Vegetation modification and resource competition in grazing ungulates

Martyn G. Murray and Andrew W. Illius

Murray, M. G. and Illius, A. W. 2000. Vegetation modification and resource competition in grazing ungulates. – Oikos 89: 501–508.

The prevalence of interspecific competition in animal communities is the subject of a long-running debate, chiefly because the underlying processes of resource exploitation and resource supply are often poorly understood. To provide some insight into these processes within a guild of grazing herbivores, two hypothetical mechanisms of exploitation competition were tested by measuring food intake of topi (*Damaliscus lunatus*) and wildebeest (*Connochaetes taurinus*) when foraging on different sward structures in the Serengeti National Park. According to our bite quantity hypothesis, wildebeest, which have relatively wide mouths, can graze down vegetative swards to a height below that which can be tolerated by topi; and according to our bite quality hypothesis, the narrower-mouthed topi can reduce the leafy component of differentiated swards (i.e. swards in which seed-bearing stems have developed) through selective feeding to a level below that which can be tolerated by wildebeest.

On differentiated swards with erect growth form, the topi selected 20% more green leaf in their diet, as measured by a calibrated visual technique, and also obtained higher short-term intake rates. Greater selectivity alone provided topi with a metabolisable energy intake estimated to be 16% higher than that of wildebeest. On vegetative swards, it was estimated that wildebeest could maintain positive energy balance on 2-cm swards, 1 cm shorter than the threshold height for topi. Our findings indicate the conditions under which each ungulate species may limit the other's use of natural pastures through interspecific competition: bite quantity competition may apply on short grazing lawns; bite quality competition is expected on differentiated swards with a limited supply of green leaf.

We suggest that herbivory by one species can modify the vegetation in a way that makes it less profitable to competing species. In effect the vegetation is 'captured' as a resource by one species. Thus modification of vegetation is argued to be a critical component of resource competition in herbivores.

M. G. Murray, Research Group in Mammalian Ecology and Reproduction, Physiological Laboratory, Univ. of Cambridge, Downing Street, Cambridge, UK CB2 3EG (present address: Inst. of Cell, Animal and Population Biology, Ashworth Laboratories, Univ. of Edinburgh, West Mains Road, Edinburgh, UK EH9 3JT [m.murray@ed.ac.uk]). – A. W. Illius, Inst. of Cell, Animal and Population Biology, Ashworth Laboratories, Univ. of Edinburgh, West Mains Road, Edinburgh, UK EH9 3JT.

Interspecific competition was perceived initially with confidence as a self-evident axiom of life's evolution (Lyell 1832, Darwin 1859, Hutchinson 1959, 1978, MacArthur 1972) soon to be reported in a wide range of organisms (Connell 1983, Schoener 1983), only to recede gradually from view during the slow forward march of empirical research (Connor and Simberloff 1979, 1984, Simberloff and Boecklen 1981, Lawton 1984, Strong et al. 1984, Connell 1990). Opinion today remains divided and ambivalent as to the prevalence and importance of interspecific competition in plant and animal communities (Begon et al. 1996) with much of the enigma arising from repeated attempts to infer causality from community patterns, without first having

501

gained sufficient knowledge of the actual mechanisms by which one species might compete with another (Tilman 1987).

Some of the best demonstrations of the influence of morphology on resource intake rate come from studies of birds (Smith 1987, 1990, Wheelwright 1985) and, in relation to interspecific competition, particularly from the studies of beak sizes and food characteristics in Darwin's finches (Geospizinae) of the Galápagos Islands (Grant et al. 1976, Abbott et al. 1977, Boag and Grant 1981, Grant 1986). The profitability, or energy return per unit handling time, is apparently highest for all species when feeding on the largest seeds they can crack (Schluter 1982), and patterns of bill morphology between sympatric and allopatric populations have upheld Lack's interspecific competition hypothesis by consistent agreement with its predictions (Lack 1947, Schluter et al. 1985). But as Grant (1986) has pointed out, the relatively strong evidence for competition in Darwin's finches still relies upon indirect tests which leave some uncertainties in the explanation of morphological and distributional features in the subfamily. The literature on ungulate community ecology reveals similar uncertainties over the role of competition. Evidence for the importance of interspecific competition is claimed from observation of overlap in diet and use of habitats, population responses (in size and location) to a reduction in the number of a competitor, the influence on production of foraging by a competitor; interspecific separation in body size; intersexual separation of body sizes; and the change in body size distributions of equids and ruminants during the Miocene (Eltringham 1974, Sinclair 1977, 1983, Clutton-Brock and Harvey 1983, Owen-Smith 1985, de Boer and Prins 1990, Janis et al. 1994, Hobbs et al. 1996, Prins and Olff 1997). Evidence that different forms of community interaction (notably predation, facilitation and intraspecific competition) have a more dominant role in shaping community structure is claimed from a number of other observations, including overlap in use of resources and habitats, the interspecific pattern of herd spacing, the intra-community pattern of population dynamics of ungulate species; and simulation modelling of diet and morphology (McNaughton 1976, Owen-Smith 1982, 1989, Sinclair and Norton-Griffiths 1982, Sinclair 1985, 1995, Illius and Gordon 1987, Gordon and Illius 1989, Dublin et al. 1990, Du Toit 1990).

As with other animal communities, few mechanistic studies of resource exploitation have been undertaken in the ungulates, but some progress has been made from single species studies of foraging which have revealed that major constraints on energy intake arise from variations in the quantity and quality of forage in the sward (Murray and Illius 1996). On short uniform swards, food intake has been shown to become limiting through reductions in bite frequency or bite size (Hodgson 1985, Murray and Brown 1993), and it has been predicted in theory that quite small differences in sward height, of the order of 1 or 2 cm, may lead to large differences in bite volume and the exclusion of larger ungulates from short swards (Illius and Gordon 1987). On differentiated grass swards (i.e. swards in which seed-bearing stems have formed), the energy content of food ingested has been shown to become limiting through reduction in bite quality which is related to the digestibility of plant parts (Murray and Illius 1996). Some ungulate species are better able than others to avoid this constraint by feeding selectively within differentiated sward structures (Murray 1993, Murray and Brown 1993). It has been suggested that the width of the mouth determines the level of selection for high quality items of food (Jarman 1974, Owen-Smith 1982), and that consequently different ungulate species are more proficient when feeding on grass swards in particular growth stages (Murray and Brown 1993). However, a mechanism of resource competition involving bite quality has not previously been specified or tested, perhaps because the cost of selective feeding in sparse, differentiated swards has been little appreciated and rarely incorporated into models of diet selection or intake (Murray 1991). We hypothesise that selective feeding by narrow-mouthed ungulates may reduce the frequency of green leaf in the sward causing the leaf intake of less selective (wide-mouthed) species to decline, forcing them to accept a lower quality diet, and a lower energy intake, or to move elsewhere.

Earlier work has revealed that grazing ungulates with differing morphology occupy separate feeding niches, but it has not been established whether resource competition has importance in structuring ungulate communities. Whilst it is obvious that vegetation will be modified by selective grazing, it is not known whether this modification will have a competitive effect on other species. In this paper, we investigate the consequences of sward state for the intake rates in topi (*Damaliscus lunatus*) and wildebeest (*Connochaetes taurinus*). In so doing, we develop and test the aforementioned mechanisms of exploitation competition, drawing on results of feeding trials conducted with these two species in the Serengeti National Park, Tanzania. The two ungulates are well known for their occupation of different ecological niches, despite similarities in body size and major predators, their being members of the same subfamily (Alcelaphinae), and their sympatric occurrence in large herds in the Serengeti.

Methods

Grazing trials were conducted with topi, which has an average adult female body size of 109 kg (Sachs 1967) and a comparatively curved and narrow incisor row of 50 mm width (Bell 1969), and wildebeest, which has an

average adult female body size of 143 kg in the migratory Serengeti population (Watson 1967) and a comparatively flat and wide incisor row of 70 mm width. Measurements of leaf selection were obtained from two yearling topi (74 and 77 kg) and two yearling wildebeest (86 and 108 kg) during "selection trials", and measurements of short-term food intake were made on one animal for each species during "intake trials" (Murray and Brown 1993). The animals were housed at night in stables at the Serengeti Wildlife Research Centre (SWRC) in the Serengeti National Park, Tanzania, and taken each day to feed on nearby pastures. Plots of 12×12 m were marked out in the vicinity of the stables on uniform swards in natural pastures. We deliberately chose to use plots at the height, greenness and structure that animals would experience in the wild to make the tests relevant to natural foraging choices: inevitably therefore, plant species were confounded with height, structure and greenness. Most plots were dominated by grass species of erect habit, principally *Themeda triandra*, *Bothriochloa insculpta* and *Panicum coloratum*. The shortest sward was dominated by mat-forming grasses: *Chloris pycnothrix* and *Cynodon dactylon*. Plots with either vegetative or differentiated swards were employed for grazing trials. Vegetative swards were developed by slashing or burning differentiated swards before the feeding trials, followed by daily watering.

Immediately before each feeding trial, 30 recordings of the canopy height of leaf in the plot were taken using a metre rule equipped with a sliding pointer. Leafiness of plots was determined by clipping herbage to a height of 1–2 cm in four (intake trials) and eight (selection trials) 25×25-cm quadrats, sorting samples by hand, drying, and weighing.

All animals were provided with freshly cut grass in the stables at night, and the grazing trials were held from 07.00 to 09.30 each morning. For intake trials, the subject animals were weighed, walked to the experimental plot (up to 100 m distance) and allowed to graze. The duration of the grazing period (20–30 min) was timed and adjusted to allow subject animals to take approximately 1000 bites, after which the animal was led back to the stables and weighed again. Radiant temperature was recorded at 1-min intervals. Intake was estimated from the difference in body mass before and after grazing, with a correction made for insensible mass loss (Penning and Hooper 1985). Live mass was recorded on a Mettler weighing platform (± 10 g), after waiting for a constant reading from a completely stationary animal. By choosing quiet animals for the trials, the delay in obtaining a reading was no more than a few seconds. Insensible mass loss was estimated from regressions of mass loss against radiant temperature which were previously established for each subject animal (Murray and Brown 1993). Approximately 10% of feeding trials were abandoned because of urination or defecation by the subject animal before weighing.

The green leaf content of bites taken by topi and wildebeest was estimated using a visual method whilst animals were feeding on grass plots. The observer stood within 1 m of the animal's mouth and noted the proportion of green leaf in each bite just before prehension, calling the assessment (one of seven classes corresponding to the following proportions of green leaf: 0–0.01, 0.02–0.1, 0.11–0.33, 0.34–0.66, 0.67–0.89, 0.90–0.98 and 0.99–1) into a micro-cassette recorder. The mean of the estimates for 200 sequential bites was accepted as the proportion of green leaf in the diet of the subject animal on that plot. We tested the accuracy of this method on a rough sward of *Festuca* and *Agrostis* species in UK using one of the authors (AWI) as a surrogate ungulate who rapidly grabbed, cut and bagged bite-sized grass samples from the sward, using a pair of sheep shears. The same observer as in the Serengeti trials (MGM) estimated the proportion of green leaf in each sample. The true proportion of green leaf in each grab sample (p) was determined by drying 50 bagged samples in an oven at 65°C, sorting by hand into leaf and non-leaf components, and weighing. At the average visual class (3.88), we found that a sample of 50 bites provides an estimate of p which 95% of the time falls within a confidence interval of ± 0.04, rising to ± 0.096 at the lowest visual class (1). Since the standard deviation of means is an inverse function of the square root of sample size, we expect estimates of p based on 200 bites of real ungulates to have confidence intervals of approximately half this magnitude (i.e. 0.02–0.048).

Data on intake were obtained from ten vegetative and seven differentiated plots; data on selection were obtained from six differentiated plots. The data for both ungulate species were analysed by regression and the significance of different intercepts and slopes tested. Initially the response of the proportion of green leaf in the diet to the proportion of green leaf in the sward was analysed using the method of residual maximum likelihood (REML, Patterson and Thompson 1971) to account for the separate sources of variation due to individual animals, plots, grazing order within plot, and plant species. However, it soon became apparent that the estimated variance component for random terms was negative, indicating that individual differences within species and plot, and due to grazing order, could be ignored. This conclusion was verified by Anova, fitting animal as a block effect. The same applied to analysis of intake rate on short swards: plot and order effects could be ignored. Thereafter, data were analysed by standard regression modelling. Data on nutritional properties of Serengeti grasses were obtained from grass samples collected throughout the ecosystem (Table 1). All samples were oven-dried, sorted by hand and flown to UK for analysis by the Agricultural Development and Advisory Service.

Table 1. Protein, digestibility and energy values of grass parts in the Serengeti National Park. Samples were collected from representative habitats within the central and northern woodlands, western corridor and south-eastern plains.

	Green leaf			Brown leaf			Stem		
	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Crude protein (%)	12.0	4.54	4.9–24.4	4.4	1.61	2.7–10.6	3.8	1.75	1.1–9.5
Digestibility (% NCD)[1]	51.0	6.61	35.0–69.6	43.4	6.71	27.5–56.6	32.5	5.16	22.8–46.4
Gross energy (E_I)[2]	18.5	0.28	18.0–19.3	18.0	0.10	17.9–18.4	18.0	0.11	17.8–18.3
Metabolizable energy (E_M)[2]	8.9	0.73	7.1–11.0	8.1	0.75	6.3–9.5	6.9	0.57	5.8–8.4
q (E_M/E_I)	0.48	0.035	0.38–0.59	0.45	0.040	0.35–0.53	0.38	0.031	0.32–0.47
N	152			35			82		

[1] NCD: neutral cellulase digestibility (Murray and Brown 1993).
[2] Expressed as MJ kg^{-1} DM.

Results

The nutritional quality of the herbage in Serengeti N.P. is highly differentiated according to plant part, with green leaf containing 2.5–3 times the crude protein content of brown leaf or stem (Table 1). The digestibility of brown leaf is approximately midway between that of green leaf and stem. The relationship between crude protein content and digestibility in herbage is also dependent on plant part (Fig. 1). Before grazing trials, the average height of green leaf in the experimental plots varied from 2 to 33 cm, and the proportion (by dry weight) of green leaf varied from 10 to 38%.

Leaf selection by both topi and wildebeest led to depletion of the green leaf % in differentiated swards ($t_{10} = 4.6$, $P < 0.001$). On senescent swards which have little green leaf there was not much selection by either topi or wildebeest, but on the greener plots, both species selected strongly for green leaf. Data on the proportion of green leaf in the diet (d) appear sigmoidal when plotted against the proportion of green leaf in the sward (s), and are well described by a logistic transformation. The logistic function $f(d) = \ln[d/(1 - d)]$ is sometimes referred to as logit(d) (Colquhoun 1971). Using this transformation, the selectivity of wildebeest and topi can be expressed in parallel regression equations:

$$\text{logit}(d_t) = -5.78 + 45.1s \quad (1)$$

and

$$\text{logit}(d_w) = -6.83 + 45.1s (\text{SE} = 0.571; R^2 = 0.91), \quad (2)$$

where d_t and d_w are the proportions of green leaf in the diet of topi and wildebeest, respectively. The slopes of separate regression equations for each species do not differ ($P = 0.802$), but the intercepts are significantly different ($P = 0.001$), indicating that topi are more selective of green leaf than wildebeest, and particularly when grazing on sites with high average grass height and low average percent green leaf, where topi can obtain 20% more green leaf in their diet (Fig. 2).

We now test whether selectivity has associated costs in terms of reduced short-term rates of food intake. Regression of intake rate (mg DM body mass$^{-0.75}$ min^{-1}) on the proportion of green leaf in the sward (s) gave:

$$i_{f,t} = 213.5 + 2129s \quad (3)$$

and

$$i_{f,w} = 290.5 + 591s \quad (\text{Residual SD} = 51.7, R^2 = 0.72), \quad (4)$$

where $i_{f,t}$ and $i_{f,w}$ are short-term intake rates on differentiated swards of topi and wildebeest, respectively. After fitting s, inclusion of the term to account for leaf height (h) was not significant. The slope of the above
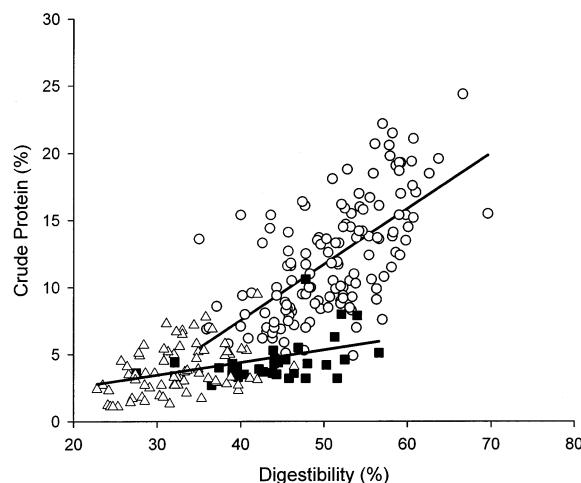

Fig. 1. Prediction of crude protein concentration of grass parts according to neutral cellulase digestibility in samples taken from the major habitats of Serengeti N.P. (See Table 1): green leaf – open circles; brown leaf – filled squares; stem – open triangles. According to regression analysis the intercepts and slopes are significantly different at $p < 0.001$ between green leaf and the rest. The data are described by the regression CP(%) = $a + b \times$ NCD(%) where $a = -9.07$ or 0.63 and $b = 0.416$ or 0.094 for green leaf and the rest respectively; $R^2 = 0.74$, residual SD = 2.704 and $N = 248$.
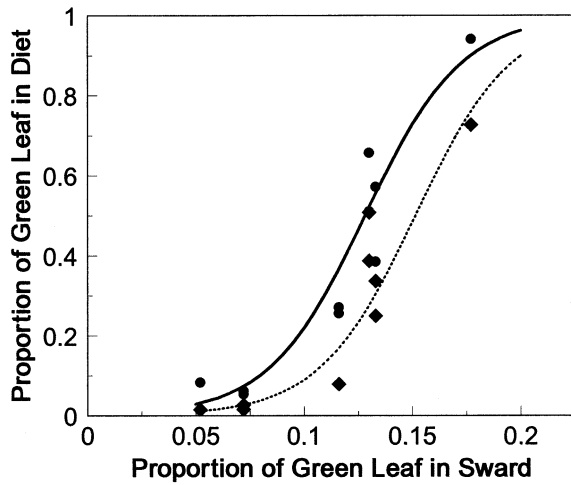
504

Fig. 2. Selection for green leaf by individual topi (filled circles) and wildebeest (diamonds) feeding in differentiated grass swards.

regression differs significantly between species ($F_{1,10} = 7.64$, $P = 0.02$) indicating that topi obtain higher intake rates from the swards on which they are capable of being more selective than wildebeest (Fig. 3).

Grazing by topi and wildebeest on vegetative swards caused a reduction of sward height ($t_{10} = 3.9$, $P = 0.003$). On the shortest swards, dominated by the semi-prostrate species, *Chloris pycnothrix*, wildebeest obtained twice the intake rate of topi (Fig. 4). Differences in intake rate due to sward structural effects (i.e. plots containing prostrate or differentiated vegetation) were not significant ($P = 0.16$). Parallel regression equations were fitted to the data collected from individual intake trials:

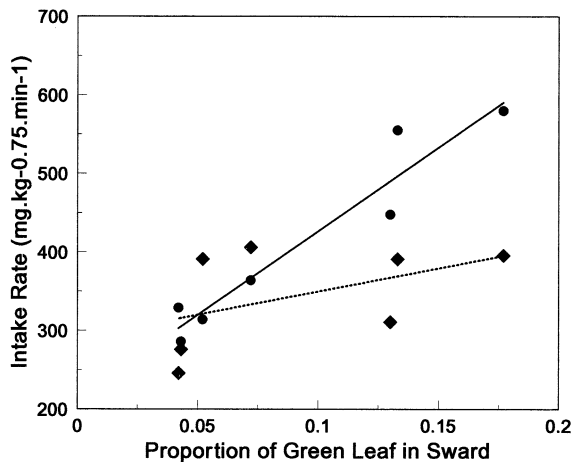$$i_{s,t} = -77.2 + 69.6h \qquad (5)$$

Fig. 3. Short-term intake rate of topi (filled circles) and wildebeest (diamonds) on tall grass in relation to leaf content of the sward.
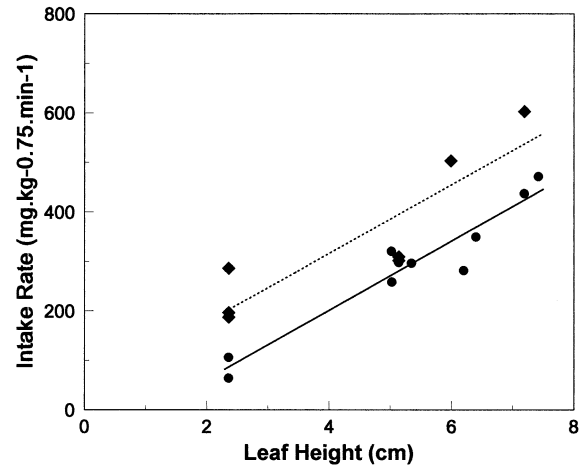

Fig. 4. Short-term intake rate by individual topi (filled circles) and wildebeest (diamonds) feeding on grass swards in an early (vegetative) growth stage.

and

$$i_{s,w} = 37.3 + 69.6h \qquad (\text{Residual SD} = 53.9; R^2 = 0.85),$$
$$(6)$$

where $i_{s,t}$ and $i_{s,w}$ are the dry matter intake rates (mg body mass$^{-0.75}$ min^{-1}) on vegetative swards of topi and wildebeest, respectively, and h is the mean canopy height (cm) of green leaf in the sward. As with the leaf selection data, the slopes of separate regression equations for each species do not differ ($P = 0.971$), but the intercepts are significantly different ($P = 0.001$), indicating in this case that wildebeest achieve a significantly higher rate of food intake than topi when grazing on short vegetative swards with a leaf canopy of 2–7 cm.

Discussion

Mechanisms of grazing competition

Observations of free-ranging wildebeest and topi in Serengeti show a distinctive niche divergence with wildebeest utilising short grasslands and topi utilising mid-length grasslands with high leaf biomass. Topi are well known to be selective feeders acquiring up to seven times the green leaf content of the sward in their bites, whilst the broad muzzle of wildebeest has long been recognised as an adaptation to feeding on short swards (Bell 1969, Duncan 1975). However, the precise mechanisms of herbivory in ungulates, and their application to interspecific grazing competition, have remained obscure.

Our experiments show that small differences in the structure of grass swards, perhaps barely noticeable to the casual observer, can produce large differences in food intake rate: a decrease of 1 cm (from 3 to 2 cm) in

the height of short vegetative swards can halve the intake rate of topi, whilst a decrease of 0.025 (from 0.15 to 0.125) in the proportion of green leaf in the tall differentiated swards can reduce the wildebeest's intake of green leaf by 24%. Knowing that the metabolic energy requirements of topi and wildebeest are closely similar (Murray 1993), we can easily calculate that an intake rate of 19 MJ d^{-1} will provide the maintenance requirement (MR) of animals of the size used in our feeding experiments (Murray 1991). To show the competitive disadvantage of the less efficient species, we first estimate the sward conditions that would allow the more efficient species to satisfy its MR, and then estimate the disadvantage experienced by the competitor species under the same conditions. We estimate that vegetative swards of height 2 cm, which more than satisfy the wildebeest's MR (assuming 600 min per day grazing time), would only provide 60% of the topi's MR. Likewise for green leaf selection, we calculate that the topi can satisfy their MR on differentiated swards with a proportion of 0.145 green leaf (assuming that daily intake is determined by forage quality in tall swards, see eq. 4 in Murray 1991) but the wildebeest encounter a shortfall of 16% of MR on the same swards.

Our argument that these results can be generalised to large-scale competition interactions depends on a number of assumptions: (1) that differences in profitability arising from grazing efficiency are not masked by disparities between the two species in metabolic rate or digestive efficiency; and (2) that the animals used in the experimental trials are representative of their species. The daily intake of the study animals was measured during digestibility trials held immediately after the grazing trials. Intake of both topi and wildebeest was found to fit the same linear relationship with apparent digestibility, suggesting that digestive efficiency and energy requirements at maintenance are closely similar for the two species (Murray 1993). As yearlings, our experimental animals were approximately 55% (range 43–68%) of adult body size; however, incisor breadth is a rapidly maturing character, and in Soay sheep, for example, it is nearly 96% of the adult value in yearlings (Illius et al. 1995). Moreover, yearling animals are an important component of the populations of large ungulates and may experience higher nutritional stress and natural mortality than adults (Dunham and Murray 1982, Murray 1982). Consequently, we have no reason to believe that yearlings are not a suitable study animal for the investigation of resource competition.

These results provide the first field evidence in support of Illius and Gordon's (1987) hypothesis that small differences in the height of short pastures can generate large differences in intake between ungulates with different incisor breadths. In comparing the short-term intake rate of wildebeest and topi in an earlier paper, Murray and Brown (1993) combined data from short

vegetative swards with longer differentiated ones, where bite size limitation does not apply, masking this significant difference between the two species. Our results also confirm greater selectivity in narrow-mouthed ungulates when feeding in differentiated swards, as has been frequently postulated (Jarman 1974) but not hitherto demonstrated. We have shown that topi are not only more selective but also achieve a greater intake rate on these swards. The remarkable ability of topi to maintain a rapid bite rate whilst feeding selectively in high biomass and stemmy swards has been commented upon previously (Murray and Brown 1993).

By comparison with the large differences between topi and wildebeest in their intake rate on short swards, the difference in net energy attributed to selectivity (16%) is small, suggesting that bite quality competition may be less severe than bite quantity competition. In both cases, a greater time spent foraging detracts from an animal's ability to contend with a variety of costs and constraints (Illius and Fitzgibbon 1994, Owen-Smith 1997). But whereas a constraint on bite quantity can be compensated for by an increase in the daily grazing time, no such compensation is possible for a limitation in bite quality, as daily intake is limited by digestive constraints rather than consumption constraints (Murray 1991). Hence bite quality competition may be just as exacting as bite quantity competition.

Our findings suggest that wildebeest herds may be capable of grazing vegetative swards closer to the ground than the minimum height that can be tolerated by topi, and that topi herds may be capable of progressively defoliating differentiated swards down to a level that cannot be tolerated by wildebeest. The question remains as to whether vegetation modification by herbivores within the Serengeti-Mara ecosystem gives rise to interspecific competition, and if so whether it has an important influence on the structure of the ungulate community.

The mechanism of bite quantity competition that we have demonstrated could explain the observed absence of buffalo from grazing lawns created by migratory wildebeest on the Serengeti Plains, in their wet-season range (Murray and Illius 1996), and also shifts in the distribution of residential topi in response to the influx of wildebeest into the Masai Mara, in the dry-season range (Sinclair 1985). In which case, spatial segregation of these herds constitutes part of an overall process of interspecific competition which is being underpinned by localised competitive intereactions (cf. Prins 1996).

Our mechanism for bite quality competition could apply wherever resident ungulates graze medium and tall grasslands for a sustainable yield, although we know of no field reports suggestive of this form of competition. The lack of corroborative evidence may reflect the greater difficulty of detecting small differences in the leaf content as compared with the surface height of swards, but it may also signify a real inequal-

ity in the strength of the two types of competition. By virtue of their large population size and high herd densities, wildebeest dominate natural pastures in the Serengeti, exerting a greater influence on other ungulate species than they, in return, exert upon wildebeest. Competition could therefore be viewed as one-way with topi having adapted to the taller swards left ungrazed by wildebeest.

We suggest that modification of vegetation, as brought about by the foraging of ungulates themselves, can be an important factor in locally limiting species diversity. By capturing the energy or nutrient flow of a resource, herbivores may effectively preclude the utilisation of that resource by other species. Localised competitive interaction may in turn give rise to wider spatial segregation of herds in which the ultimate consequences of interspecific competition are revealed by differences in mortality and natality.

References

Abbott, I., Abbott, L. K. and Grant, P. R. 1977. Comparative ecology of Galápagos Ground Finches (*Geospiza* Gould): evaluation of the importance of floristic diversity and interspecific competition. – Ecol. Monogr. 47: 151–184.

Begon, M., Harper, J. L. and Townsend, C. R. 1996. Ecology – individuals, populations and communities, 3rd ed. – Blackwell Science.

Bell, R. H. V. 1969. The use of the herb layer by grazing ungulates in the Serengeti National Park, Tanzania. – Ph.D. thesis, Univ. of Manchester.

Boag, P. T. and Grant, P. R. 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galápagos. – Science 214: 82–85.

Clutton-Brock, T. H. and Harvey, P. H. 1983. The functional significance of variation in body size among mammals. – Spec. Publ. Am. Soc. Mammal. 7: 632–663.

Colquhoun, D. 1971. Lectures on biostatistics. – Clarendon Press.

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. – Am. Nat. 122: 661–696.

Connell, J. H. 1990. Apparent versus 'real' competition in plants. – In: Grace, J. B. and Tilman, D. (eds), Perspectives on plant competition. Academic Press, pp. 9–26.

Connor, E. F. and Simberloff, D. 1979. The assembly of species communities: chance or competition? – Ecology 60: 1132–1140.

Connor, E. F. and Simberloff, D. 1984. Neutral models of species' co-occurrence patterns. – In: Strong, Jr., D. R.,
Simberloff, D. Abele, L. G. and Thistle, A. B. (eds), Ecological communities: conceptual issues and the evidence. Princeton Univ. Press, pp. 316–331.

Darwin, C. 1859. The origin of species. – John Murray, London.

de Boer, W. F. and Prins, H. H. T. 1990. Large herbivores that strive mightily but eat and drink as friends. – Oecologia 82: 264–274.

Dublin, H. T., Sinclair, A. R. E., Boutin, S. et al. 1990. Does competition regulate ungulate populations? Further evidence from Serengeti, Tanzania. – Oecologia 82: 283–288.

Duncan, P. 1975. Topi and their food supply. – Ph.D. thesis, Univ. of Nairobi.

Dunham, K. M. and Murray, M. G. 1982. The fat reserves of impala. – Afr. J. Ecol. 20: 81–87.

Du Toit, J. T. 1990. Feeding-height stratification among African browsing ruminants. – Afr. J. Ecol. 28: 55–61.

Eltringham, S. K. 1974. Changes in the large mammal community of Mweya Peninsula, Rwenzori National Park, Uganda, following removal of hippopotamus. – J. Appl. Ecol. 11: 855–865.

Gordon, I. J. and Illius, A. W. 1989. Resource partitioning by ungulates on the Isle of Rhum. – Oecologia 79: 383–389.

Grant, P. R. 1986. Ecology and evolution of Darwin's finches. – Princeton Univ. Press.

Grant, P. R., Grant, B. R., Smith, J. N. M et al. 1976. Darwin's finches: population variation and natural selection. – Proc. Natl. Acad. Sci. USA 73: 257–261.

Hobbs, N. T., Baker, D. L., Bear, G. D. and Bowden, D. C. 1996. Ungulate grazing in sagebrush grasslands: effects of resource competition on secondary production. – Ecol. Appl. 6: 218–227.

Hodgson, J. 1985. The control of herbage intake in the grazing ruminant. – Proc. Nutr. Soc. 44: 339–346.

Hutchinson, G. E. 1959. Homage to Santa Rosalia, or Why are there so many kinds of animals? – Am. Nat. 93: 145–159.

Hutchinson, G. E. 1978. An introduction to population ecology. – Yale Univ. Press.

Illius, A. W. and Gordon, I. J. 1987. The allometry of food intake in grazing ruminants. – J. Anim. Ecol. 56: 989–999.

Illius, A. W. and Fitzgibbon, C. 1994. Costs of vigilance in foraging ungulates. – Anim. Behav. 47: 481–484.

Illius, A. W., Albon, S. D., Pemberton, J. M. et al. 1995. Selection for foraging efficiency during a population crash in Soay sheep. – J. Anim. Ecol. 64: 481–492.

Janis, C. M., Gordon, I. J. and Illius, A. W. 1994. Modelling equid/ruminant competition in the fossil record. – Historical Biology 8: 15–29.

Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. – Behaviour 48: 215–266.

Lack, D. 1947. Darwin's finches. – Cambridge Univ. Press, Cambridge.

Lawton, J. H. 1984. Different ways of being a mouse. – Nature 309: 112.

Lyell, Sir C. 1832. Principles of geology, vol. II, 1st ed. – John Murray, London.

MacArthur, R. H. 1972. Geographical ecology. – Harper and Row.

McNaughton, S. J. 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. – Science 191: 92–94.

Murray, M. G. 1982. The rut of impala: aspects of seasonal mating under tropical conditions. – Z. Tierpsychol. 59: 319–337.

Murray, M. G. 1991. Maximising energy retention in grazing ruminants. – J. Anim. Ecol. 60: 1029–1045.

Murray, M. G. 1993. Comparative nutrition of wildebeest, hartebeest and topi in the Serengeti. – Afr. J. Ecol. 31: 172–177.

Murray, M. G. and Brown, D. 1993. Niche separation of grazing ungulates in the Serengeti: an experimental test. – J. Anim. Ecol. 62: 380–389.

Murray, M. G. and Illius, A. W. 1996. Multispecies grazing in the Serengeti. – In: Hodgson, J. and Illius, A. W. (eds), The ecology and management of grazing. CAB Int., Wallingford, pp. 247–272.

Owen-Smith, N. 1982. Factors influencing the consumption of plant products by large herbivores. – In: Huntley, J. and Walker, B. H. (eds), Ecology of tropical savannas. Springer-Verlag, pp. 359–404.

Owen-Smith, N. 1985. Niche separation among African ungulates. – In: Vrba, E. S. (ed.), Species and speciation. Transvaal Museum Monograph No 4, Transvaal Museum, Pretoria, pp. 167–171.

Owen-Smith, N. 1989. Morphological factors and their consequences for resource partitioning among African savanna ungulates: a simulation modelling approach. – In: Morris, D. W., Abramsky, Z., Fox, B. J. and Willig, M. R. (eds), Patterns in the structure of mammalian communities. Texas Tech Univ. Press, pp. 155–165.

Owen-Smith, N. 1997. Control of energy balance by a wild ungulate, the kudu (*Tragelaphus strepsiceros*) through adaptive foraging behaviour. – Proc. Nutr. Soc. 56: 15–24.

Patterson, H. D. and Thompson, R. 1971. Recovery of inter-block information when block sizes are unequal. – Biometrika 58: 545–554.

Penning, P. D. and Hooper, G. E. 1985. An evaluation of the use of short-term weight changes in grazing sheep for estimating herbage intake. – Grass Forage Sci. 40: 79–84.

Prins, H. H. T. 1996. Ecology and behaviour of the African buffalo: social inequality and decision making. – Chapman and Hall.

Prins, H. H. T. and Olff, H. 1997. Species richness of African grazer assemblages: towards a functional explanation. – In: Newberry, D. M., Prins, H. H. T. and Brown, N. D. (eds), Dynamics of tropical communities. Blackwell Science, pp. 449–490.

Sachs, R. 1967. Liveweights and body measurements of Serengeti game animals. – East Afr. Wildl. J. 5: 24–36.

Schluter, D. 1982. Seed and patch selection by Galápagos ground finches: relation to foraging efficiency and food supply. – Ecology 63: 1106–1120.

Schluter, D., Price, T. D. and Grant, P. R. 1985. Ecological character displacement in Darwin's finches. – Science 227: 1056–1058.

Schoener, T. W. 1983. Field experiments on interspecific competition. – Am. Nat. 122: 240–285.

Simberloff, D. and Boecklen, W. 1981. Santa Rosalia reconsidered: size ratios and competition. – Evolution 35: 1206–1228.

Sinclair, A. R. E. 1977. The African Buffalo. – Univ. of Chicago Press.

Sinclair, A. R. E. 1983. The adaptations of African ungulates and their effects on community function. – In: Bourlière, F. (ed.), Tropical savannas. Elsevier, pp. 401–426.

Sinclair, A. R. E. 1985. Does interspecific competition or predation shape the African ungulate community. – J. Anim. Ecol. 54: 899–918.

Sinclair, A. R. E. 1995. Serengeti past and present. – In: Sinclair, A. R. E. and Arcese, P. (eds), Serengeti II – dynamics, management and conservation of an ecosystem. Univ. of Chicago Press, pp. 3–30.

Sinclair, A. R. E. and Norton-Griffiths, M. 1982. Does competition or facilitation regulate migrant ungulate populations in the Serengeti? A test of hypotheses. – Oecologia 53: 364–369.

Smith, T. B. 1987. Bill size polymorphism and intraspecific niche utilization in an African finch. – Nature 329: 717–719.

Smith, T. B. 1990. Resource use by bill morphs of an African finch – evidence for intraspecific competition. – Ecology: 1246–1257.

Strong, D. R., Jr., Lawton, J. H. and Southwood, T. R. E. 1984. Insects on plants: community patterns and mechanisms. – Blackwell Scientific.

Tilman, D. 1987. The importance of the mechanisms of inter-specific competition. – Am. Nat. 129: 769–774.

Watson, R. M. 1967. The population ecology of the wildebeest (*Connochaetes taurinus albojubatus* Thomas) in the Serengeti. – Ph.D. thesis, Univ. of Cambridge.

Wheelwright, N. T. 1985. Fruit size, gape width and the diets of fruit-eating birds. – Ecology 66: 808–818.