

RESOURCE-RATIO THEORY APPLIED TO LARGE HERBIVORES

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Abstract. The theoretical description of exploitation competition, known as resource competition theory (RCT) or resource-ratio theory, has been tested in terrestrial plant communities and microorganisms in laboratory cultures. Applications in animal ecology have been rare, although the theory itself is generic. A major difficulty is that the description of resources in RCT is fundamentally different from that used in classical studies of animal competition. In presenting the first fully specified RCT models for terrestrial animals, we distinguish between positive attributes (mineral elements) and negative attributes (plant defenses) as indicators of quality in animal resources. Using the latter we apply RCT to ungulate communities that exploit just two resources: the cell wall and cell contents of plant material. We show how coexistence in the same habitats depends on the strategy of resource exploitation. Ungulate species that differ in body size adopt a “demand-minimizing” strategy that permits them to coexist on ratios of the two resources by acquiring less of the resource that most limits their competitor. Ungulates that differ in mouth width adopt an “extraction-maximizing” strategy that leads to competitive exclusion because they acquire more of the resource that most limits their competitor. We conclude that differential resource utilization permits grazing herbivores of different body size to coexist on the same grassland habitats, but that the full diversity of grazing communities depends on spatial heterogeneity in plant defenses at the landscape level.

Key words: *body size; coexistence; competitive exclusion; grazing community; plant defenses; resource-ratio theory; Serengeti; ungulate.*

INTRODUCTION

By defining resource use distributions, MacArthur and Levins (1967) developed a resource-based theory of competition coefficients that could be applied to motile animals such as ants, lizards, birds, and herbivorous mammals. 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. The competition coefficient remains, however, an essentially descriptive parameter, correlated to resource use overlap but not mechanistically derived from it. This limitation is the fundamental reason classical competition theory (CCT) can predict the intensity of competition, but not the outcome. CCT cannot predict in a given case whether exclusion will occur, and if so, which species will be excluded (Tilman 1982, 1986, 1987, Abrams 1983, Grover 1997, Miller et al. 2005).

Resource competition theory (RCT) has been developed to predict the outcome of competition. Two vital components lie at its heart. First, the growth of each competing species is explicitly related to its consumption

of resources. Second, the outcome of resource consumption is determined by a species interaction rule that either causes competitive exclusion or allows coexistence (León and Tumpson 1975): coexistence requires that each species consumes less of the resource that contributes more to its competitor's growth. If this condition is satisfied, numerous species can coexist whilst competing for just two resources, given spatial variability in the availability and therefore ratios of those resources (Tilman 1982).

A variety of resource types have been analyzed by RCT, including those that are essential for growth and those that can be substituted for each other (Tilman 1982). Curiously, there has been no equivalent analysis of consumer types, reflecting perhaps the early application of the theory in studies of microorganisms and higher plants (Miller et al. 2005). A useful classification of plant and animal consumers can be founded on adaptations to resource scarcity and the León and Tumpson rule. Under conditions of resource scarcity, plants and animals may adapt to competition either by increasing their potential to extract a limiting resource or by decreasing their demand for that resource. For instance, the tongues of certain pollinating insects have elongated because small extensions increase their nectar extraction capability (Darwin 1862). Similarly, the deep and robust bill of the Large Ground Finch (*Geospiza magnirostris*) enables it to feed more rapidly on hard seeds than its competitors (Grant 1986). We classify

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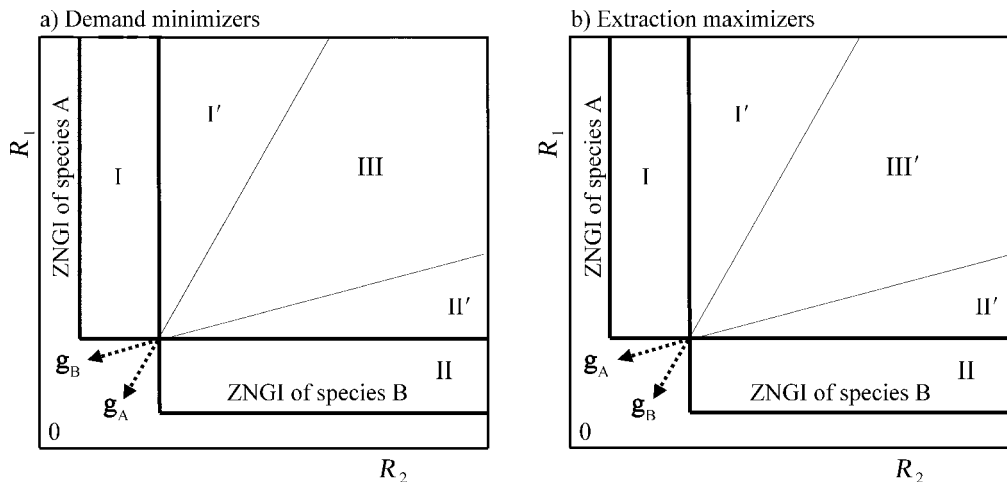


FIG. 1. Graphical models of species competing for the essential resources, R_1 and R_2 (after Tilman 1982). In both cases the zero net growth isoclines (ZNGIs) cross at a two-species equilibrium point. (a) Species A with consumption vector \mathbf{g}_A consumes less of R_2 , which is its competitor's limiting resource. Similarly species B with consumption vector \mathbf{g}_B consumes less of R_1 , which is its competitor's limiting resource. Both species can coexist in region III; species B will be excluded from regions I and I', and species A will be excluded from II and II'. Neither species is sustained in region 0. This pattern of competition can be expected where species have adapted to resource scarcity by minimizing demand for a limiting resource. Here species A has minimized its demand for R_2 (enabling it to persist where R_2 occurs at low density, and to require little uptake of the resource), and likewise species B has minimized its demand for R_1 . (b) In this model, each species consumes relatively more of its competitor's limiting resource. The outcomes of competition are identical to those for (a) except that in region III', either species can displace the other, depending on starting conditions. This pattern of competition can be expected where species have adapted to resource scarcity by maximizing the rate of extraction of a limiting resource. Here species A has maximized its uptake of R_2 , enabling it to persist where R_2 occurs at low density by extracting more of the resource than its competitor.

organisms displaying the extractive kind of adaptation as "extraction maximizers." On the other hand, they may adapt by increasing the efficiency with which they utilize resources, thereby reducing the required intake or demand for a limiting resource. An animal's demand for sodium, calcium, or other metabolites, for instance, may be reduced by conservation mechanisms that decrease losses in urine and feces, effectively increasing the residence time of the limiting nutrient within the organism. Many plants have conservation mechanisms that improve the efficiency of nutrient use in their growth and reproduction (Chapin 1980). We classify organisms that have reduced resource requirements as "demand minimizers." Naturally, some organisms may have evolved greater efficiency in both mechanisms.

If two extraction maximizers compete for a resource within the same habitat, one will eventually reduce its availability to a level at which the other is excluded. A demand minimizer, by contrast, can persist in a habitat that has too little of some limiting resource for a competitor to survive, yet at the same time use so little of the resource that it does not compete aggressively for it when sharing richer habitats with a competitor (Fig. 1). Provided these consumer strategies are applied exclusively to the resources that are currently limiting, they offer an ecological interpretation of the León and Tumpson (1975) rule.

Tilman (1980, 1982) showed how many species of demand minimizer can coexist by specializing on ratios of just two resources, given variation in their supply rate

(Fig. 2). Furthermore, he predicted a distinctive pattern in species richness along a resource gradient. As the mean supply rate increases, variability in supply rates often remains constant such that the variability relative to the mean (i.e., the coefficient of variation) falls. Therefore in moving along a productivity gradient from the origin to progressively richer habitats (A, B, and C in Fig. 2), he predicted that species richness will initially rise rapidly, peak in habitat A, and slowly decline through habitats B and C.

RCT has seldom been applied to animal communities, even though it is essentially generic in nature. Grover (1997) knew of only one such experiment, that of Rothhaupt (1988) using rotifers. One reason for the failure with animals is the prodigious data required to test RCT's predictions. But the main reason perhaps is that animal and plant resources are entirely different in character. Plants and microorganisms absorb their food as simple soluble chemicals, surrounding them in the soil or in a growth medium. Plants require space, light, water, CO_2 , and some 20 or 30 mineral elements, such as nitrogen and phosphorus, any one of which may limit population growth (Tilman 1988). Because plants take up simple metabolites and specialize in how efficiently they are utilized, Tilman (1982) expected them to meet the León and Tumpson conditions for coexistence. Plants often use smaller quantities of their particular limiting resource because they have specialized in the ability to conserve them (Chapin 1980); for this reason they are more likely to be demand minimizers. On the

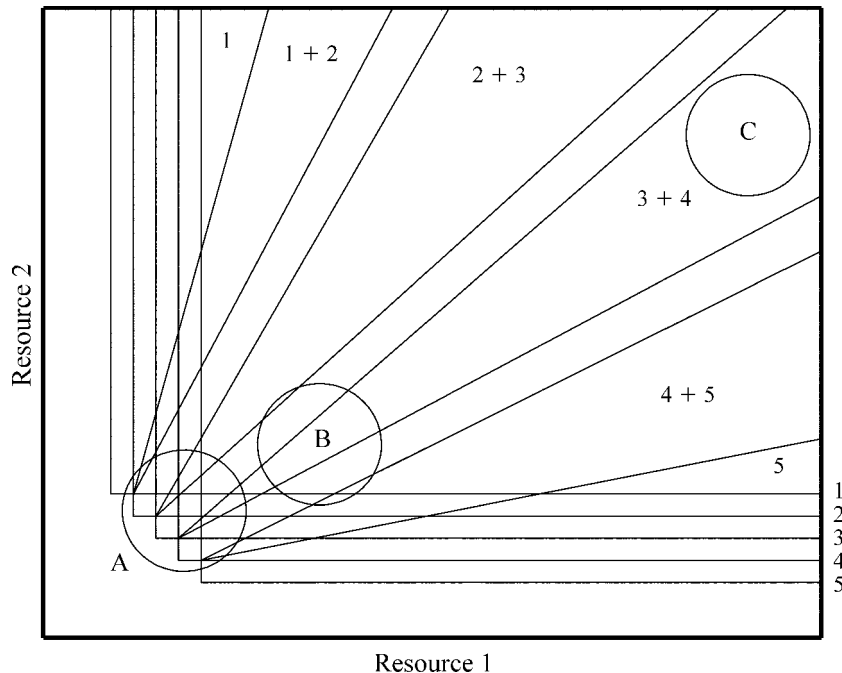


FIG. 2. The graphical model of Tilman (1980, 1982, 1986), which represents a range of habitats, varying in the supply rates of two resources. The circles (A, B, C) represent specific habitats. The lines (1–5) are the zero net growth isoclines (ZNGIs) of five species (1–5). Above and to the right of its 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 center 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.

other hand, some plants maximize resource extraction by adjusting shoot:root ratios or through association with mycorrhizae, so that further investigation is needed to better establish the relative importance of the two consumer strategies.

Although the range of minerals that an animal requires is limited and fixed just as for plants, the various macroelements and trace elements are bundled together in the cells of plants and animals (Robbins 1983). The complex digestive system of animals allows them to extract minerals and simple organic nutrients from a wide range of different foods. As with plants, the growth of herbivore populations can be limited directly by minerals such as phosphorus, calcium, and nitrogen (McNaughton 1988, Murray 1995, Elser et al. 2000), but it is often dependent on energy metabolism alone. In many cases it reduces to the problem of how to secure a sufficient energy intake. Since animals primarily need digestible energy and are specialized in extracting bundled nutrients in complex resources out of difficult environments, they are more likely to be extraction maximizers. They are more likely than plants to meet the León and Tumpson (1975) conditions for exclusion.

The food of herbivores contains complex mixtures of plant species and plant parts that are not ordered in a simple optimal way (Crawley 1983). Herbivores select food items with high energy and nutrient content, but they also avoid plant material with antiherbivore

defenses such as toxins, repellents, and digestibility-reducing substances (Rosenthal and Janzen 1979, Harborne 1988, Bryant et al. 1991). Plants with powerful toxins can remain virtually free of herbivore damage; others rely on lignin, tannin, or resins to deter rather than prevent feeding. The concentration of these deterrents varies according to the plant part (e.g., leaf, stem, fruit, or seed), plant phenology (especially age of leaf or shoot), and plant life history, rather than with the taxon of the plant, enabling edible and inedible food items to be readily distinguished (Feeny 1970, 1976). Plant defenses are considered better indicators of high-quality food in herbivores than are mineral elements (Feeny 1976, Rhoades and Cates 1976, Bryant and Kuropat 1980). Thus herbivores select food resources by attributes that influence energy and nutrient assimilation. Unlike mineral attributes that have a positive effect on growth, plant defenses have a negative effect, as the metabolizable energy content of the resource depends on the degree of their absence.

Assessing the quality of the grazing ungulate's diet is relatively simple, as grasses contain few secondary compounds and little tannin. The quality of forage is most often determined by just two components, one weakly and the other strongly defended: the cell contents (CC) are free from fiber and are soluble and easily digested, while the cell wall (CW) is largely insoluble and requires fermentation before digestion is possible. The

ratio in the supply rates of these two complex resources determines the digestibility of plant material and, as we will show, the ability of two ungulates to coexist. Our aim in this paper is to model consumption of CC and CW by grazing ungulates to determine conditions for coexistence and exclusion. We suppose that body size and mouth size are key determinants of community assembly outcomes in ungulate communities, and we incorporate them as parameters in our RCT models.

The ability to ingest and digest the CC and CW components of forage varies according to the body size of herbivores, and this property underpins the classical description of ungulate communities. In their application of Kleiber's rule to wild ungulate communities, Bell (1969, 1970) and Jarman (1968, 1974) noted that the rate of minimal metabolism of mammals increases according to body mass (M) as $M^{0.75}$. Consequently, small ungulates with a high metabolic rate per unit of body mass would be more frequently limited by the energy concentration of forage (i.e., by the availability of the CC component), and large ungulates with a high overall metabolic rate would be more frequently limited by the biomass of forage (i.e., by the availability of the CW component). Hence they predicted that small ungulates would be more limited by food quality and large ungulates by food quantity and used this relationship to account for niche differentiation in African ungulates. The Bell-Jarman hypothesis does not, however, predict the outcome or even assume the existence of competition.

Another approach to the investigation of ungulate communities is based on the allometric scaling of the mouth dimensions of grazing ungulates; it also explains the mass-related separation of feeding niches (Illius and Gordon 1987). In essence, short swards impose greater constraints on the bite depth of large species, relative to their metabolic requirements, despite their having broader incisor arcades and hence larger bite areas. By relating consumption rates to the availability of resources, this model can predict the outcome of competition between two species occupying overlapping niches. The result is that smaller species are expected to competitively exclude larger ones whenever defoliation is sufficient to deplete jointly used resources. In agreement with this prediction, wider-mouthed ungulates in the Serengeti of East Africa exclude narrower-mouthed ones with similar body mass from grazing lawns (Murray and Illius 1996). Thus past approaches to modeling community structure in ungulates either fail to predict the outcome of competition altogether or else predict single-species outcomes wherever competition plays a significant role.

SIMULATION MODELS OF RESOURCE COMPETITION THEORY IN UNGULATES

Much of the empirical research on resource competition theory (RCT) has been carried out using microorganisms growing in a chemostat in the labora-

tory, and with good reason. A fully specified experiment to test the predictions of RCT in nature requires a formidable amount of information and years of fieldwork (Chase and Leibold 2003). Fortunately, simulation modeling provides an effective tool with which to explore the predictions of RCT for vertebrates. In the case of ungulates, much of the data required to set up the RCT models are already available from studies of foraging behavior and digestive physiology. Previous modeling work has utilized an optimal foraging approach, for instance maximizing 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 (Owen-Smith 1985, Belovsky 1986, 1997, Illius and Gordon 1987, 1992, Murray 1991, Gordon and Illius 1996). The RCT approach uses the same data on profit and cost to predict the outcome of competition between ungulate species. The growth of each ungulate species is represented by its growth isoclines. The zero net growth isocline, or ZNGI, is the growth isocline at which reproductive rate equals mortality rate (Tilman 1980). Two simulation models are presented. The first concerns competition between antelope that differ in mouth size; the second concerns competition between ungulates of different body mass.

MOUTH SIZE COMPETITION MODEL

The mouth size competition (MSC) model derives the zero net growth isoclines (ZNGIs) and consumption vectors of topi and wildebeest (representing a green-leaf selector with a narrow mouth and an intake maximizer with a broad mouth, respectively) whilst they forage together on a single grass sward varying in its content of green leaf and stem. The model is based on data from Murray (1991), Murray and Brown (1993), and Murray and Illius (2000). Metabolizable energy intake is constrained either by the height of the sward or (where swards are tall enough) by the proportion of green leaf in the sward. Energy expenditure is based on an energy budget calculated for a moderately selective ruminant grazing for 10 h/d in the Serengeti (Murray 1991). The model was programmed in Waterloo Maple Release 9.5 (Maplesoft 2004). The code is given in the Supplement, and details of equations and parameter derivations are provided in Appendix A.

The model predicts an equilibrium point where the ZNGIs of wildebeest and topi cross one another (Fig. 3). Wildebeest at this point are more limited by the availability of green leaf. Topi are limited by the total availability of forage, but stem contributes more to their growth than green leaf. The steep vertical slopes of the consumption vectors show that both species are highly selective of green leaf, with topi being even more selective than wildebeest. At equilibrium, each species is consuming relatively more of the resource that is most limiting the other species (the species are not self-limiting), and therefore the equilibrium coexistence

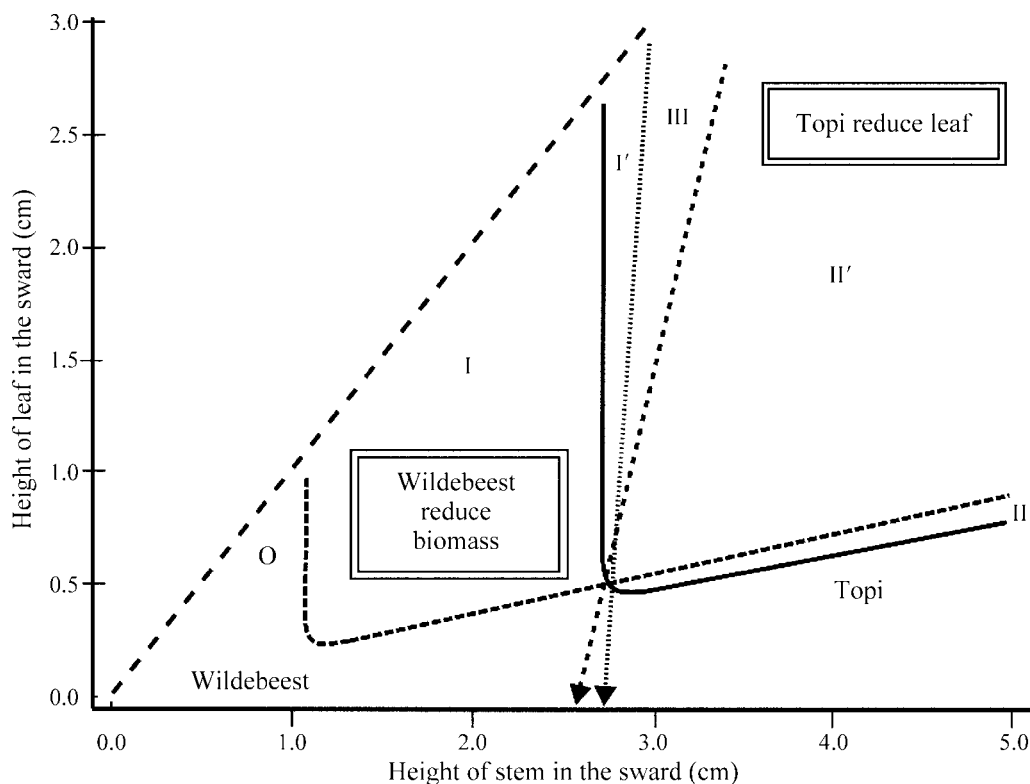


FIG. 3. Competition between topi and wildebeest within a homogeneous sward of grass. The height of green leaf is constrained to be less than or equal to stem height, indicated by the dashed line. The zero net growth isoclines (ZNGIs; solid for topi, close dashes for wildebeest) run nearly parallel to both axes, demonstrating that each resource is essential to the ungulates (Tilman 1982). The upward slope to the ZNGIs on the right-hand side of the diagram reveals the inhibition nature of stem as a resource. The consumption vectors (with arrows) show that both species are strongly selective of green leaf, with topi (barred line) slightly more selective. Topi capture almost all the tall, stemmy swards (region II'), where their narrower mouth gives them an advantage at selecting leaves. In region II', topi reduce the availability of green leaf so that there is too little for wildebeest. Wildebeest control the short, leafy swards (region I), where they reduce the total biomass of forage by cropping the grass very close to the ground. The topi's mouth is inefficient at harvesting such short swards. Coexistence is possible in region III but is unstable.

point is unstable. Furthermore, the range of habitat types that could lead to coexistence (region III) is narrow.

The figure shows that wildebeest can crop short swards down to a level that is too short to sustain topi (region I). If the sward is long enough to support topi, however, there is only a very narrow region (I') in which wildebeest can capture the sward from topi. In almost all swards with stem >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 at the supply point that will ultimately, through selective grazing, follow a trajectory into this region is large (region II', see also Fig. 5), and topi will capture virtually all tall swards. In the 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 (Tilman 1982).

Recognizing that specialization in the mouth, particularly in the width of the dental arcade, enabled grazing ungulates to maximize their extraction of particular resources, not to minimize their need (or demand) for them, Murray and Illius (1996) concluded that the grazing community of ungulates in the Serengeti National Park would not be stable within any given location due to the competitive process of sward capture. The MSC model supports their conclusion, but it is not the whole story.

BODY SIZE COMPETITION MODEL

In the body size competition (BSC) model we simulate the resource competition between ungulates of different body size whilst foraging together in the same habitat. The model does not contain a specific structural description of the environment, but predicts growth responses of animals to the availabilities of two resources in plants: cell wall and cell contents. The model uses allometric relationships for the energy requirements of the ruminant animal and for its intake

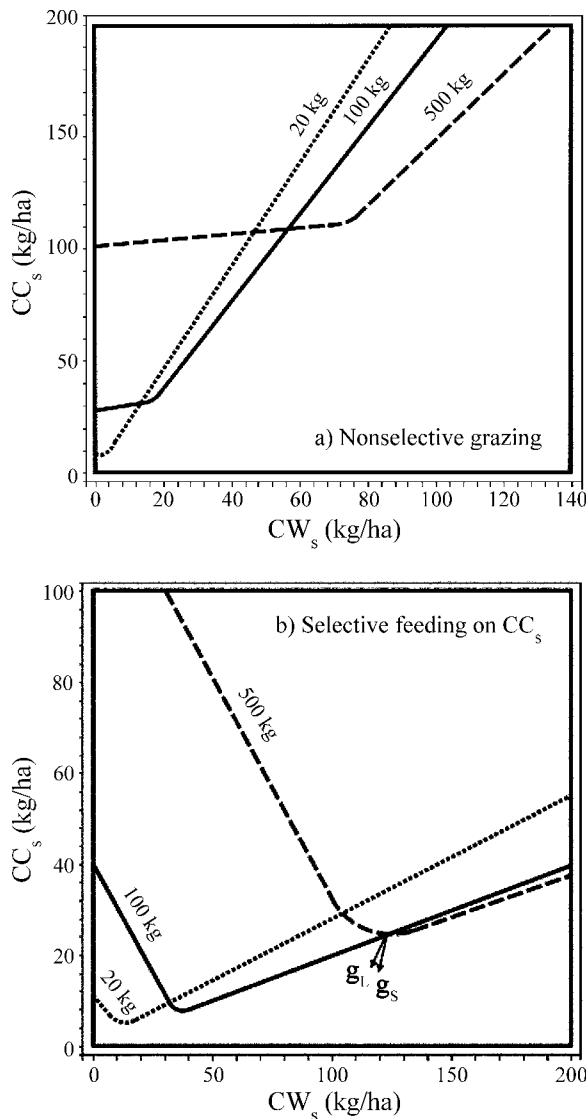


FIG. 4. Zero net growth isoclines predicted by the model for ungulates of different body sizes: (a) with nonselective grazing, and (b) with ungulates selectively feeding on cell contents. CC_s and CW_s are the supply rates (or standing biomasses) of cell contents and cell wall, respectively. Three crossover equilibrium points can be distinguished. Consumption vectors for the smaller 100-kg (g_S) and larger 500-kg (g_L) ungulates are shown at their equilibrium point in (b); all vector slopes are given in Table 1. Although three species pair interactions were modeled and three pairs of vectors were generated (Table 1), only one pair of vectors is shown in (b) for readability.

and digestion of food; these are based on the literature of ungulate foraging behavior and digestive physiology.

The intake component of the model calculates the daily intake of dry matter as the lesser value produced by two constraints, gut capacity and eating rate. Its structure (Appendix D) is based on the models of Fryxell (1991) and Wilmshurst et al. (1999, 2000), and uses their function to describe the eating rate constraint. The digestion component of the model calculates the

energy intake from the cell contents and cell wall fractions of the diet. The amount of cell wall digested depends upon its fiber content and on the ruminant's body size through its effect on the passage time of food. Most of the parameters and equations in this component are taken from Givens et al. (1989, 1990a, b) and from Van Soest (1994). The energy balance component of the model takes the gross digested energy intake, which is the sum of the energy contents of assimilated cell wall and cell contents as calculated by the digestion model, and deducts energy expended on 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 zero net growth isocline (ZNGI). The structure of the energy balance model is modified from Van Soest (1994).

Variables and units used in the model are listed in Appendix B. A flow diagram of model components is provided in Appendix D. Details of equations and parameter derivations are given in Appendix C, and the shapes of many of the functions used are illustrated in the Supplement. The Maple code used to specify the model is given in the Supplement.

The ZNGI diagram outputs are shown in Fig. 4 for three ruminants ranging in size roughly from gazelle to buffalo. Two versions of the model were run: with and without selective foraging. The growth isoclines in both models show that the resources are hemi-essential (Tilman 1980), intersecting the CC_s (cell contents standing biomass) axis only, signifying that this is the required resource. The ZNGIs cross the CC_s axis closer to the origin for smaller animals than for larger animals. Smaller species can therefore exclude larger species from high-quality swards. ZNGIs do not cross the CW_s (cell wall standing biomass) axis, indicating that none of the species modeled can survive purely on cell wall. Larger animals, however, can tolerate a higher abundance of cell wall.

Kink points (Tilman 1980) divide the ZNGIs into left- and right-hand regions according to which feeding constraint is active. On the left, the eating-rate constraint (dependent on the height or biomass density of the grass sward) limits intake: the animals require a minimum intake of cell contents (Fig. 4a). The ZNGIs are parallel in this region, which is consistent with limitation on intake mediated by mouth size or bite rate but not food retention in the gut. On the right, the gut capacity constraint (dependent on the fiber content and digestibility of the forage) limits intake, more so in small than in large animals. The ZNGIs rise in this region because increasing amounts of cell wall inhibit digestion, calling for an increase in cell contents. The ZNGIs also diverge as CW_s increases, which is in agreement with the Bell-Jarman hypothesis. Selective feeding lowers the ZNGIs in this region (cf. Fig. 4a, b) as the ungulates actively raise the quality of their diet. It can be seen that the kink point of large ungulates occurs at a higher level of CW_s , as they need more biomass

than smaller ungulates in order to move beyond the eating-rate constraint.

Equilibria between pairs of species occur at three crossover points. In the model without selective feeding (Fig. 4a), consumption vectors are the same (the angle being given by the proportion of cell contents in the sward), and so coexistence is not possible. In the model with selection (Fig. 4b), the proportion of cell contents in the diet at the crossover points provides the angle of the consumption vectors (Table 1). The differences in angles predicted by the model are small, except in the case of the 100/500 kg pair of animals. All grazing ungulates are selective of green leaf, but a large disparity, with one species obtaining 20% more green leaf in the diet than another, vanishes almost completely under equilibrium conditions when food items are scarce and the opportunity to select differently is highly restricted (Murray and Illius 2000). Consequently, the separation of consumption vectors narrows toward the equilibrium point. Nevertheless small differences remain, and even small differences impact on energy intake. At each equilibrium point, the model predicts that the smaller animal consumes more cell contents, as expected from comparative studies of herbivory. Furthermore, at each equilibrium point, the smaller animal's ZNGI has a positive slope, indicating that any increase in cell wall in the diet has an inhibitory effect on growth. With the larger animal, on the other hand, a small increase in cell wall at equilibrium has a positive effect on growth. Since the larger ungulate consumes more cell wall, which is the resource that more limits it, and conversely since the smaller ungulate consumes more cell contents, which is the resource that more limits it (at each equilibrium point), the León and Tumpson condition for stable coexistence is satisfied.

The BSC model predicts a change in the composition of ungulate communities along a productivity gradient. Low-productivity habitats can only support small species; high-productivity habitats only support larger species because forage quality is low. For instance, at CC_s and CW_s of 10 kg/ha and 20 kg/ha, respectively, the habitat will only sustain a 20-kg ungulate, while at 100 and 200 kg/ha, the habitat is dominated by the 500-kg ungulate (Fig. 4b).

DISCUSSION

Modeling herbivore communities

The ungulate resources that we modeled are distinguished from one another by the fiber content of the food, which has a negative effect on energy assimilation. In the case of the mouth size competition (MSC) model, the resources are essential in character. There is a minimum stem height, and for each stem height a minimum leaf height to sustain growth. Under zero-growth conditions, wildebeest cannot take advantage of taller swards if they contain less green leaf, and topi cannot take advantage of leafier swards if they are shorter (Fig. 3). It is these reciprocal foraging con-

TABLE 1. Slopes of consumption vectors for the body size competition model given by the percentage of cell contents ingested (% CC_i) by ungulates at the equilibrium points in Fig. 4b.

Species pair masses (kg)	% CC_i	
	Smaller animal	Larger animal
100/500	42.95	40.66
20/500	44.91	44.56
20/100	44.94	44.86

straints of selectivity and intake that generate the essential character of the growth isoclines.

The resources of the body size competition (BSC) model are hemi-essential but with a distinctive inhibition quality (cf. Fig. 2 in Tilman 1982). The cell contents are an essential resource in that the zero net growth isoclines (ZNGIs) cross the y -axis. When there is little cell wall in the diet (left of the kink points in Fig. 4b), the cell wall can partially substitute for cell contents. Above a threshold level (i.e., to the right of the kink points), increasing cell wall in the diet inhibits digestion, leading to an increase in the requirements for cell contents. This in turn leads to facilitation as the large species can deplete the long grass (high CW_s) to a point where the small species is able to invade.

As with other resource competition theory (RCT) models, the supply point of the herbivore models is determined by the rate of supply of the two resources in the habitat, and is defined as the equilibrium resource availability in the absence of the consumer species. It is the maximum amounts of resources R_1 and R_2 that can occur in the environment at a steady state (Fig. 3 in Tilman 1980). When a mature sward is heavily grazed by a large ungulate, the supply of plant material often moves toward younger, leafier growth, at least temporarily. In this respect the dynamic supply point of herbivores differs from the static supply point assumed for plants and microorganisms (Tilman 1980, 1982). With herbivores, the supply vectors maintain the ambient supply point's position close to the limiting resource axis. Supply from a grazed lawn (S_2 in Fig. 5) is weighted toward production of cell contents, reflecting the highly digestible leaves and shoots of the immature growth stages. Conversely, supply from a mature sward (S_3 in Fig. 5) is weighted toward the formation of cell wall. Consequently both supply vectors have a curved trajectory, which increases the resilience of the captured state. As our RCT models assume that plant regrowth is static and proportional to the original ratio of leaves and stem, they may underestimate the influence of resource capture and resource facilitation. The outcome of competition, however, depends on the shape of the ZNGIs and the stability of equilibria: these conditions are unaffected by changing supply rates.

The resources that we model vary in abundance but not in quality. In the MSC model, for instance, the standing biomass of leaf (represented by canopy height)

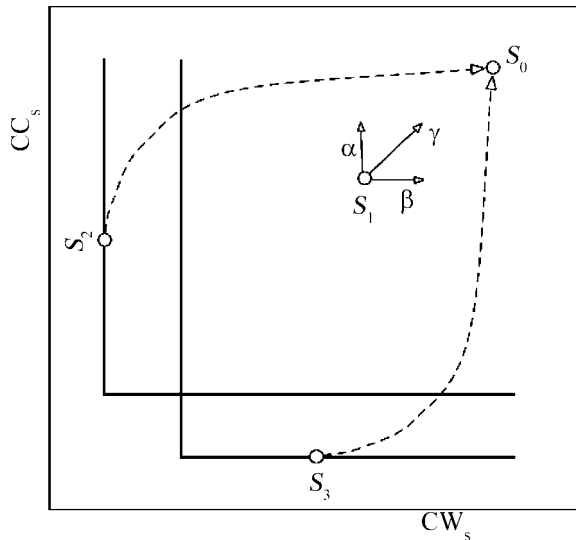


FIG. 5. Resource supply points and supply vectors under different levels of grazing intensity. The resource supply point S_0 represents the maximal amounts of cell contents (CC_s) and cell wall (CW_s) that can occur in the environment at a steady state. If the ungulates shift the actual amounts of resources to the supply point S_1 , the supply of resource CC_s at rate α and of CW_s at rate β gives rise to a resource supply vector γ . It is usually assumed that α and β are identical and that the supply vector points toward S_0 (Tilman 1980). With intense herbivory, the ambient resource supply point is shifted toward the zero net growth isoclines of the dominant consumer (supply points S_2 or S_3). Supply from a grazed lawn (S_2) is weighted toward production of cell contents reflecting the highly digestible leaves and shoots of the immature growth stages. Conversely, supply from a mature sward (S_3) is weighted toward the formation of cell wall.

varies, but the energy content per kilogram of leaf is fixed. This simplification is in line with much of the ruminant literature and facilitates the calculation of both ZNGIs and consumption vectors. It is critical to the RCT models that the resource can be consumed; in our model, for instance, the standing biomasses of leaf and stem are reduced when ungulates forage over the sward. By contrast, classical competition theory (CCT) models often use resource indices that vary in quality but that cannot be consumed. The fiber content of leaf has been used as a classical axis of herbivore niche space (Bell 1970, Demment and Van Soest 1985), and food item size is sometimes used to define the niche space of bird communities (e.g., MacArthur 1972). Neither index is appropriate to RCT models because the quality measures are not in themselves reduced when competitors harvest resources (although the frequency of items with high or low values of the index may be reduced). The actual availability of nutrients to an ungulate depends on both the fiber content of a food item (its quality) and the abundance of items across the spectrum of fiber contents (Demment and Van Soest 1985). Quality measures on their own have utility in CCT

because of their effectiveness in separating competing species and their mathematical simplicity. Their suitability for CCT but not RCT is a source of confusion in community ecology (Chase and Leibold 2003).

Our leaf and stem resources impose different constraints on the energy intake of grazing herbivores. Suitable resource indices in other herbivore communities might be the biomasses of shrubs, fruits, or a class of leaves that has a common type of defense against herbivory. Yet other resource indices could relate to constraints on energy expenditure. For example, the cost of travel to water points may constitute a significant component of an ungulate's energy budget in water-limited landscapes (Pennycuik 1979, Murray 1991). Small pans that hold water in African savannas dry out quickly because of heavy water consumption by ungulates (M. Murray, *personal observation*) making the density of water points a potential resource indicator for water-limited communities.

Competitive exclusion and coexistence

The MSC simulation model considers two species foraging in habitat patches that may be defined as areas small enough to be modified by the grazing activity of a herd of ungulates. The species adopt the extraction-maximizing strategy, and consequently, as the model shows, either ungulate can capture the grass sward by taking more of the resource that limits its competitor. This does not mean that one species will necessarily exclude the other from the entire landscape. Externally generated variability, in the form of topographic features, local rainfall events, fire, or other perturbations, can reasonably be expected to generate sufficient sward heterogeneity for coexistence at the larger scale under average conditions. Extrinsic heterogeneity is not even necessary to ensure coexistence. The intrinsic effect of complementary feeding strategies can create feeding niches in the landscape that will enable different grazing species to coexist (Farnsworth et al. 2002). 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, as exclusion only occurs locally. The predictions of the MSC model are consistent with observations of some natural ungulate communities, such as those in the Serengeti-Mara ecosystem where wildebeest and topi forage broadly over the same area but maintain a degree of spatial separation (Sinclair 1985).

The actual limit on species diversity that the MSC model predicts concerns the coexistence of multiple species when they are in equilibrium with their habitats across the entire landscape. This might occur when ungulate populations reach high density or during a prolonged drought. As equilibrium points between extraction maximizers are not stable, the community will then be restricted in its diversity to not more than one species per resource, even at the landscape level.

However, contrary to the assumptions of Murray and Illius (1996), who expected competitive exclusion to be the prevalent outcome of intensive competition in African ungulate communities, the results of our BSC model show that differences in body size are indicative of a demand-minimizing strategy in which each ungulate can specialize on a different ratio of the cell contents and cell wall resources. Consequently we predict that two or more species of different body size can coexist in the same habitat, despite intense grazing competition.

Typical productivity ranges (standing biomasses) for African grazing systems are from 0 to ~1500 kg/ha (McNaughton 1985). Fig. 4b predicts that if productivity is high but 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. Variable habitats (portrayed as circles in Fig. 2) would support the maximum number of ungulate species at moderately low productivities of around 100 kg/ha cell wall and just 20 kg/ha cell contents (Fig. 4b). 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 at higher productivities. Fig. 4b 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 is in agreement with the predictions of Bell (1982), East (1984), and Olf et al. (2002), who provide data in support of the hypothesis that in high-rainfall areas of Africa, nutrients have been leached out of the soil so that vegetation, whilst highly productive, is of low quality and only capable of supporting a community of large-bodied herbivores. Where rainfall is lower, the vegetation standing biomass is lower but of higher quality, and small-bodied herbivores dominate the fauna.

Previous approaches to understanding ungulate communities showed the importance of the digestion constraint in relation to body size (Bell 1969, 1970) and intake constraint in relation to mouth size (Illius and Gordon 1987). These constraints were subsequently integrated in models of foraging energetics (Fryxell 1991, Wilmshurst et al. 1999, Wilmshurst et al. 2000). Our models unify the state of knowledge of ungulate foraging ecology and digestive physiology with RCT. They demonstrate that the pattern of herbivore coexistence and exclusion under equilibrium conditions is determined by the core strategy of resource consumption (i.e., demand minimizing or extraction maximizing).

The dichotomy in consumption strategy also illuminates the spatial pattern of resource use in animal communities with both migratory and residential species. Migratory species are extraction maximizers that specialize on early growth stages; they move seasonally between areas with high nutritional quality,

reducing plant resources to a low level through unselective feeding before moving on (McNaughton 1976, Albon and Langvatn 1992, Murray 1995). The migrant strategy maximizes intake of energy and nutrients when overall conditions on the range are poor. Competition on the feeding sites can be severe with one species displacing another in a grazing succession governed by mouth size (Murray and Illius 1996). Residential species, on the other hand, are demand minimizers that feed selectively from a differentiated food resource (i.e., from swards in which seed-bearing stems have formed). Except under unusually harsh conditions, they do not leave their traditional ranges when food is scarce, coping instead by picking out higher-quality food items (Murray and Brown 1993). In some cases the reduced locomotion costs of residents are supplemented by a lower metabolic rate and more flexible timing of breeding to further minimize energy requirements in drought conditions (Murray 1991, 1993, Spurway et al. 1996). Competition between different-sized residents enables long-term coexistence.

Our models assume that exploitation competition predicts the pattern of ungulate distribution and coexistence, but other kinds of explanation may apply under certain conditions. Territorial behavior arising from mate competition may restrict antelope to localities with a higher green biomass; life history constraints or antipredator tactics may likewise influence habitat selection. Currently there is much interest in the various ways that spatial heterogeneity can promote coexistence of competitors (e.g., Chesson 1985, 2000, Ritchie 2002, Cromsigt and Olf 2006). Elucidating how foraging constraints interact with such mechanisms will further improve our understanding of ungulate community assembly.

We consider that an understanding of consumption strategies can shed light on the mechanism of competition in both plant and animal communities. Demand minimizers will tend to be frugal exploiters with efficient means of using resources. They may have mechanisms for conserving heat, water, or a metabolite, or alternatively they may have access to an external source of nutrients (e.g., Weir 1972, McNaughton 1988). Such frugal competitors will be able to coexist in multispecies communities on just two resources (given spatial variability in resource availability) because they use less of the resources that their competitors most need. Extraction maximizers, on the other hand, are superior users of their competitor's most needed resources. They will tend to be denuding exploiters with an enhanced capacity to extract resources that they eventually capture from competing species. Adaptations may include taller growth form (in plants), specialized mouthparts that are closely adapted to extracting a particular resource, better means of overcoming feeding deterrents, or novel biochemical methods for controlling toxic compounds. For these acquisitive competitors, there will be a limit of one such species per resource. It

should be noted, however, that the same species can display different kinds of consumption strategies when acquiring different resources. For instance, several herbivore species may be adapted to feeding from the same toxic plant (showing a typical extraction-maximizing strategy in coping with toxicity), but may exploit different parts of that plant using the demand-minimizing strategy.

Diversity in plants and herbivores

The ability of motile animals to switch between different resources is thought to account for the low ratio of animals to resources relative to that of plants (Tilman 1982). Such a strategy is occasionally observed at the landscape level in ungulate communities inhabiting natural ecosystems. For example, African ungulates will leave mature or senescent pastures to exploit temporary patches of new grass that spring up following the passage of dry-season storms, only to abandon them again as the ground dries and growth stops. But switching is not expected within the sward where stem and leaves are found together, and this is supported by the shape of the ZNGIs (Figs. 3 and 4). Rather than a difference in switching, our herbivore models suggest that patterns of diversity arise from adaptations affecting the extraction rate and internal conservation of resources: higher diversity is associated with the demand-minimizing strategy. Even with a demand-minimizing strategy, however, the number of herbivores that can coexist on ratios of CC: CW will be constrained, as there is an observed limit to the similarity in body size that has been attributed to classical competition (Prins and Olf 1998, Baird 2001).

The grazing communities of African vertebrate herbivores are the most diverse of their type in the world; ~100 species >2 kg occur in the continent. The number of these species that can fit into a fully packed community, specializing only on ratios of cell wall and cell contents, can be found by ranking species according to size (M) and calculating the average size ratio between neighboring species. May (1973) provides an appropriate model: $\ln(M) = ai + b$, where i is the body size rank order ($i = 0$ being the smallest species), a is $\ln(\text{size ratio})$, and b is $\ln(M_0)$. The average size ratio between subsequent grazing species (if ordered from light species to heavy) in species-rich locations of East Africa is ~1.39 (Prins and Olf 1998). This would enable a maximum of 24 species to coexist between the size of a hare (2 kg) and an elephant (4000 kg). We may extend the weight range downward to that of a grass mouse (20 g), whereupon the total rises to 38 species, and further down to a grasshopper (0.2 g), whereupon the total reaches 52 species.

While this is an appreciable assemblage of species, it does not necessarily compare with the richness of plant assemblages. Plant communities located on nutrient-poor soils can be highly diverse, containing many hundreds of species by virtue, at least in part, of

specialization on different soil types. If both plants and animals adopt the demand-minimizing strategy, yet the diversity of plant communities structured by soil nutrients is higher than that of herbivores structured by defense resources, it would suggest either some relaxation in limiting similarity effects in plants relative to animals or some difference of scale in the heterogeneity of resources.

The structure of plant and herbivore communities depends on heterogeneity in their habitats at the level of limiting resources. In the case of plant communities, heterogeneity is maintained by local productivity gradients in soil nutrients within old fields, forest stands, or other similar habitats (Tilman 1988). Diversity in the plant community depends on resource variation within the habitat. In the case of herbivore communities, heterogeneity in plant defenses and antiherbivore deterrents is maintained by gradients and disturbances that affect the phenology and life history of plants. Grass swards at different growth stages, and discrete plant communities in different stages of succession, are examples of "plant defense habitats" for a vertebrate herbivore. Diversity in the herbivore community depends on resource variation between such habitats. Differences in diversity between plants and animals may therefore reflect differences in the scale of resource gradients and disturbances.

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APPENDIX A

The mouth size competition model (*Ecological Archives* E089-087-A1).

APPENDIX B

Variables and units used in the model of body size competition (*Ecological Archives* E089-087-A2).

APPENDIX C

The body size competition model (*Ecological Archives* E089-087-A3).

APPENDIX D

Flow diagrams of the body size competition model (*Ecological Archives* E089-087-A4).

SUPPLEMENT

Maple code implementing the mouth size and body size competition models, along with graphical output from running the models (*Ecological Archives* E089-087-S1).