbivores who want to exploit browse have to draw heavily on the cell contents, of which there is more than in grasses, and which contain much better digestible substances like proteins, sugars and lipids. The two forage classes also differ in their chemical defence structures (see Box 11.2 for different defence mechanisms). Grasses contain considerably fewer secondary compounds than browses. They tend to have a higher silica concentration, which increases tooth wear, but in many browse species, a whole array of chemical substances can be found, ranging from polyphenols (tannins) to toxins like alkaloids. These compounds generally have negative effects on the herbivores through, for example, the lowering of the digestibility of nutrients (tannins), effecting reproduction, appetite and the immune system (see overview in Van Soest 1994; Bailey and Provenza, Chapter 2).

Table 11.4. Relative differences between chemical and structural characteristics of grasses (monocots) and woody and herbaceous plants (dicots) (Iason and Van Wieren 1999; Van Soest 1994; Shipley 1999).

Characteristic	Grasses (monocots)	Browses (dicots)
Cell wall	High cell wall content	Low cell wall content
	Thick	Thin
	Low in lignin	High in lignin
	Moderate to high digestibility	Low to moderate digestibility
Defence	Low chemical defence (silica)	High chemical defence (e.g., tannins, terpenes, alkaloids)
Plant architecture	Fine-scaled heterogeneity in nutritional quality within plant	Coarse-scaled heterogeneity in nutritional quality within plant
	New growth added at base	New growth added at tip
	Low growth form	Low to high growth form
Dispersion	Uniform	Dispersed/discrete

Apart from these differences in morphology and chemistry, grasses and browses also differ in architecture, growth form and spatial arrangement. Grasses consist of leaves and stems that differ in quality only over a very small spatial scale. Further, the low growth form of grasses, in which new tillers are added to the base of the plant, creates a rather continuous three-dimensional layer of vegetation with a relatively constant density (Jarman 1974). A grass sward also frequently consists of a mix of different species. These characteristics make that grasses provide a rather homogeneous food source for larger herbivores that face difficulties in selecting the good parts from it, if possible at all (Drescher 2003). Browse on the other hand, tends to contain a more heterogeneous assembly of plant parts of various nutritional quality with buds, leaves and stems. Also the individual browse plants are dispersed in a more discrete fashion and are thus more spread out in space. In browse, the change in quality when bite size increases is also much greater than in grass (Van Wieren 1996a).

Food adaptation in ungulates

Diet overlap can, however, be misleading since species may converge in diet toward the more productive resource type as competition intensifies (Abrams 1990; Ritchie and Tilman 1993) and diet overlap may change with species density. Moreover, it will not be surprising that ungulates have adapted themselves to utilise the various plant resources (Owen-Smith, Chapter 8) and more in particular to the two main

Diet overlap can be misleading since species may converge in diet toward the more productive resource type as competition intensifies

forage classes discussed above. It has long been recognised that ungulates differ in the preference they show for certain food categories and that these preferences are related to a number of characteristics which involve both adaptations to the cropping and to the processing of the food base. Cropping and processing abilities have been attributed both to body size and special adaptations irrespective of size. The idea that there are different categories of ungulates, like typical browsers and grazers, which fundamentally differ in their anatomy and digestive system, has both been advocated (Hofmann 1973, 1989; Van Wieren 1996a; Iason and Van Wieren 1999) and challenged (Gordon and Illius 1994; Robbins et al. 1995; Gordon 2003). Fact is that for most characteristics, body size always plays a role because of the enormous range in body sizes that can be found in most ungulate communities (Table 11.1) and because body size affects almost every ecological parameter (Peters 1983). Here we have tried to disentangle the effects of body size and categorical difference (Tables 11.5 and 11.6) but note that there is always an interaction.

Table 11.5. *Some relative differences in characteristics related to the cropping and processing of plants between small and large ungulates (Van Soest 1994; Van Wieren 1996a).*

Characteristic	Small	Large
Absolute energy requirements	Low	High
Relative energy requirements (per kg $^{0.75}$)	High	Low
Absolute food intake	Low	High
Relative food intake (per kg $^{0.75}$)	High	Low
Gastro-intestinal tract	Small	Large
Muzzle width	Narrow	Broad
Selectivity in feeding	High	Low

In absolute terms, small herbivores need less energy and food than large ones (Table 11.5). Because of allometric scaling, however, small animals require more energy per unit weight, which they can accomplish by eating more or selecting food items of a higher quality. It has been found that relative food intake of smaller ungulates is higher than that of larger ones (Van Wieren unpublished data), but smaller animals are also more selective.

This is facilitated by a smaller muzzle width that allows them to crop smaller food items. High-quality food items are in general both more scarce and smaller than low-quality food items. Although it seems evident that large herbivores are better suited to digest cell walls than smaller ones (Demment and Van Soest 1985), an analysis of more than 200 feeding trials with various ungulate species did not reveal significant differences in the capacity to digest cell walls between small and large animals (Van Wieren 1996a). The various characteristics within a certain size range are, logically, related, and we can state that different sizes produce different adaptive syndromes, which are suited to the exploitation of a certain part of the plant food base. Although size alone has great explanatory power, there are still a number of differences to be found between browsers and grazers (Table 11.6).

Table 11.6. *Relative differences in characteristics related to the cropping and processing of plant material between grazers and browsers, corrected for body-weight effects (Van Wieren 1996a; Iason and Van Wieren 1999; Mendoza et al. 2002; Hofmann 1973; Clauss et al. 2003)*

Characteristic	Grazers	Browsers
Hypsodonty index	High	Low
Skull length relative to body size	Large	Short
Shape of incisor arcade	Straight	Curved
Muzzle width	Broad	Narrow
Digestive capacity	High	Low
Salivary glands	Small	Large
Liver	Small	Large
Retention time of food	Long	Short
Reticular orifice	Small	Large

Some of these are related to harvesting. Grazers have teeth with higher crowns than browsers, which enables them to utilise the more fibrous and silica-laden grasses (Mendoza et al. 2002). Grazers and browsers also differ in other craniodental features, which make them suitable to exploit either grasses or browses better. Grazers have a relatively large skull, the shape of the incisor arcade is straighter and they have a broader muzzle that makes them fit to exploit the more continuous grass sward, but at the same time reduces their ability to select the smaller, more nutritious parts within the sward (Illius and Gordon 1987; Janis and Ehrhardt 1988). Note that there also are differences related to phylogeny. Suids and equids, in contrast with ruminants, have upper incisors that make them better equipped for tearing off grass leaves.

Browsers, on the other hand, tend to have narrower muzzles and a relatively larger mouth opening that permits sideways stripping of leaves. They frequently have a longer tongue and prehensile lips, which enables them to negotiate thorns and take small bites that are difficult to reach. Browsers also have larger salivary glands and a larger liver (Hofmann 1989; Robbins et al. 1995), both seen as adaptations to deal with the secondary compounds so characteristic of the browse world. Proteins in saliva can bind tannins while many toxic compounds can be detoxified in the liver. Browsers have lower digestive capacity than grazers (Iason and Van Wieren 1999) and are more adapted to utilising cell content than cell wall. Cell content fermentation is rather quick and permits a higher throughput of food through the digestive tract (Clauss et al. 2003), which is facilitated by a large reticular orifice, the opening between the reticulum and omasum.

Diet specialisation within ungulates

The structural differences between grasses and browses have led to various adaptations within ungulates, and this has led to the recognition of a number of dietary strategies (see also Owen-Smith, Chapter 8). A number of classifications
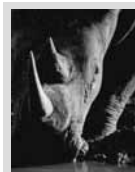

Structural differences between grasses and browses have led to various adaptations, which has led to the recognition of dietary strategies

based on food preference of ungulates have been proposed (Gagnon and Chew 2000; Hofmann and Stewart 1972; Janis 1995; Langer 1988; Mendoza et al. 2002), but there is no consensus. Here we adopt the classification into six classes of Gagnon and Chew (2000) as it is based on the most extensive survey of the literature (Table 11.7).

Table 11.7. *Classification of Kruger National Park ungulates based on diet preference (Gagnon and Chew 2000; Van Wieren 1996a).*

Code	Diet
OG	obligate grazers (>90% monocots)
VG	variable grazers (60-90% monocots)
BG	browser-grazer intermediates (30-70% of dicots and monocots, <20% fruits)
GE	generalists (>20% of all food types)
BR	browsers (>70% dicots)
FR	frugivores (70% fruits, little or no monocots)

The various classes of diet specialisation are not randomly distributed across the body size range. Figure 11.2 clearly demonstrates that small animals are more likely to be frugivores and browsers while the very large ones are more of the grazer type. This again points to the important effect that body size has on the structuring of adaptive syndromes. Substantial overlap, however, can be expected in a large portion of the medium size range. We have evidence that browsers are more obligate in their food preference than both pure grazers and animals of the more mixed types (Van Wieren 1996a). This would indicate that pure browsers can be clearly distinguished and separated from all other types. The question how diet preference structures the Kruger ungulate community is illustrated in Table 11.8.
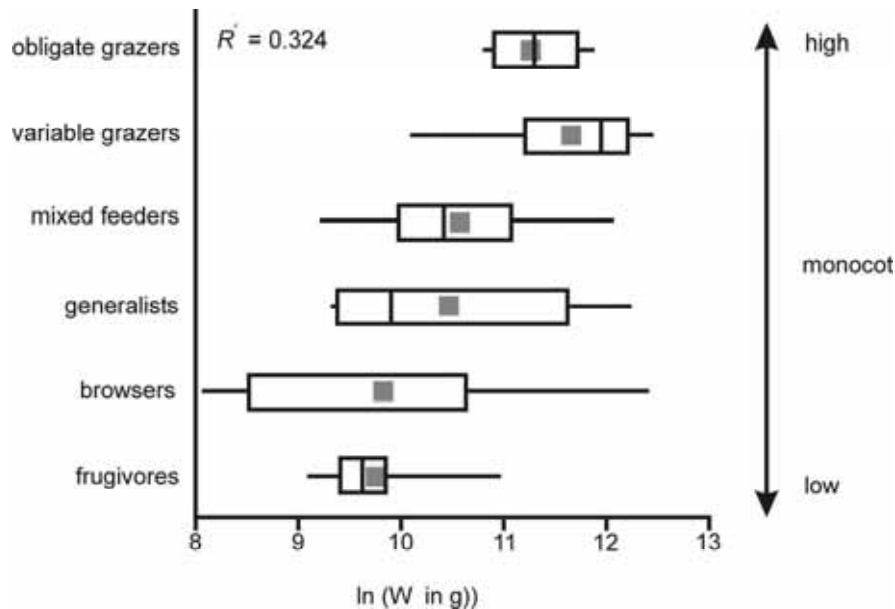
Figure 11.2. *Box plot showing the relationship between body mass (g) and dietary preferences for 76 species of African bovids (Gagnon and Chew 2000).*

Table 11.8. *Classification of Kruger NP ungulates based on dietary preference (for legend see Table 11.7; Gagnon and Chew 2000; Van Wieren 1996a).*

Species	Diet class					
	OG	VG	BG	GE	BR	FR
suni					●	
Sharpe's grijsbok			●			
common duiker					●	
red duiker						●
klipspringer				●		
steenbok			●			
oribi		●				
vaal rhebok			●			
mountain reedbuck	●					
bushbuck					●	
impala			●			
common reedbuck	●					
warthog		●				
bushpig				●		
nyala				●		
tsessebe	●					
hartebeest (Licht.)		●				
waterbuck		●				
sable antelope		●				
greater kudu				●		
blue wildebeest		●				
Burchell's zebra	●					
roan antelope		●				
eland				●		
African buffalo		●				
giraffe					●	
black rhino					●	
common hippo		●				
white rhino	●					
African elephant				●		

Apart from the frugivores, each category contains a number of species. It can further be seen that the 'size rule' is violated in almost each diet category. The small oribi is very much a grazer while the giraffe and the black rhino are obligate browsers. Similar to the classification in habitat, the classification in diet preferences brings about some differentiation but does, in itself, not clearly separate all the species.

HABITAT AND DIET COMBINED

Now we can combine the two most important resource axes into one picture (Table 11.9). The two axes separate more species than either one of them. Quite a few species show no overlap with quite a few other species. According to this analysis,

Table 11.9. *Classification of Kruger National Park ungulates based on both habitat and diet preference. For legend see Tables 11.2 and 11.7. Body weight classes: S = 5-50 kg, M = 51-200 kg, L= >200 kg.*

Habitat class	Size class	OG	VG	Diet class BG	GE	BR	FR
LS	S	m-reedbuck	oribi	rhebok			
	M	c-reedbuck tsessebe	warthog hartebeest waterbuck	impala			
	L	zebra	wildebeest buffalo hippo	eland elephant		giraffe	
WS	S			grijsbok steenbok			
	M	tsessebe	warthog hartebeest waterbuck	impala			
	L	zebra	roan wildebeest buffalo	eland elephant		giraffe	
Wo	S					suni	r-duiker
	M		hartebeest		nyala		
	L		sable buffalo	eland elephant			
Fo	S					suni	
	M				bushpig		
	L		buffalo	elephant			
SB	S			steenbok			
	M	tsessebe	waterbuck				
	L	w-rhino		elephant		giraffe	
BS	S			steenbok		bushbuck	
	M	tsessebe			nyala		
	L	w-rhino	sable wildebeest roan	elephant		giraffe	
Bu	S			steenbok		c-duiker bushbuck	r-duiker
	M		hartebeest		bushpig nyala		
	L			elephant	kudu b-rhino		
Th	S				klipspringer	c-duiker suni bushbuck	r-duiker
	M				bushpig nyala		
	L		sable	elephant	kudu		

m = mountain; c = common; w = white; r = red; b = black

however, separation is far from complete. Groups of species can still be found in the various diet–habitat classes. This is not surprising as, in particular, the diet classification is quite general and each class comprises a whole range of plant species. Much more detailed study is needed to try and separate the 'remaining' species while incorporating detailed observations on diet selectivity and a further differentiation in resource axes by including spatial and temporal heterogeneity, and the species' response on these. The effects of size may play an important role here as we will discuss below, but it is furthermore evident that habitat and diet choice most likely are not sufficient to explain the ungulate community completely and that other resource dimensions have to be included too. Nevertheless, this exercise can be used to point to certain combinations of species that likely show large overlap, especially when they are similar in size (e.g., sable antelope – roan antelope – wildebeest – zebra or bushbuck – nyala – common duiker). To explain these combinations poses the greatest challenge to students of ungulate community. In the remainder of this chapter, we will focus on a number of other characteristics of the niche space which need to be incorporated in the analysis and which can help to further separate the species in our ungulate community.

RESOURCE HETEROGENEITY AND BODY SIZE

Especially in the green world resources are not homogeneous entities. Animals can make choices in heterogeneous environments with difference in food types, variation in distribution and density of these food types, differences in food patch size, etc. These possibilities of choice by foraging animals suggest that heterogeneity in the distribution of resources and habitat play a large role in competitive coexistence, because greater heterogeneity implies more available resources (Ritchie 2002).

As indicated in Table 11.4, both grasses and browses are heterogeneous in architecture. Within a sward, patches of different height can be found, and within a plant, different plant parts with frequently varying quality are apparent. This

Heterogeneity in the distribution of resources plays a large role in competitive coexistence, because greater heterogeneity implies more available resources

variation in a single resource leads to a further possible niche differentiation within the herbivores exploiting the resource. The factor that best seems to describe this differentiation is body mass. In Table 11.5, a number of vital differences between being either a small or a large animal is given. These differences can be used to explain why small and large herbivores exploit different dimensions of the same resource. Of great importance is the variation in height/biomass of the resource. It is easy to envisage that the giraffe and the steenbok can be separated along a vertical gradient while exploiting the same resource. But separation can also occur when the vegetation is within reach of species of different size (e.g., 0-100 cm). The separation is based on the difference
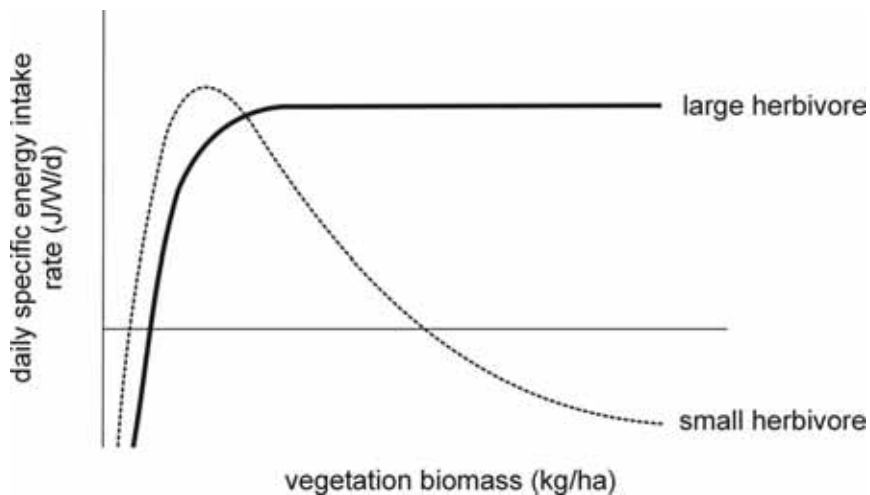
in the functional response between small and large herbivores when foraging on vegetation of varying height/biomass. This has been best studied in grass swards (Prins and Olff 1998; Drescher 2003).

A schematic representation of the functional response of small and large herbivores across a biomass gradient is given in Figures 11.3 and 11.4. From Figure 11.3, it is clear that in an absolute sense (i.e., per animal), intake rates of larger herbivores are always higher than those of smaller herbivores. However, per unit body mass, intake rates at low plant biomass are higher in small herbivores (Figure 11.4). The reason for this lies in the allometric relationship between body mass and mouth size whereby small species are able to take relatively larger bites at low grass height (Gordon 2003). The asymptote is also reached earlier in small species, to decline thereafter and to become much lower than that of larger species at higher biomass. The reason for this decline may be a relatively larger increase in vigilance behaviour or a relatively greater problem in coping with a decrease in the availability of high-quality food items (Stobbs 1973; Van de Koppel et al. 1997; Drescher 2003). Small herbivores are thus better able to exploit the lower biomass/height ranges of the vegetation and large herbivores the higher.
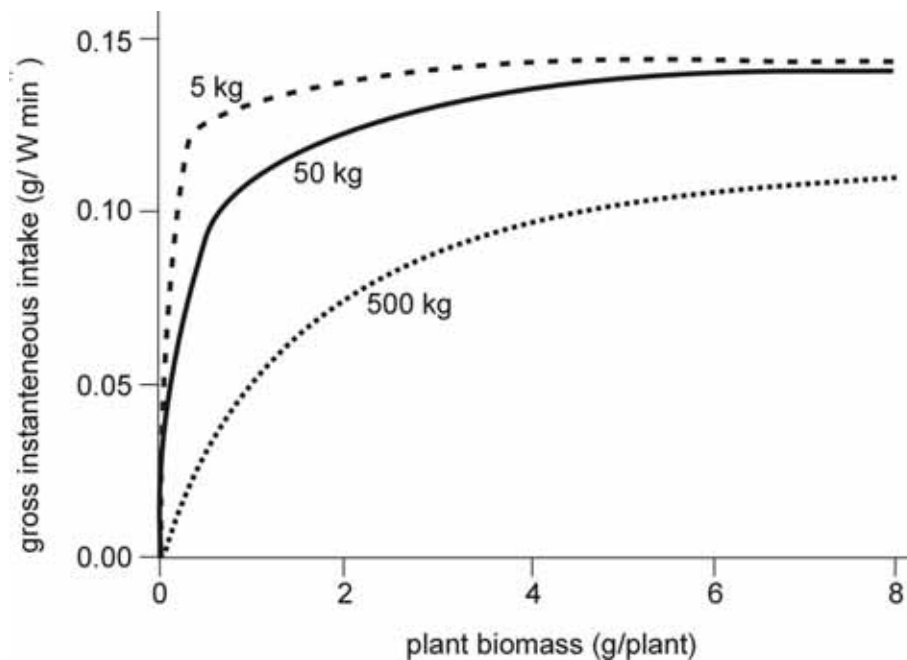
Figure 11.3. *Gross instantaneous intake rate as a function of plant biomass at different body mass (Gross et al. 1993, Prins and Olff 1998).*

Figure 11.4 can also serve as model for some important interactions between herbivores. Species of similar size are, on the basis of the similarity in their functional response, much more likely to compete than when species differ largely in weight. Further, we can hypothesise that when two species of different size show considerable overlap in diet preference, the smaller species is more likely to suffer from competition from the larger one than *vice versa* because the smaller species is much more overlapped by the larger one than that the smaller one overlaps the larger. On the other hand, it can be envisaged that a large species, by changing the grass biomass/height to a lower level, can facilitate smaller species. Facilitation has been reported between hippo and kob (Verweij et al. 2006), and between other large and small grazers (see Prins and Olff 1998 for more examples). Box 11.3 further discusses facilitation.

Figure 11.4. Predicted pattern of functional response of daily specific net energy intake of grazers towards vegetation biomass for a small and a large herbivore, assuming a negative relationship between vegetation biomass and forage quality, and larger problems in the small species in coping with poorer quality forage (Prins and Olff 1998).

RESOURCE HETEROGENEITY AND SCALE

Heterogeneity in resources exists at different spatial and temporal scales (Skidmore and Ferwerda, Chapter 4). In such heterogeneous environment, the resource distribution is perceived differently by species that differ in body size (Ritchie 1998). In a specific environment, one species, which detects variation at a very small scale of resolution, finds many choices. Another species, which detects variation at a very large scale, may find the environment to be very homogeneous because this species averages across the detailed variation detected by the smaller-scaled species. Size not only determines food requirements, it apparently also determines the scale of resolution at which animals perceive the environment.

Box 11.3. *Facilitation between herbivores*

Facilitation among species is the process whereby one species benefits from the (feeding) activities of another. For herbivores, the interaction is thus strongly mediated through grazing and browsing impacts on the vegetation. Facilitation is generally brought about by the larger species having a positive effect on the smaller ones. Large species have the ability to utilise low-quality food and therefore they can sustain on tall vegetation, while small species require high forage quality, but can tolerate low food levels. Small species may thus benefit from the grazing impacts of the larger species because biomass is reduced and food quality is enhanced. It is well established that grazing stimulates grass regrowth, thereby increasing the nutritional quality of the forage (Vesey-Fitzgerald 1974; McNaughton 1976). Facilitation may act on the population level and, perhaps, even may affect species richness (Prins and Olff 1998; Arsenault and Owen-Smith 2002).

Facilitation may increase access to and quality of resources. On the Island of Rum, Scotland, Gordon (1988) found that areas grazed by Highland cattle during winter had a significantly higher standing crop of green vegetation in the spring, and had a greater proportion of green material, than areas without cattle grazing. Red deer (*Cervus elaphus*) preferred the areas previously grazed by cattle while females produced more calves per female in areas where cattle were reintroduced. Although perhaps not so common, facilitation can also be brought about by small herbivores. On a salt marsh in the Netherlands, it was found that brown hares (*Lepus europaeus*) facilitated brent geese (*Branta bernicla*) by selectively removing the shrub *Atriplex portulacoides*, making the preferred forage grass *Festuca rubra* more accessible (Van der Wal et al. 2000). Because of their size, gregariousness and rather unselective mode of grazing, large grazers are able to create grazing lawns which provide short, high-quality forage over larger areas, attracting smaller grazers (McNaughton 1976, 1986; Fryxell 1991). Especially grazing megaherbivores (>1000 kg) like hippopotamus (*Hippopotamus amphibius*) and white rhinoceros (*Ceratotherium simum*) have been found to create grazing lawns, benefiting short-grass-preferring species like wildebeest, zebra, impala and warthog (Owen Smith 1988).

For facilitative effects on the ecosystem level, affecting community structure and species richness, a keystone species, *sensu* Paine (1969), is needed. This megaherbivore, then, should be able to alter vegetation structure profoundly so as to 'lower the canopy', as the result of which more primary production becomes accessible while variation in available niches should increase. To date, only the elephant has been hypothesised to be able to accomplish this. It is well known that elephants can transform savanna woodlands into either open parkland or shrubland (Laws 1970; Bell 1981; Dublin et al. 1990). The vast increase of elephants in the Tsavo region in Kenya during the 1960s, and consequent opening of dense shrubland, was followed by increases in the abundance of grazers like oryx (*Oryx gazella*) and zebra (*Equus burchelli*), while browsers such as lesser kudu (*Tragelaphus imberbis*) and gerenuk (*Litocranius walleri*) declined (Arsenault and Owen-Smith 2002; Parker 1983). The reverse has also been reported: a decline in some grazing ungulates following the extermination of elephants (Owen-Smith 1989). In a recent analysis of 31 ungulate communities from East and Southern Africa, Fritz et al. (2002) studied the relationship between megaherbivores and mesoherbivores. First, it was established that megaherbivores indeed generally make up the bulk of the ungulate community. Further, the study showed that the various guilds of mesoherbivores reacted differently to the most dominant megaherbivore, the elephant. No relation between elephants and the mesograzers was detected but both the mesobrowsers and the mesomixed feeders were negatively affected by elephants. In this study, the effect on the mesograzers was thus neutral while, like above, the effects on the more browsing species were more competitive. The potential facilitative keystone effect of elephants on the ungulate community at large has thus not unequivocally been substantiated. Furthermore lacking, still, is evidence that megaherbivores can have an effect on the composition and species richness of ungulate communities.

Ritchie and Olff (1999) argue, therefore, that it seems likely that body size, which is often different among coexisting species, influences how much heterogeneity is detected and what choices are available to a species. They provide a mechanism of niche differentiation that could explain coexistence of different-sized animals. This mechanism is based on the assumption that larger-scaled species may only select resource clusters that exceed a certain density, so that small resource clusters are ignored effectively. For non-randomly moving foragers attempting to maximise their encounter with resources, smaller-scaled species should experience a higher average resource density per patch (volume sampled) and greater numbers of acceptable resource patches (Ritchie 1998). Larger species encounter fewer acceptable patches, which contain absolutely more resources per patch (volume sampled), but the resources occur at a lower density per unit volume sampled. If large and small species search the same number of patches per unit time, then the larger species should also sample a greater total volume per unit time. These mathematical outcomes predict that species measure different qualities of a single resource by virtue of their different scales, and may thus differ in the rate of consumption of resources. However, trade-offs in number, resource density and size of resource patches encountered or accepted, as well as search rate, suggest that differences in foraging scale among species provide some potential for coexistence (Ritchie 1998; Ritchie and Olff 1999; Ritchie 2002). These trade-offs generate exclusive resources for species of different size: each species has a unique set of food patches of a particular size and resource concentration.

Body mass of animals could explain exclusive resource use and coexistence

Although this prediction is untested, Ritchie (2002) argued that some field experiments support the assumption that larger-scaled animals select larger resource clusters. In the Negev desert, large gerbils (*Gerbillus* sp.) left patches with more seeds remaining than smaller gerbils (higher giving-up densities, GUDs) (Brown et al. 1994; Garb et al. 2000). This could suggests that larger foragers select only large seed patches and thus perceive the environment in a more coarse-grained manner than smaller rodents. These GUDs directly correspond to a minimum seed consumption rate, and thus could conceivably be used to calculate a minimum patch size.

On a larger scale, Redfern et al. (2006) recently analysed the associations of seven herbivore species (three grazers and four browsers) in the Kruger National Park on three different spatial scales: $5\times5km^2$, $10\times10km^2$ and $15\times15km^2$. It was expected that all herbivore distributions would be similar at large scales because of the influence of abiotic factors, but that at smaller scales the relative importance of guild aggregation versus competition in structuring assemblages would become apparent. For instance, similar-sized species with similar diets are expected to associate less on smaller scales. It was indeed found that similarity was greatest at large scales and that spatial distributions became increasingly disjoint at smaller scales. Larger species had a more even spatial distribution than small species, presumably because of a higher tolerance for low-quality foods.

OTHER NICHE DIMENSIONS

When body mass (through its relationship with resource heterogeneity) is added to the habitat-diet niche space, the community becomes much more structured. Oribi and buffalo will most likely be separated now, like steenbok and elephant, and bushbuck and giraffe, to name a few examples (Table 11.8). Yet, various combinations of species with similar body size remain present in the same habitat-diet group. Apparently more and other niche axes need to be invoked to explain these combinations. Some of these niche axes that can possibly act as niche separators are briefly described below.

Morphological differences

Similar-sized species may differ in mouth structure, which leads to differences in the part of the resource base that can be exploited. Sometimes, these differences are related to phylogeny. So have equids relatively narrower muzzles than ruminants of similar size (Janis and Ehrhardt 1988; MacFadden and Schockey 1997), but

Similar-sized species may differ in mouth structure, which leads to differences in the part of the resource base that can be exploited

differences can also occur within the same taxonomic group. Murray and Brown (1993) compared similar-sized wildebeest, hartebeest and topi, the latter being the same species as the tsessebe from Kruger National Park. From these three species, the wildebeest has the greatest muzzle width, while the muzzle width of topi and hartebeest are similar. Its broad muzzle makes wildebeest better suited for short leafy grasslands while topi, with their relatively pointed jaw, are expected to be better as selective feeders in medium-height upright grasslands (Illius and Gordon 1987). These expected differences were also found in field observations (Bell 1970; Duncan 1975; Murray and Brown 1993).
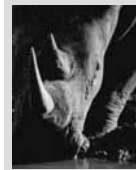
Although the muzzle width of hartebeest is similar to that of topi, their foraging behaviour is nevertheless different. Hartebeest were always less successful in a series of feeding trials, selecting less leaf, securing smaller bites at a slower bite rate (Murray and Brown 1993). Also in the field, hartebeest and topi differ in foraging behaviour, especially in the dry season. Thus, even while hardly distinguishable morphologically, topi and hartebeest are specialised on a different growth stage of the grass sward (Stanley Price 1974), indicating that spatial and vertical arrangements in and between grass swards are thus additional dimensions of niche space.

More differences and Gause's axiom

When species, even after the most important resource axes have been applied, still show considerable overlap, then the analysis becomes fuzzier. To circumvent the Gausian paradigm that two completely overlapping species cannot coexist, ever more niche dimensions need to be invoked because, by definition, they must be

there. And, indeed, the more we study and compare species, we will always find plenty of differences because no two species are alike! Species may differ in water dependence (Sahid 2003), in efficiency with which they utilise acquired resources (e.g., similar-sized ruminants versus non ruminants, Van Wieren 1996a), in efficiency with which they can cope with predation (Sinclair et al. 2003.), in metabolic rate (e.g., wildebeest, eland and hartebeest, Owen-Smith 1985), in heat tolerance (oryx and wildebeest: Sahid 2003), and a host of other characteristics.

Problem is to end up in the tautological backwater of the Gaussian axiom with a never-ending search for the niche axis along which two species might differ

No doubt, all these differences are real but the problem is that we may end up in the tautological backwater of the Gausian axiom with a potentially never-ending search for the niche axis along which two species might differ. Although this problem has been considered real (Hubbell 2001; Chase and Leibold 2003), solutions have been sought and found (for a review see Chase and Hubbell 2003).

SYNTHESIS

In this chapter, many factors that possibly shape the (co)existence of ungulate communities have passed by. Although we can not yet predict the composition and structure of a community in a given biome, we can hypothesise about the principal processes involved and put them in a coherent framework. From this scheme, testable hypotheses can be generated.

Despite difficulties, our starting points are the niche concept and the strive between species for the acquisition of resources. Our principal hypothesis is that species can only exist if they have exclusive access to resources that cannot be used by others. The playing field for competition is then confined to resources shared with other species, and coexistence and equilibrium densities of populations become a function of the amount of shared resources and the exclusive resources of other species (Ritchie 2002).

The second crucial factor affecting community richness and structure is related to the distribution of resources in space: spatial heterogeneity. Resources are not homogeneously distributed in space but density and extent of density vary, leading to a patchy landscape with patches of varying size and resource density. This patchiness can be described by fractal geometry (Ritchie 1998, 2002). Especially for mobile animals like ungulates this patchiness is important because they can move through the landscape and are thus able to make choices. By making choices they may try to evade competition with others and, even more important, the scale of resolution with which animals perceive the landscape depends on their size, leading to differential use of a patchy landscape by small and large species (Ritchie 2002). Adding heterogeneity thus both underlines the fundamental role of body size and also can explain the presence of the large body weight ranges so characteristic of the richer ungulate communities. It can also be deduced that heterogeneity and ungulate

species richness are positively related. Most of this is, however, still hypothetical, and although the structure of a number of communities could be explained by this theory (Ritchie 2002), for ungulate communities the work still has to be done. A complicating factor here is that the resource (grass, browse) is not so discrete (unlike seeds) and that foraging can change the amount and quality (density) of the resource, possibly affecting the amount of exclusive resources for species.

Therefore, much still needs to be done, and we suggest that in order to make real progress in this field, future research should focus on the following topics. First, define the fundamental niche (adaptive syndrome) of species regarding resource and habitat requirements, based on predominantly physiological and morphological characteristics. A start has been made by Chase and Leibold (2003). Second, describe the heterogeneity of the landscape in terms of patchiness and patch resource density using fractal geometry, and, third, estimate the minimum threshold patch size and the minimum resource density for each species. If the above programme can be executed, then the road is open to analyse fundamental relationships and to test crucial hypotheses which are now coming up in the mind of the reader. Some hypotheses for future research are formulated in Box 11.4.

Box 11.4. *Testable hypotheses for future research*

Hypothesis 1. A species can only exist if it has exclusive access to resources that cannot be used by others.
Hypothesis 2. Increasing heterogeneity leads to a higher species packing, greater species richness, and greater size range of ungulate communities.