

Niche separation of grazing ungulates in the Serengeti: an experimental test

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Summary

1. The niche separation of three species of alcelaphine antelope (wildebeest, topi and hartebeest) with similar body size was compared by measuring bite weight, bite rate, intake rate and selectivity of tame animals in plots containing grass at different growth stages.
2. On growing swards, hartebeest had a smaller bite weight and lower intake rate, and were also less selective of green leaf, than either topi or wildebeest. On senescent swards, hartebeest were more selective of leaf than the other two species.
3. Wildebeest had a faster bite rate than either topi or hartebeest on swards with low biomass and high protein content of green leaf (green flush). Bite weight and intake rate of wildebeest and topi were similar despite the difference in breadth of their incisor rows.
4. Topi were significantly more selective of green leaf than the other two species and were the only species to maintain a rapid bite rate on swards with high green leaf biomass.
5. The feeding experiments did not reveal significant cross-overs between species in the rate of food intake on different grass types, but each species was most proficient either in leaf selection or bite rate when feeding on grass swards in a particular growth stage. We suggest that growth stage is a primary determinant of niche separation.
6. In Serengeti, grazing ungulates which migrate are specialists of the earlier growth stages of grass which tend to be transient, while those that are residential specialize on late growth stages which are more enduring. The mobility of species, and the spatial and temporal dynamics of pastures containing different growth stages of grass, contribute to niche separation.

Key-words: bite, intake, migration, niche, ungulate.

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Introduction

Some 30 ungulates species occur in the Serengeti–Mara ecosystem of northern Tanzania and south-western Kenya, making up one of the most diverse assemblages in the world. The area is particularly renowned for its herds of grazing ungulates. If the list is restricted to those ungulates which subsist largely or completely on grass, 12 species remain. In order of increasing female body size, these are: oribi *Ourebia ourebi* (20 kg); mountain reedbuck *Redunca fulvorufula* (25 kg); Bohor reedbuck *Redunca redunca* (45 kg); topi *Damaliscus lunatus* (110 kg); hartebeest *Alcelaphus buselaphus* (125 kg); wildebeest *Connochaetes taurinus* (160 kg); waterbuck *Kobus ellipsiprymnus* (175 kg); oryx *Oryx gazella*

(200 kg); zebra *Equus burchelli* (220 kg); roan antelope *Hippotragus equinus* (250 kg); buffalo *Syncerus caffer* (450 kg); and hippopotamus *Hippopotamus amphibius* (2000 kg) (Sachs 1967; Haltenorth & Diller 1980).

The explanation for how so many species of grazing ungulate can share the same natural pastures, without overwhelming competition for their common food resource, has intrigued ecologists working in the Serengeti for more than 25 years. In the 1960s, Richard Bell demonstrated how different species of ungulate select different plant parts from the same plant species, and then postulated ecological separation of African grazing ungulates on the basis of differential efficiency of feeding on different grass types (Bell 1969, 1970, 1971; Gwynne & Bell 1968).

Bell (*ibid*) proposed two underlying adaptations: dissimilar diets were determined firstly by differences in ruminant and non-ruminant digestive systems (see Janis 1976 and Duncan *et al.* 1990 for more developed arguments), and secondly on the basis of size-dependent energy requirements (see Demment & Van Soest 1985 for a mechanistic explanation of this hypothesis).

Differences in diet selection by grazing ruminants of similar body size were also investigated by Bell (1969, 1970) who hypothesized that wildebeest, with their greater breadth across the incisors, would be most successful on short leafy swards, but that topi, with a relatively pointed jaw, would be most successful as selective feeders in medium height, upright grasslands. Subsequently, the influence of dentition on feeding efficiency has been investigated in simulation models by Owen-Smith (1985) and by Illius & Gordon (1987), both models confirming the advantage of species with broad muzzles on short grassland.

Topi and hartebeest have similar body size and incisor breadth, and in the Serengeti they are often found feeding together in mixed herds. The causation of grazing separation between these two species has remained an enigma. Topi occupy a whole spectrum of grassland habitats in the course of a year. The species association of grassland is of secondary importance in predicting habitat selection, the primary factor being growth stage: topi prefer an intermediate growth stage (semi-mature) when this is available (Duncan 1975). Hartebeest on the other hand are more successful in habitats with lower quality food (Stanley Price 1974).

In this paper, we report on differences in intake rate and selectivity of wildebeest, topi and hartebeest when grazing experimental grass swards in the Serengeti National Park. In addition to their taxonomic affiliation and their similarity in body size, the three alcelaphines share many similar features of their digestive system, leading Hofmann (1973) to classify all three as bulk and roughage feeders which specialize on a diet composed almost entirely of grass. Topi and hartebeest have a near identical breadth across the front of the mandible (5.0 cm), but wildebeest have a wider jaw (7.0 cm) (Bell 1969). In East Africa wildebeest are associated with short grass 'lawns' and a plentiful supply of water, topi with taller wetland grasses in valley bottoms or flood plains, and hartebeest with drier wooded savannas in medium or long, coarse grassland (Kingdon 1982). The geographic ranges of the three species overlap within the Serengeti-Mara ecosystem.

Methods

FEEDING TRIALS

Animal to be used in feeding trials were caught as yearlings and stabled at the Serengeti Wildlife

Research Institute (SWRI) which is located 5 km east of Seronera in the Serengeti National Park, Tanzania (see Kreulen 1977). Trials were conducted from late June to early August 1989, in a period with little rain when natural grass swards were becoming progressively drier. Two wildebeest (average weights of 86 and 108 kg), two topi (74 and 77 kg) and one hartebeest (92 kg) took part in the trials. All animals were in possession of adult dentition. The number of animals in the intake trials was limited to one of each species in order to increase the precision of intake measurements. Each of the individuals chosen stood quietly on the weighing platform allowing accurate and repeatable measurements of body weight (see below).

Food intake was estimated from the difference in body weight before and after grazing, with individual correction for insensible weight loss brought about by steady loss of moisture in respired air and from external surfaces. Insensible weight loss per minute was determined for each individual from regression equations relating this variable to radiant temperature. Data for regression equations were obtained from an investigation of weight loss in animals standing outside on bare ground. Live weight was measured at half-hourly intervals and radiant temperature (thermometer in the sun), shade temperature, relative humidity and wind velocity were noted at 1-min intervals. Live weight was recorded on a Mettler weighing platform with digital output (± 10 g) to a microcomputer. The platform was set into one of the stalls in the stable to reduce interference from the wind. The mean weight could be computed over any convenient period of time (Penning & Hooper 1985), but best results were achieved with animals that stood completely still providing a constant reading.

Using these methods, differences in weight before and after feeding could be corrected for the insensible weight loss expected if the experimental animal had been standing outside under equivalent climatic conditions. Any additional weight loss attributable solely to movement between stables and plots (up to 100 m distance) was ignored.

During the feeding trials, animals were housed in stables at night, where they were provided with freshly cut grass, and grazed on nearby pastures during the day. Feeding trials were conducted from 07.00 to 09.30 h each morning. When measuring intake rate, subject animals were weighed in the stables, walked to the experimental plot and allowed to graze until they had taken 1000 bites, usually requiring 20–30 min. At this point, the animal was immediately led back to the stables and weighed again. Radiant temperature was recorded at 1-min intervals throughout the trial.

By entering the time of each bite into a computerized event recorder, bite rate (bites s^{-1}) and bite weight (intake/number of bites) could be deter-

mined. Bite rate was calculated over the time period in which the animal was actually feeding, i.e. foraging time less the time spent walking and looking about. Approximately 10% of trials were terminated following urination or defecation by the subject animal. Intake rate was measured on 15, 20 and 22 plots for wildebeest, topi and hartebeest, respectively.

In a parallel series of trials, the degree of selection for green leaf in the diet was determined subjectively by estimating the % of green leaf in each of 200 sequential bites. In this procedure, the observer (MGM in all instances) stood within 1 m of the animal's mouth and recorded his assessment of the percentage of green leaf in each bite into a micro-cassette recorder at the moment of prehension. Selectivity was subsequently calculated as % green leaf in the diet/% green leaf in the sward (Duncan 1975), and was measured on 21, 21 and 19 plots for wildebeest, topi and hartebeest, respectively. Selectivity on swards in a late growth stage (containing small quantities of green leaf) was calculated as % leaf (green or brown) in the diet/% leaf in the sward, and determined for each species on four plots.

Selection and intake trials took place on a variety of naturally occurring grass swards, and on green flushes induced by cutting, near to SWRI. Plots of 12 × 12 m were marked out on uniform grass swards and the perimeter was scraped bare to discourage the subject animal from leaving during the trial. The herb layer in the plots was dominated by *Themeda triandra*, a forage species of widespread importance in Serengeti, in association with *Bothriochloa insculpta* and occasional tillers of *Panicum coloratum* and *Aristida adoensis*. All these species have an erect growth form. On one plot the herb layer was dominated by *Chloris pycnothryx*, a species with a prostrate, mat-forming growth form.

Prior to each feeding trial, 15 measures of the sward were obtained by clipping all herbage to a height of 2 cm within four quadrats of 25 × 25 cm: biomass of green leaf (g m^{-2}); biomass of brown leaf; biomass of stem; total biomass; % green leaf in sward; % brown leaf in sward; % stem in sward; mean weights of 100 green and 100 brown leaves (mg); neutral cellulase digestibility, ash content and crude protein content of green leaf and of stem (the latter six measures as a % of dry matter). The herbage samples were sorted by hand, dried at 65 °C and flown to the UK for chemical analysis by the Agricultural Development and Advisory Service (Murray 1991). In addition, canopy height of leaf was determined from 50 measurements made with a metre rule equipped with a sliding pointer. Moisture content of grass samples was also determined for estimation of dry matter intake, but it was not included as a variable for describing the grass sward.

STATISTICAL ANALYSIS

The initial dataset comprised four dependent variables describing foraging efficiency (bite rate, bite weight, intake rate and green leaf selectivity) and 16 explanatory variables describing the grass sward (listed above). The dependent variables were transformed using logs because the residual variability of the untransformed variable increased with the mean, whereas the residual variability of the logarithmically transformed variable was more uniform. By log-transforming the explanatory variables as well, coefficients of the fitted multiple regression corresponded to powers of the original explanatory variables (after both sides of the regression equation have been anti-logged). They therefore have more generally applicability and are easier to interpret than those in a model involving a sum of terms.

The number of explanatory variables was reduced by seeking a multiple regression model which had the highest predictive power, but contained no redundant terms (as determined by statistical significance). The minimal model was determined by a graphical analysis of variance technique (Brown 1992). For each dependent variable, the resulting minimal model contained just three explanatory variables: the biomass of green leaf (*glb*), the percentage of crude protein in green leaf (*glcp*) and the percentage weight of stem in the grass sward (*stem*).

Results

EXPERIMENTAL PLOTS

The experimental plots could be broadly divided into two classes: plots with new growth which had been stimulated by cutting, and plots with old growth which were not managed. Further subdivision on the basis of growth stage and form revealed five categories of grass sward (Table 1). New growth was characterized by short height, low biomass, high moisture content, low percentage of brown leaf and high crude protein content of green leaf. Semi-mature swards were taller with higher biomass, and contained heavier green leaves. Mature swards were tall with high biomass, a high percentage of brown leaf, and a low crude protein content and digestibility of green leaf. Senescent growth was lower in height and biomass with a low percentage of green leaf and a high percentage of brown leaf and stem. The latter two categories of sward (mature and senescent) were provided exclusively by unmanaged swards).

INSENSIBLE WEIGHT LOSS

Radiant temperature proved to be the best climatic variable for predicting insensible weight loss per minute (Table 2). Adding the other variables (shade

Table 1. Composition* of the grass sward in experiment plots according to growth stage and form

Measurements	New growth, mat-forming	New growth, erect	Semi-mature, erect	Mature, erect	Senscent, erect
Biomass (g m ⁻²)	68.0	104.7 (80.4–133.6)	163.3 (106.8–200.2)	450.8 (151.6–794.8)	89.8 (68.0–111.6)
Leaf height (cm)	2.4	4.9 (2.6–7.2)	6.4 (3.9–8.3)	40.3 (18.1–56.2)	9.8 (8.9–10.8)
Moisture content (%)	75.1	67.8 (63.8–71.6)	66.7 (63.8–71.6)	39.9 (23.0–57.6)	21.1
Indiv. green leaf (mg)	5.5	6.7 (5.1–8.5)	9.1 (5.5–11.8)	13.4 (9.7–15.9)	10.7 (6.5–14.9)
Green leaf (%)	25.3	22.1 (15.3–33.1)	31.1 (21.6–40.0)	11.3 (5.2–17.7)	4.2 (4.2–4.3)
Green leaf cp (%)	18.1	15.1 (11.7–19.3)	16.1 (10.8–20.7)	7.3 (5.8–8.9)	
Green leaf ncd (%)	51.0	52.3 (40.0–59.2)	56.2 (50.5–61.0)	41.7 (36.2–45.5)	
Green leaf ash (%)	14.6	14.5 (12.8–16.6)	14.8 (12.2–16.7)	13.2 (11.2–15.7)	
Stem (%)	69.0	63.8 (54.0–75.3)	61.6 (54.8–70.5)	57.7 (52.4–62.6)	67.6 (63.6–71.5)
Stem cp (% of DM)	9.5	5.0 (2.7–7.3)	5.3 (2.9–7.8)	2.6 (1.4–3.6)	3.3 (3.2–3.3)
Stem ncd (% of DM)	42.0	32.3 (28.4–34.9)	33.4 (26.4–38.1)	29.1 (26.6–35.0)	37.5 (36.1–38.8)
Stem ash (%)	10.1	10.0 (9.1–10.9)	9.9 (8.1–11.3)	8.5 (7.6–9.5)	6.8 (6.4–7.2)
Indiv. brown leaf (mg)	3.7	6.3 (4.6–9.3)	6.1 (5.3–7.5)	8.0 (6.1–9.8)	11.2 (9.8–12.6)
Brown leaf (%)	3.4	9.4 (4.3–20.0)	5.7 (3.0–8.8)	26.1 (18.0–30.9)	22.3 (21.6–23.0)
Number of plots	1	9	9	6	2

* An average value is given together with the range in parentheses.

Table 2. Prediction of the insensible weight loss (I , g min⁻¹) in wildebeest, topi and hartebeest from the radiant temperature (T , °C)

Species	Regression equation	Accountable variance [†]	Significance level	Observations fitted
Wildebeest	$I = -0.314 + 0.792\exp(T/10) - 0.000464T^3$	68.4	***	32
Topi	$I = 0.07 + 0.393\exp(T/10) - 0.000254T^3$	60.2	***	20
Hartebeest	$I = 0.425 + 0.131\exp(T/10)$	74.4	***	26

*** $P < 0.001$.

[†] Adjusted for degrees of freedom.

temperature, relative humidity and wind velocity) did not significantly improve the predictive power of regression equations for any of the three species.

FEEDING TRIALS

The relationship between bite weight of wildebeest and topi, and canopy height of leaf, using data that has not been log-transformed, is illustrated in Fig. 1a. In these two species, and also in hartebeest, bite weight rose rapidly reaching an asymptote in swards with a leaf canopy of approximately 15 cm height. On the other hand, bite rate of wildebeest and hartebeest declined with increasing canopy height of leaf. Only topi were able to maintain a relatively rapid bite rate in tall swards (Fig. 1b).

Considering now the multiple regression analysis using log-transformed data, 40–90% of variance in the dependent variables is accounted for in the models (Table 3). Most of the variance is accounted for by a pooled model, in which there is one intercept and the same slopes for each ungulate species against the explanatory variables, demonstrating that the composition of the grass sward affects the foraging efficiency of each ungulate in a similar way. However, significant between-species variation was found in

the intercepts and in the slopes of the models fitted to bite rate and intake rate (Table 4).

The bite weight of hartebeest was smaller than that of wildebeest ($P < 0.01$) or topi ($P < 0.01$). The bite weight of wildebeest was similar to that of topi ($P > 0.1$; Fig. 2a,d). The bite rate of wildebeest was very sensitive to the composition of grass swards (see Table 3). On swards of low biomass and high crude protein content, wildebeest had a faster bite rate than either of the other two ungulates ($P < 0.01$; Fig. 2b,e). On the other hand, topi were able to maintain a constant bite rate even on high biomass and stemmy swards ($P > 0.1$) whereas wildebeest could not ($P < 0.05$; Table 3).

The net result of these trends was that in the mid-range of explanatory variables, i.e. when $glb = 40 \text{ g m}^{-2}$, $glcp = 12\%$, and $stem = 60\%$, the intake rate of hartebeest was lower than that of wildebeest and topi ($P < 0.01$; Table 3), the latter two species having similar intake rates. The intake rate of topi was the highest of the three ungulates on swards with a high biomass and low crude protein content of green leaf (mature swards), whilst that of wildebeest was highest on swards of low biomass and high crude protein content (green flush) (Fig. 2c,f), but the differences failed to achieve signifi-

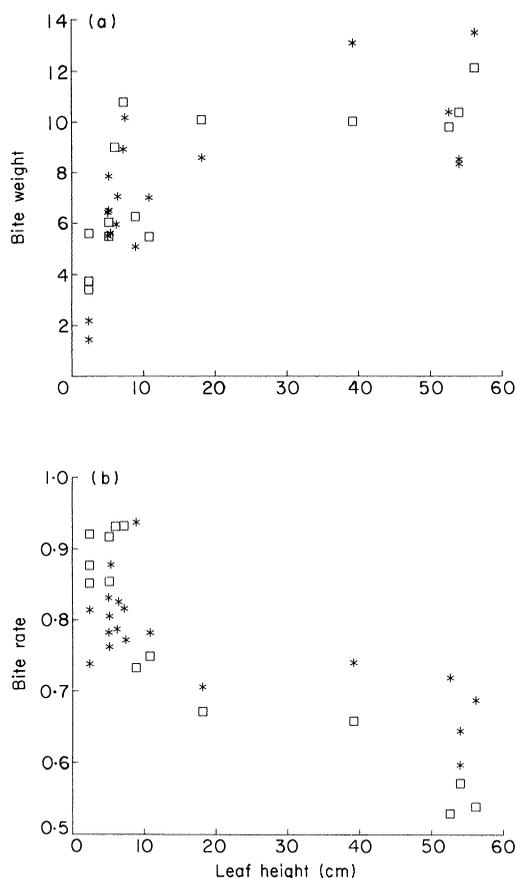


Fig. 1. Relationship between (a) bite weight ($\text{mg W}^{-0.75}$) and (b) bite rate (bites s^{-1}) of wildebeest (\square) and topi (*), and the height of leaf in the sward. Variables are not log-transformed.

cance due to the greater variability in measures of intake rate.

All three species were more selective of green leaf

in swards with a high biomass of green leaf (Fig. 3a; Table 3), reflecting in part the greater opportunity for selection in these swards (Table 1). Significant between-species variation was found in the intercepts of the regression equation fitted to green leaf selection, but not in the slopes (Table 4). On most grass swards, topi were more selective of green leaf than either wildebeest ($P < 0.01$) or hartebeest ($P < 0.01$), but wildebeest were more selective than topi on some swards with high crude protein content (Fig. 3b), i.e. on new growth.

As the mature swards dried out and were grazed over by free-ranging herbivores, the biomass of green leaf declined and the proportion of stem rose. Although the replication of trials on these dry swards was limited to four for each species, it was apparent from casual observation and systematic measurement that hartebeest were selecting strongly for leaf (green or brown) and against stem, but that topi and wildebeest were not feeding selectively (Fig. 4). The hartebeest was most selective of leaf when grazing on senescent swards with a low biomass of green leaf.

Discussion

GRAZING EFFICIENCY

With their remarkably wide dental pad and incisor row, it has been suggested that wildebeest obtain a higher intake of forage on short and leafy grass swards, but that topi with their narrow incisor row feed more selectively and efficiently in longer grass (Bell 1970; Jarman & Sinclair 1979; Owen-Smith 1985). Applying the logic of Illius & Gordon's (1987) simulation model, we should expect differences

Table 3. Regression coefficients for dependent variables describing the intake and selectivity of wildebeest (W), topi (T) and hartebeest (H). All coefficients are \log_{10} values with standard errors in brackets. The predicted mid-range value of each dependent variable is given for *glb* (green leaf biomass) = 40 g m^{-2} , *glcp* (crude protein content of green leaf) = 12%, and *stem* (percentage of stem in the sward) = 60%

Dependent variable	Mid-range predicted values	Intercept	Slopes			% Variance accounted for
			<i>glb</i>	<i>glcp</i>	<i>stem</i>	
Bite weight						
W	0.890 (0.036)	4.84 (1.63)	0.192 (0.108)	-0.320 (0.242)	-2.200 (0.965)	67.5
T	0.854 (0.033)	7.34 (1.66)	0.271 (0.106)	-0.432 (0.179)	-3.627 (0.923)	74.7
H	0.698 (0.037)	4.05 (1.70)	0.193 (0.123)	-0.522 (0.225)	-1.741 (0.945)	55.4
Bite rate						
W	-0.119 (0.006)	0.564 (0.278)	-0.056 (0.018)	0.519 (0.041)	-0.649 (0.165)	95.6
T	-0.123 (0.007)	-0.109 (0.353)	-0.007 (0.023)	0.190 (0.038)	-0.117 (0.196)	58.7
H	-0.155 (0.008)	-0.287 (0.371)	-0.049 (0.027)	0.160 (0.049)	0.021 (0.206)	53.2
Intake rate						
W	2.549 (0.036)	7.18 (1.61)	0.136 (0.107)	0.199 (0.239)	-2.849 (0.954)	47.9
T	2.509 (0.035)	9.01 (1.78)	0.264 (0.114)	-0.243 (0.192)	-3.744 (0.992)	67.8
H	2.322 (0.036)	5.54 (1.67)	0.144 (0.172)	-0.362 (0.222)	-1.720 (0.930)	43.8
Selectivity						
W	0.283 (0.063)	-7.88 (2.50)	1.073 (0.186)	0.595 (0.308)	3.260 (1.43)	65.2
T	0.380 (0.041)	-6.24 (1.53)	0.697 (0.114)	-0.348 (0.233)	3.306 (0.882)	66.6
H	0.267 (0.063)	-4.77 (2.64)	0.750 (0.196)	0.445 (0.347)	1.890 (1.46)	43.7

Table 4. Comparison of the intercepts and slopes of regression equations for food intake and green leaf selection in three antelope species. In the common model, there is one intercept and three slopes (one for each of *glb*, *glcp* and *stem*); in the different intercepts model, there are three intercepts (one for each antelope species) and three slopes as in the common model; in the different slopes model, there are three intercepts and nine slopes (three sward variables for each of three antelope species). Significant improvements in fit from adding different intercepts or slopes to the model are indicated

Dependent variable	Statistic	Model		
		Common	Different intercepts	Different slopes
Bite weight	df	46	44	38
	Residual SS	1.117	0.784	0.704
	F_s		8.99	0.72
	P		***	NS
Bite rate	df	46	44	38
	Residual SS	0.073	0.063	0.031
	F_s		6.30	6.65
	P		**	***
Intake rate	df	46	44	38
	Residual SS	1.332	0.896	0.728
	F_s		11.38	7.16
	P		***	***
Selection	df	54	52	46
	Residual SS	2.545	2.074	1.736
	F_s		6.24	1.49
	P		**	NS

** $0.001 < P < 0.01$; *** $P < 0.001$.

in bite weight between topi and wildebeest to be greatest on short swards, where bite width will contribute relatively more than bite depth to bite volume. In our experiments with the two species, we found that wildebeest and topi had similar bite weights when feeding on light swards. The lack of agreement between observed and expected differences in bite weight may be due to the spatial distribution of green leaf in unsown swards. If most leaf bunches in light swards can be fully encompassed by a small mouth then bite weight can be independent of incisor breadth.

Our experiments were conducted mostly with plots containing *Themeda triandra* and other grass species with erect growth form, which predominate in the central and northern wooded areas of Serengeti (Sinclair 1977). Grass species with a prostrate mat-forming growth style occur in the wet season range of wildebeest on the southern short grass plains (Kreulen 1975; McNaughton 1984). On the single experimental plot dominated by a mat-forming species (*Chloris pycnothryx*) in an early growth stage, the bite weight of wildebeest averaged 2.6 times that of topi (leftmost points in Fig. 1a), in agreement with expectation. Higher leaf density, and other structural differences, may enable wildebeest to obtain heavier bites from mat-forming species (D.A. Kreulen personal communication; Illius & Gordon 1987).

Unexpectedly, topi were found to have slower bite rates than wildebeest when grazing light swards. This was not due to differences in time spent looking about in-between grazing bouts, as this time was

discounted in the measurement of bite rate. Nor was the difference related to greater selectivity for green leaf by wildebeest in the vertical plane. The two species were apparently biting down to the same depth, and topi obtained at least as high a proportion of green leaf in their bites as did wildebeest (Fig. 3a). The difference could be related to greater selectivity by topi in the horizontal plane. Topi may have been seeking larger leaves on the light swards in an attempt to maintain bite weight, and this could account for their slower bite rate, and higher than expected bite weight relative to that of wildebeest.

The preference of topi for grass in a semi-mature growth stage was established by Duncan (1975) who found that bite weight increased with the length of leaf in the sward, reaching an asymptote at about 70 mm leaf length. We found similar asymptotic relationships between bite weight and average leaf weight in all three alcelaphines, and no significant differences between species in the relationship between bite weight and biomass of green leaf. The relationship between bite rate and green leaf biomass did vary between species. Topi was the only species able to maintain rapid bite rates in heavy swards, although this advantage was not sufficient to produce a significantly higher intake rate. Topi also proved to be more selective of green leaf than the other two species. Especially when grazing mature swards with a high biomass of green leaf (Table 1), topi probably procured a diet higher in energy and protein content than did wildebeest.

The hartebeest was the 'odd-one-out' in this three-way comparison, despite the fact that its muzzle

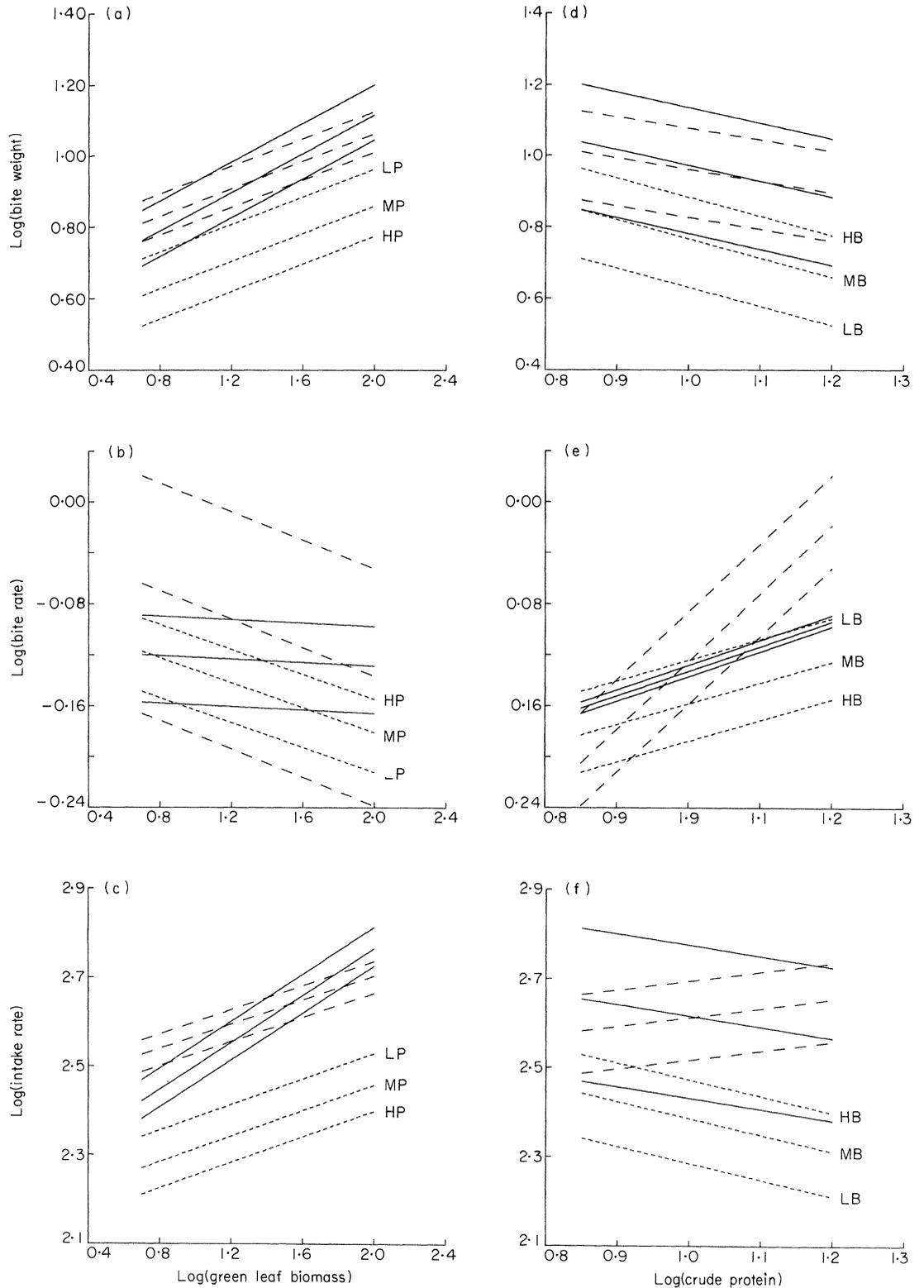


Fig. 2. Variation in dry matter intake of topi (—), wildebeest (---) and hartebeest (.....), as predicted by the regression model, against two parameters of the grass sward: green leaf biomass ($\text{g dry matter m}^{-2}$) and protein content of green leaf (% CP). Dependent variables are (a,d) bite weight per kg metabolic weight ($\text{mg dry matter} \times \text{weight}^{-0.75}$); (b,e) bite rate (bites per s^{-1}); (c,f) rate of intake ($\text{mg dry matter} \times \text{weight}^{-0.75} \text{ min}^{-1}$). Values of the explanatory variables used in the predictions were set as follows: in graphs (a, b & c) $\log_{10}(\text{stem}) = 1.74$ and $\log_{10}(\text{glcp}) = 0.85$ (LP), 1.04 (MP) and 1.20 (HP); in graphs (d, e & f) $\log_{10}(\text{stem}) = 1.74$ and $\log_{10}(\text{glb}) = 0.7$ (LB), 1.4 (MB) & 2.0 (HB).

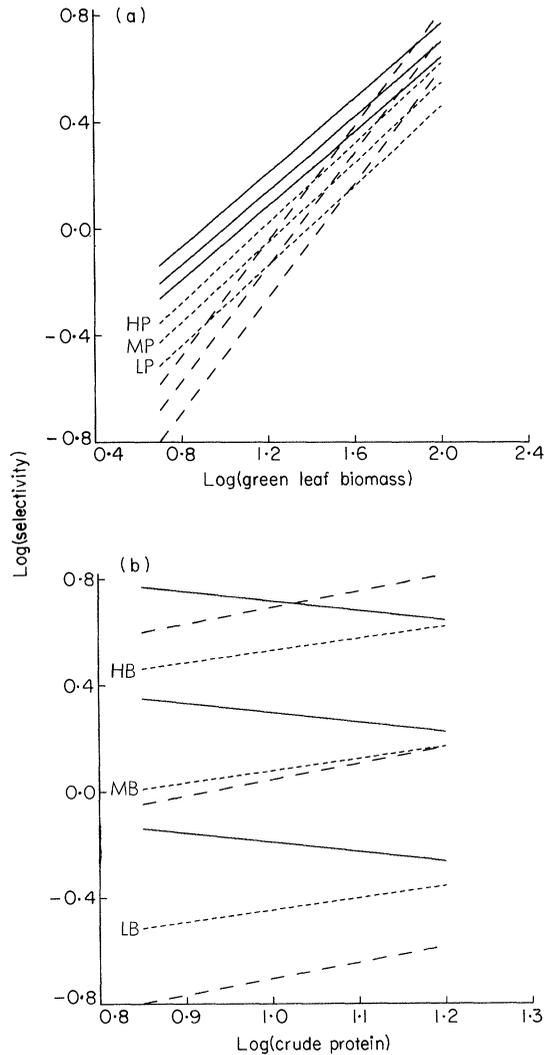


Fig. 3. Variation in the level of selection for green leaf by topi (—), wildebeest (---) and hartebeest (···), as predicted by the regression model: (a) against biomass of green leaf ($\log_{10}(\text{stem}) = 1.80$ and $\log_{10}(\text{glcp}) = 0.85$ (LP), 1.04 (MP) and 1.20 (HP)); and (b) against crude protein content of green leaf ($\log_{10}(\text{stem}) = 1.80$ and $\log_{10}(\text{glb}) = 0.7$ (LB), 1.4 (MB) and 2.0 (HB)).

width, ruminant digestive system and body size is very similar to that of topi. In almost all feeding trials, hartebeest performed less successfully than either topi or wildebeest, selecting less green leaf and securing smaller bites at a slower bite rate. The first indication of grazing specialization in hartebeest came towards the end of the feeding trials after a prolonged period of dry weather. The tame hartebeest was observed plucking small tufts of dry leaf out of a senescent sward that had been heavily defoliated in previous weeks by free-ranging wildebeest. The other two species were noticeably less choosy. Systematic observation confirmed that the hartebeest was feeding much more selectively in dry grass swards than either topi or hartebeest. Selective feeding by hartebeest under similarly dry conditions was observed by Stanley Price (1974) on the Athi

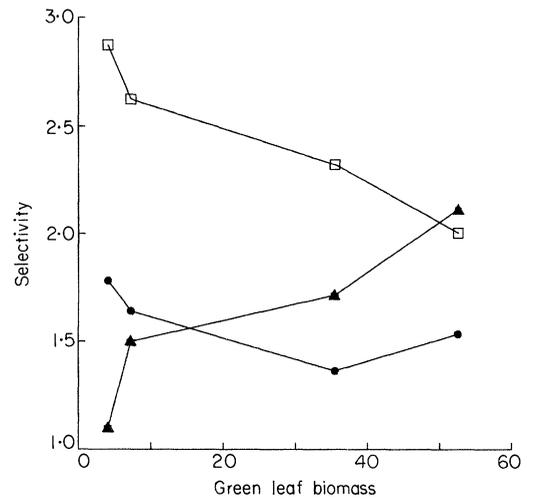


Fig. 4. Relationship between the level of selection for leaf (either green or brown) by topi (\blacktriangle), wildebeest (\bullet) and hartebeest (\square) and the biomass of green leaf in mature and senescent grass swards.

Plains of Kenya. He describes how hartebeest removed sheath from defoliated dry swards by nibbling in a vertical plane from the base of grass clumps. Compared with other ruminants, hartebeest have a relatively low daily intake of dry matter (Stanley Price 1978). Their weak appetite may be related to their low requirement of energy for maintenance and growth (Murray, in press), and this in turn may account for their greater selectivity on senescent grass swards in which daily intake is potentially limited by food availability.

NICHE SEPARATION

According to the theory of resource competition, two similar species can coexist provided that the food which each harvests most efficiently is different (MacArthur 1972). Our results show that each of the alcelaphines was most efficient on grass swards with a high biomass of green leaf (Figs 2c & 3a), and this could be taken as evidence for specialization by all three species on the same resource type. An alternative explanation can be derived from Tilman's (1982) hypothesis for resource competition in plant communities. If one species of herbivore is able to reduce the biomass of grass (by biting to a low horizon in the sward) below the level at which another can maintain zero growth, then resource competition will occur. If the other herbivore can reduce the protein or energy content of the grass (by selective feeding) below that at which the first herbivore can maintain zero growth, then the two herbivores may be able to co-exist on the same pastures.

Viewing resource competition in this way, it can be seen that two herbivores may each be most efficient on the same favourable resource type (heavy and leafy grass swards, for example), but we expect

to find cross-overs on less favourable resource types, such that species A is more efficient than B on resources of type a, and species B is more efficient than A on resources of type b.

The significant difference in slopes for intake rate between alcelaphines (Table 4) is suggestive evidence for niche separation, but a clear picture fails to emerge when each component slope is examined in isolation from the others. We found that each species was more proficient than the other two species, either in leaf selection or bite rate, when grazing in a particular growth stage. We did not find significant cross-overs in the intake rate between species feeding on different grass types. While the picture of resource competition which emerges from our experiments is therefore preliminary, it does provide some indication of how resources are structured within the grazing community. We found that foraging behaviour was strongly influenced by the growth stage of grass, and we suggest that each alcelaphine has specialized on a different growth stage of grass: wildebeest on early growth stages, topi on green growth at an intermediate or mature stage, and hartebeest on late growth stages in which the sward is dry and senescent.

The spacing between pastures of different growth stage, the duration of a given growth stage, and the mobility of ungulate species may be additional constituents of niche space. In the Serengeti, green growth in the dry season is localized and temporal, sprouting forth in the wake of rainstorms and following the passage of fire, but soon drying and browning without persistent rainfall. The ungulates exploiting the early and intermediate growth stages (wildebeest, topi and Thomson's gazelle *Gazella thomsoni*) are nomadic and renowned as migratory species in some areas. By contrast, swards in the later and drier growth stages are more stable: transformation of growth stage being accelerated by fire, or heavy grazing pressure, but not by the absence of rain. Species exploiting the later growth stages of grass in the Serengeti (hartebeest, waterbuck and buffalo) are residential.

The recognition of a dichotomy in ungulate grazing strategy related to species-specific specialization on the growth stages of grass provides a further tool for wildlife managers. Expansion of herds of residential species will be assisted by management practises (such as fire exclusion) that maintain stands of mature or senescent grass during dry periods; conversely, management for early growth stages (by burning or mowing, for example) will favour migratory species, especially where green pastures are patchily distributed and temporal.

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References

- Bell, R.H.V. (1969) *The use of the herbaceous layer by grazing ungulates in the Serengeti National Park, Tanzania*, PhD thesis, University of Manchester.
- Bell, R.H.V. (1970) The use of the herb layer by grazing ungulates in the Serengeti. *Animal Populations in Relation to their Food Supply* (ed. A. Watson), pp. 111–123. Blackwell Scientific, Oxford.
- Bell, R.H.V. (1971) A grazing ecosystem in the Serengeti. *Scientific American*, **224**, 86–93.
- Brown, D. (1992) A graphical analysis of deviance. *Applied Statistics*, **41**, 55–62.
- Demment, M.W. & Van Soest, P.J. (1985) A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. *American Naturalist*, **125**, 641–672.
- Duncan, P. (1975) *Topi and their food supply*. PhD thesis, University of Nairobi.
- Duncan, P., Foose, T.J., Gordon, I.J., Gakahu, C.G. & Lloyd, M. (1990) Comparative nutrient extraction from forages by grazing bovids and equids: a test of the nutrient model of equid/bovid competition and coexistence. *Oecologia*, **84**, 411–418.
- Gwynne, M.D. & Bell, R.H.V. (1968) Selection of vegetation components by grazing ungulates in the Serengeti National Park. *Nature*, **220**, 390–393.
- Haltenorth, T. & Diller, H. (1980) *A Field Guide to the Mammals of Africa*. Collins, London.
- Hofmann, R.R. (1973) *The Ruminant Stomach*. East African Literature Bureau, Nairobi.
- Illius, A.W. & Gordon, I.J. (1987) The allometry of food intake in grazing ruminants. *Journal of Animal Ecology*, **56**, 989–999.
- Janis, C. (1976) The evolutionary strategy of the equidae and the origins of rumen and cecal digestion. *Evolution*, **30**, 757–774.
- Jarman, P.J. & Sinclair, A.R.E. (1979) Feeding strategy and the pattern of resource partitioning in ungulates. *Serengeti, Dynamics of an Ecosystem* (eds A.R.E. Sinclair & M. Norton-Griffiths), pp. 130–163. University of Chicago Press, Chicago.
- Kingdon, J. (1982) *East African Mammals, Vol III D*. University of Chicago Press, Chicago.
- Kreulen, D.A. (1975) Wildebeest habitat selection on the Serengeti plains, Tanzania, in relation to calcium and

- lactation: a preliminary report. *East African Wildlife Journal*, **13**, 297–304.
- Kreulen, D.A. (1977) Taming of wild-captured wildebeest for food habit studies. *Journal of Wildlife Management*, **41**, 793–795.
- MacArthur, R.H. (1972) *Geographical Ecology*. Harper & Row, New York.
- McNaughton, S.J. (1984) Grazing lawns: animals in herds, plant form, and coevolution. *American Naturalist*, **124**, 863–886.
- Murray, M.G. (1991) Maximizing energy retention in grazing ruminants. *Journal of Animal Ecology*, **60**, 1029–1045.
- Murray, M.G. (in press). Comparative nutrition of wildebeest, hartebeest and topi in the Serengeti. *African Journal of Ecology*.
- Owen-Smith, R.N. (1985) Niche separation among African ungulates. *Species and Speciation* (ed. E.S. Vrba), pp. 161–171. Transvaal Museum Monograph No 4, Transvaal Museum, Pretoria.
- Penning, P.D. & Hooper, G.E. (1985) An evaluation of the use of short-term weight changes in grazing sheep for estimating intake. *Grass and Forage Science*, **40**, 79–84.
- Sachs, R. (1967) Liveweights and body measurements of Serengeti game animals. *East African Wildlife Journal*, **5**, 24–36.
- Sinclair, A.R.E. (1977) *The African Buffalo*. University of Chicago Press, Chicago.
- Stanley Price, M.R. (1974) *The feeding ecology and energetics of Coke's hartebeest*. DPhil thesis, University of Oxford.
- Stanley Price, M.R. (1978) The nutritional ecology of Coke's hartebeest (*Alcelphus buselaphus cokei*) in Kenya. *Journal of Applied Ecology*, **15**, 33–49.
- Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton.

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