PLANT ANIMAL INTERACTIONS

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Bush selection along foraging pathways by sympatric impala and greater kudu

Abstract In order to identify the selection mechanism of two sympatric African browsers, we analysed encounter rates and selection of bushes along foraging pathways. We monitored the tracks, left overnight, by kudu and impala on an experimental plot of natural *Acacia nilotica* and *Dichrostachys cinerea* in the highveld of Zimbabwe, and recorded the number of bushes attacked in each category. Both ungulates were selective for the bush categories, but kudu were consistently more selective than impala, and showed a higher preference for the larger *A. nilotica* and *D. cinerea* bushes, which had a significantly greater number of bites which were not reachable by impala. For both kudu and impala, the probability of attacking larger bushes increased significantly with the proportion of large bushes encountered along the foraging pathways, whereas the consumption of smaller bushes was apparently unpredictable. For the most abundant food item (medium *D. cinerea*), the probability of attack by impala along a pathway decreased with increasing proportions of larger bushes in the experimental area, but was also dependent on impala group size and season. In addition, we found that encounter rates with larger bushes were significantly higher for kudu than for impala. Experimentally reducing the availability of the larger bushes had little effect on both impala and kudu during the following rainy season. However, during the following cool dry season, kudu showed an increased selectivity with a strong preference for the remaining large bushes (large *A. nilotica*), followed by a sharp decrease in selectivity in the hot dry season when they also fed from significant numbers of medium trees. Impala had little reaction to the experimental changes in the availability of bush categories in either season. We suggest that both kudu and impala selected bushes on the basis of the potential number of bites they can provide, and this resulted in different search strategies. Kudu focussed on the larger bushes which have a larger number of twigs which are out of reach of impala and kudu also probably directed their path preferentially towards the few larger bushes to maximize encounter rates with this favoured bush category. These differences in bush selection process lead to a low overlap in resource use between the two browsers in this type of savanna.

Keywords *Aepyceros melampus* · Browsing · Competition · Feeding height stratification · *Tragelaphus strepsiceros*

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Introduction

Among the foraging models which have been proposed for herbivores, browsing behaviour has often been referred to as a "prey as patch" model (Stephens and Krebs 1986; Aström et al. 1990). Optimal use of the discrete food items (trees) by browsers is determined by three types of decisions (Owen-Smith and Novellie 1982): (1) whether or

not to commence feeding on a food plant; (2) when to stop feeding on a plant; (3) in which direction to walk toward the next food plant. Decisions concerning foraging path choice, which determine encounter rates with discrete food items, are also crucial, and it has been suggested that browsers would orientate their movement to maximize encounter rates with their preferred food item (Etzenhouser et al. 1998). However, the foraging behaviour of an herbivore is the outcome of numerous variables and processes, and both intrinsic and extrinsic constraints arise for browsers trying to feed in the "best" way (Perry and Pianka 1997). These constraints include morphological and physiological characteristics of the animal (Hofmann and Stewart 1972; Hofmann 1989), intraspecific and interspecific competition (e.g. Fritz and de Garine-Wichatitsky 1996), risk of predation (Illius and Fitzgibbon 1994) and weather, as well as the profitability and distribution of food items. In mammalian herbivores, both incisor breadth and energy requirements are related to body size (e.g. Gordon and Illius 1988; Illius and Gordon 1992), and these attributes explain a large amount of the differences in foraging strategies in grazers, and their ecological segregation (Illius and Gordon 1987, 1992). In browsers, body size also determines the access to resources on different tree or bush height strata (du Toit 1990; Woolnough and du Toit 2001). Comparing foraging decisions in browsers differing in body size may thus provide insights on differences in foraging decision rules, as well as hypotheses on mechanisms of resource partitioning.

Early studies documenting the feeding patterns of African browsers (Lamprey 1963; Jarman 1972; Leuthold 1978) suggested that resource partitioning was an explanation for the coexistence of species; competition was implicitly assumed to be the cause of the contrasting foraging patterns (McNaughton and Georgiadis 1986), and several mechanisms operating at different scales have been invoked: habitat use, choice of plant categories, plant species or plant parts and feeding height.

Several detailed studies have been carried out on greater kudu (*Tragelaphus strepsiceros*, a large browser with females weighing up to 180 kg) and impala (*Aepyceros melampus*, a medium-size selective mixed feeder with females weighing up to 50 kg), two relatively common antelope species in Eastern and Southern Africa. They demonstrate that sympatric kudu and impala usually differ in their habitat and food preferences, but also concluded that "Acacia habitats" are preferred by both species, at least seasonally (Jarman 1972; Fritz et al. 1996), and that several tree species, including *Acacia nilotica* and *Dichrostachys cinerea*, are also preferred by both species (Owen-Smith and Novellie 1982; Owen-Smith and Cooper 1987b; Fritz and de Garine-Wichatitsky 1996). Cooper and Owen-Smith (1986) suggested that impala may outcompete kudu on these prickly small-leaved trees, because their smaller mouth allows them to feed at a faster rate. In addition, feeding height stratification among browsing ungulates, suggested by early authors (Lamprey 1963; Leuthold 1978), has been questioned by du Toit (1990),

who found considerable overlap in the feeding height range of browsers, including kudu and impala.

This paper presents the results of a field study to describe the mechanisms of food selection by kudu and impala and evaluate the consequences for resource partitioning between sympatric browsers. Using the tracks left by kudu and impala on an experimental plot of natural bush savanna in Zimbabwe, we evaluated encounter rates and selection of bushes along foraging pathways, and tested for changes in bush preference and foraging path selection of these browsers by manipulating the availability of preferred bush categories.

Materials and methods

The study is based on the recording of tracks left by kudu and impala foraging at night in a study area where the preferred browsing resources (*A. nilotica* and *D. cinerea*) had been identified and mapped. Because of their wary nature and the perturbations induced by the observer, the direct observation of African wild ungulates in their natural habitat is difficult, and detailed studies of their foraging behaviour have often relied on the observation of tame animals (Dunham 1982; Cooper and Owen-Smith 1986; Owen-Smith and Cooper 1987a) or on a relatively limited number of observations (e.g. Fritz and de Garine-Wichatitsky 1996). However, recording tracks in natural habitats can overcome these problems and provide relevant information on the movements and foraging behaviour of wild ungulates. Although the number of bites taken for a given tree cannot be assessed by recording tracks, foraging path characteristics and the frequency of attack of the various bush categories encountered can be accurately monitored.

Study site

This work was conducted in an extensive ranch (Kelvin Grove Ranch, Agricultural and Rural Development Authority) located in the highveld of Zimbabwe (Mashonaland west province; 18°36′08″–18°43′24″S, 30°00′16″–30°05′57″E). The ranch covers 9,400 ha, situated between 1,100 and 1,180 m in altitude, with an average annual rainfall of approximately 650 mm. Three major seasons prevail (Fritz et al. 1996): wet season (November–April); cool-dry season (May–July); and hot-dry season (August–October). The vegetation of the ranch ranges from a wooded savanna to woodland, with four major communities: Miombo woodland *Brachystegia* spp. and *Julbernardia globiflora*), Mopane woodland (*Colophospermum mopane*), Terminalia bush savanna, (*Terminalia sericea*), and some patches of Acacia bush savanna on richer soils (*A. nilotica* and *D. cinerea*).

"Acacia field"

The area selected for the study was frequently visited by both kudu and impala and the ground was almost totally covered in sand and dust. Scattered patches of grass were removed from the study area, but all bush regrowth was carefully preserved. After we levelled the ground and spread some sand in areas where the soil was too compacted, the surface of the "Acacia field" was deemed suitable for a careful recording of ungulate tracks. The area of the field was 35 m×45 m, and included 72 bushes at the beginning of the experiment, both *Acacia nilotica* and *Dichrostachys cinerea* (Fig. 1). Each tree was individually identified and the following characteristics were recorded: coordinates on a map (included in a GIS), species (*A. nilotica* or *D. cinerea*), height and maximum perimeter. Almost all bush had the shape of an upside-down cone, typical of

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trees subjected to heavy utilisation by browsers, and the 72 bushes were split into six different categories according to species and volume:

1. Large *D. cinerea* (LD; volume>1.0 m³, *n*=2).
2. Medium *D. cinerea* (MD; volume 0.1–1.0 m³, *n*=17).
3. Small *D. cinerea* (SD; volume 0.01–0.1 m³, *n*=17).
4. Minute *D. cinerea* (miD; volume<0.01 m³, *n*=25).
5. Large *A. nilotica* (LA; volume>1.0 m³, *n*=6).
6. Medium *A. nilotica* (MA; volume<1.0 m³, *n*=5 including one bush which had an estimated volume of 0.05 m³).

During the course of the study, eight new miD appeared, eight miD grew to the extent that they changed to category SM, seven SM changed to category MD and one MD changed to category LD. This resulted in a slight change of the availability of each bush category, although all *A. nilotica* remained unchanged.

Wild and domestic ungulates

Cattle, *Bos indicus* (mainly Brahman and Afrikander breeds) and *B. taurus* (mainly Simmental) and cross-bred, were raised extensively on the ranch for the purpose of meat production. Wild ungulate species (including impala, greater kudu, common duiker *Sylvicapra grimmia*, blue wildebeest *Connochaetes taurinus* and Burchell's zebra *Equus burchellii*) ranged freely over the whole area of the ranch, as they easily jump over cattle fences. However, only impala, kudu and duiker entered the experimental field during the course of the study, as well as cattle and domestic horses. The most frequent and most abundant species recorded in the field during the study (*n*=217 days) was impala (64% of the time, average 6.1±0.7 individuals), followed by kudu (35% of the time, average 0.9±0.1 individuals) and cattle (28% of the time, average 2.1±0.4 individuals), domestic horses being encountered less frequently (16% of the time, average 0.3±0.1 individuals) and common duiker on rare occasions (5% of the time, average 0.05±0.01 individuals). The effects of these other species on the resources used by impala and kudu are likely to be negligible, as <10% of browse attempt by cattle recorded on the ranch were done on *Acacia* spp. or *D. cinerea* (Fritz et al. 1995), horses never browse and duiker were very rare.

Twig availability per bush categories

On two occasions (dry season in June 1997 and rainy season in February 1998) measurements were made on each bush in the field in order to estimate food availability for each bush category. All bushes were visited and measured at the same time to account for possible experiment-induced effects that could alter herbivory on visited and manipulated bushes (Cahill et al. 2001). We measured green twigs (available) and recently browsed twigs ("browsing scar" still green), and the total number of twigs potentially available (twigs available+recently browsed). For the smaller trees, exhaustive counts were made, but we had to design a sampling method to estimate the total number of twigs for the larger classes. For the larger classes, we counted the number of twigs included in a 50×50-cm grid applied to the surface of the bush and included all twigs within a maximum depth of 15 cm (considered as an average penetration depth of the herbivores inside *A. nilotica* and *D. cinerea*, as both species have thorns which efficiently prevent the penetration

Fig. 1 Map of the experimental Acacia field showing the distribution of the different bush categories and two examples of impala and kudu paths (buffer 1 m wide on each side of the path). The size (four classes) and the colour of the dots (*dark grey* for *Dichrostachys cinerea* and *light grey* for *Acacia nilotica*) define six bush categories: large *D. cinerea*, medium *D. cinerea*, small *D. cinerea*, minute *D. cinerea*, large *A. nilotica* and medium *A. nilotica*. Four bushes were removed between phases 1 and 2 (see text)
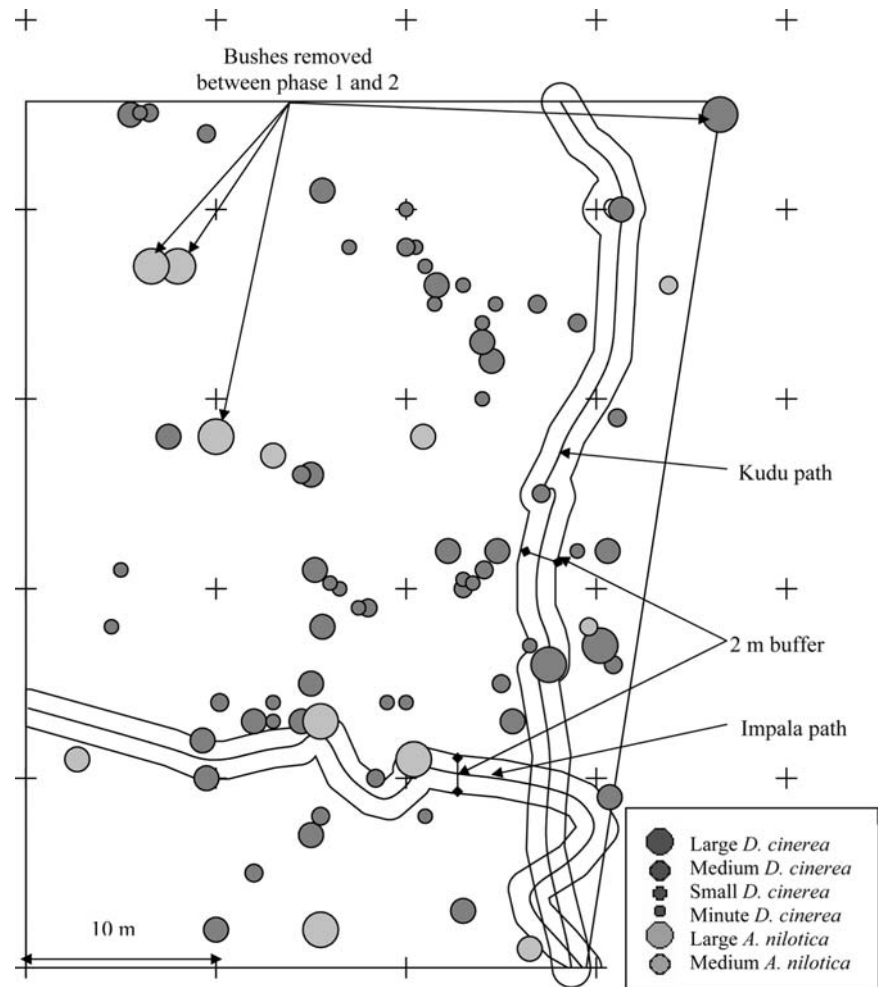
of browsers deep inside the bush). A total of three replicates were placed on different sides of a given bush. The measurements were also stratified according to height (0–50, 50–100, 100–150 and 150–200 cm when available), and the total number of bites was estimated by multiplying the surface area by the average number of bites. For the bigger bushes (LA and LD) the estimated number of twigs available for browsing was different for impala and kudu, as the latter species can feed on items which are out of reach for impala. For LA and LD bush category, we calculated the total number of twigs below 175 cm above ground level, which was considered to be the maximum height for browsing impala, and available twigs between 175 and 210 cm were added to those available below 175 cm for kudu (Leuthold 1978; du Toit 1990; personal observation).

During the course of the study, measurements were made with an electronic precision calliper on the diameter of the scars of freshly browsed twigs eaten during the night. The measurement were recorded only when there was positive evidence that the bite was made by either kudu or impala (visual observation or more often when the bush was visited that night by a single species). This resulted in 54 measurements of bite diameter on *A. nilotica* and *D. cinerea* between March 1997 and October 1998 for kudu and 134 for impala. Values of bite diameter were $\log_{10}$ transformed to homogenise variances (Sokal and Rohlf 1998). A three-way ANOVA was performed to estimate the effects of ungulate species (kudu or impala), bush species (*A. nilotica* or *D. cinerea*) and bush volume (large >1 m^3 or small <1 m^3) on the diameter of bites.

Description of the foraging path recording procedure

The evening preceding every recording session, all tracks were removed from the survey area with a broom. The next morning (between 0630 and 0730 hours) we recorded the total number of animals of each species (including wild ungulates, cattle, dogs and jackals) entering the survey area. We selected one to four focal animals (impala or kudu) for which the path was recorded in detail and reproduced on a map. Data recorded for each focal animal included an estimation of group size (4.43±0.30 for impala; 1.92 ±0.16 for kudu) and each individual bush visited along the path. A bush was considered to be visited when the tracks indicated a change in direction toward the tree (usually with trampling at the base of the tree), a position of the animal which allowed it to feed on the bush or when obvious signs of feeding activities were noticed (recent browsing scars). When we were able to establish, without any doubt, that the focal animal fed on a given tree and that no other animal had browsed it during the same night, we also measured diameters of the browsing scars if available.

In order to check the accuracy of the recording procedure, we verified the information given by the path recorded by an observer with direct visual observations made by two other observers. During nights of full-moon (nine nights between May and November 1997), two observers recorded animal movements and wild ungulates' feeding behaviour from the top of a tree-platform neighbouring the survey area (see Results).

Bush selection

Indices of preference, selectivity and diet overlap were calculated for kudu and impala, as summarised in Fritz et al. (1996). Preference index (P_{ik}) for bush type i of ungulate species k was calculated as in Hunter (1962):

$$P_{ik} = \frac{U_{ik}}{A_i}$$

where A_i is the percentage of bush i on the Acacia field and U_{ik} the percentage of bush i eaten by species k.

The overall degree of selectivity (S_k of ungulate species k) was calculated following Duncan (1983):

$$S_k = \sum |U_{ik} - A_i|$$

Diet overlap (O_{jk}) between ungulate species j and k was calculated according to Pianka's (1973) Niche Overlap formula:

$$O_{jk} = \frac{\sum_i U_{ij} \times U_{ik}}{\sqrt{\sum_i U_{ij}^2 \times \sum_i U_{ik}^2}}$$

Path analysis and bush encounter rates

Encounter rates with the various bush categories along each path were calculated using a GIS (Mapinfo Professional 7.0). Each bush, for which the trunk was included within a buffer 1 m wide on each side of the observed path, was considered to be encountered, and we calculated the percentage of bush categories encountered along each path. The proportion of bush categories encountered was transformed using an arcsine transformation, and comparisons between kudu and impala were performed using Student t-test, or with a Mann-Whitney U-test when the data were not normally distributed (Sokal and Rohlf 1998).

Probability of bush consumption along foraging pathways

Binary logistic regression models (Hosmer and Lemeshow 1989) were used to analyse the probability that kudu or impala stopped at various bush categories along the foraging pathways. We tested whether the probability of using a given bush category was dependent on its abundance, the abundance of other bush types, the characteristics of the animal and its environment. Pathways included in the dataset had at least one tree browsed and a minimum distance travelled on the experimental field was set to 15 m (n=128 paths for impala and n=48 paths for kudu). Response variables were coded as binary for the consumption of each bush category: 0=no bush of this category eaten; 1=one or more bushes of this category eaten. Predictor variables included the proportion of bushes of each category along the path (arcsine transformation), as well as two categorical variables coding for group size (three classes) and season (three seasons). Models were selected using a forward stepwise procedure based on the Wald statistic (SPSS 1999). We used the Hosmer-Lemeshow statistic to assess the adequacy of the models following the recommendations of Quinn and Keough (2002). Nagelkerke's R^2 was calculated as an indication of the explanatory power of the model (SPSS 1999).

Manipulation of the availability of bush categories

After 1 year of recordings (March 1997–March 1998; phase 1), we manipulated the availability of the different bush categories in the area by removing some of the larger bushes (LA and LD). Three LA and one LD were removed (Fig. 1). The recording procedure remained unchanged until the end of the experiment in October 1998 (March–October 1998; phase 2).

Results

Accuracy of the method

Direct visual observations were made during a total of nine nights, and the recording of the tracks were performed following the usual procedure the next morn-

ing. On four occasions, no herbivore foraged on the Acacia field and this was correctly recorded by the observer. Six groups of herbivores crossed the field during the remaining five nights. Species and pathways of the target animal were always correctly identified, but group size was under evaluated on three occasions because all the individuals of the group did not walk inside the boundary of the field, although they were correctly assigned to the broad classes used for the analysis. To minimize the underestimation of group size, we only included in our analysis pathways of a length exceeding 15 m. On all occasions the number and the identity of bush browsed by the target animal were correctly identified. However, on one occasion (possibly two because the observer was not sure on one additional occasion), the target animal took a single bite whilst passing by a bush, and this marginal feeding action remained unnoticed when the tracks were recorded.

The method proved to be efficient for monitoring bush selection by sympatric kudu and impala, and allowed the collection of extensive data on foraging pathways and food availability. The main limit was that the number of bites taken from each tree could not be accurately recorded, and the method is probably not suitable in the following cases: (1) areas with frequent rainfall or wind removing or blurring the tracks; (2) high densities of herbivores or other animals (it was difficult to follow the path when there were too many tracks); (3) when sympatric species cannot easily be identified by means of their tracks; (4) in areas with very dense shrub cover (identification of selected bush might be problematic).

Twig availability per bush category

During the dry season, the bush category MD contained the most available twigs for impala (25.8% of all twigs available on the field), followed by LA (22.9%), whereas this hierarchy was inverted for kudu (36.1% for LA and 18.6% for MD) (Table 1). However, LD also represented a significant proportion of all twigs available (14.8%) for kudu, and this bush category also accounted for 30% of all twigs situated above 1.75 m (i.e. considered to be out of reach of impala). During the rainy season, the total number of twigs available to impala was greatly increased (1,456 bites compared to 523 during the dry season). One bush category (MD) represented >50% of the total number of twigs available to impala, whereas for kudu LA also represented >25% of the total number of bites, although MD represented the greater share of the total number of bites available to kudu (42.4%). As for the dry season, LD represented a significant share of the total number of twigs solely available to kudu (24% of all twigs situated above 1.75 m), although this bush category represented only 10.7% of the total number of twigs theoretically available to kudu.

Bite size

Results of three-way ANOVA ($F_{7, 181}$= 11.784, P<0.001; Table 2) indicated that bites were significantly larger for kudu than impala (F=15.294, 1 df, P<0.001) and were taken from the larger bushes (f=4.170, 1 df, P<0.05). However, there was no difference in the average size of bites on *A. nilotica* as compared to *D. cinerea* (F=0.004, 1 df, P>0.05).

Table 2 Bite size (diameter of browsing scars in mm; mean and SD) made by impala and kudu on *A. nilotica* and *D. cinerea* bushes, classified according to volume (large bushes vs. medium, small and minute bushes; see text and Table 1 for abbreviations)

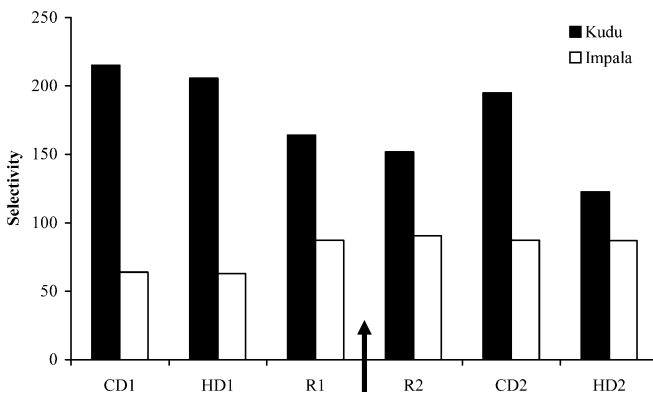| Bush species	Volume	Impala			Kudu		
		n	Mean	SD	*n*	Mean	SD
D. cinerea	L	10	1.24	0.61	29	1.79	0.59
D. cinerea	M, S, Mi	82	1.10	0.41	12	1.33	0.51
A. nilotica	L	19	1.19	0.48	13	1.66	0.53
A. nilotica	M, S	23	1.12	0.30	–	–	–

Table 1 Estimated number of twigs available to impala (0–175 cm) and kudu (0–210 cm) for each bush category measured in the dry season (June 1997) and the rainy season (February 1998). Bush categories (*n,* no. of bush/class), mean number of twigs (Mean no./bush), SD, total number of twigs for each category (Sum) and percentage of the total number of twigs available represented by each category (%). *LD* large *Dichrostachys cinerea*, *MD* medium *D. cinerea*, *SD* small *D. cinerea*, *miD* minute *D. cinerea*, *LA* large *Acacia nilotica*, *MA* medium *A. nilotica*

Season	Bush category	*n*	Impala				Kudu			
			Mean no./bush	SD	Sum	%	Mean no./bush	SD	Sum	%
Dry	LD	2	23.0	10.32	46.0	8.9	53.5	20.41	107.0	14.8
	MD	17	7.9	7.30	134.3	25.8	7.9	7.30	134.3	18.6
	SD	17	3.8	4.29	64.6	12.4	3.8	4.29	64.6	8.9
	miD	25	3.5	3.19	87.5	16.8	3.5	3.19	87.5	12.1
	LA	6	19.8	9.20	118.8	22.9	43.5	23.60	261.0	36.1
	MA	5	13.7	10.71	68.5	13.2	13.7	10.71	68.5	9.5
	Total	72			523				720	
Rainy	LD	3	37.2	18.21	111.6	7.7	63.2	35.79	189.6	10.7
	MD	23	32.8	18.15	754.4	51.8	32.8	18.15	754.4	42.4
	SD	18	10.3	7.64	185.4	12.7	10.3	7.64	185.4	10.4
	miD	24	0.9	1.12	21.6	1.5	0.9	1.12	21.6	1.2
	LA	6	33.7	15.12	202.2	13.9	74.5	38.11	447.0	25.1
	MA	6	30.1	16.09	180.6	12.4	30.1	16.09	180.6	10.2
	Total	80			1,456				1,779	

Preference and diet overlap

Both impala and kudu were selective throughout the experiment (Table 3), stopping at bushes of different categories disproportionately in relation to their availability (impala, phase 1, χ^2=71.47, 5 df, $P<0.001$; impala, phase 2, χ^2=92.68, 5 df, $P<0.001$; kudu, phase 1, χ^2=271.36, 5 df, $P<0.001$; kudu, phase 2, χ^2=177.56, 5 df, $P<0.001$). However, kudu were far more selective than impala (Fig. 2), and tended to be less selective during the rainy season than during the dry season, whereas the opposite was true for impala which tended to be slightly more selective during the rainy season.

MiD were never browsed by kudu (0/70 trees attacked) and only on a few occasions by impala (11/221 trees stopped at), which also occasionally browsed on SD (29/221 trees stopped at), whereas kudu almost never did (2/70 trees stopped at). Kudu showed a very high preference for LD (Fig. 3), although this tended to be lower during the rainy season, and for LA, whereas MD bushes were avoided during the dry season. Preferences of impala for the different bush categories were consistently lower than those of kudu, and they were relatively
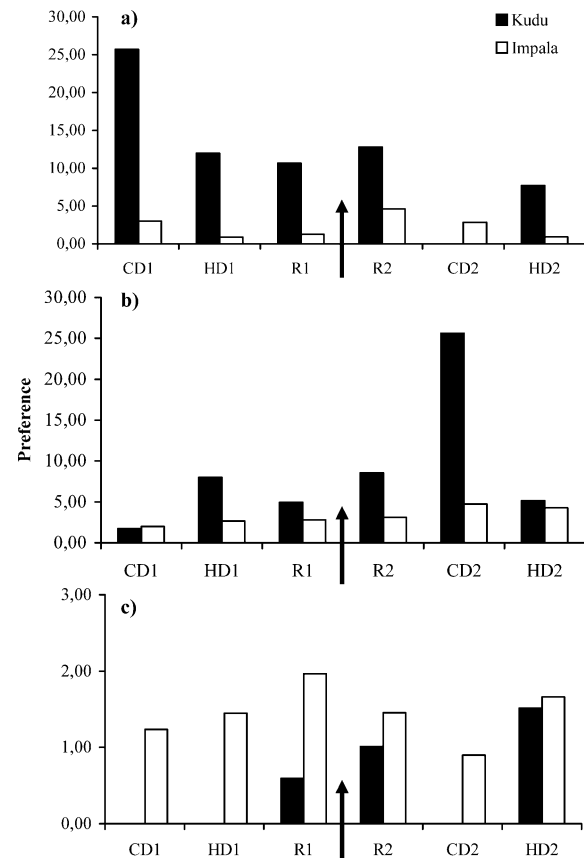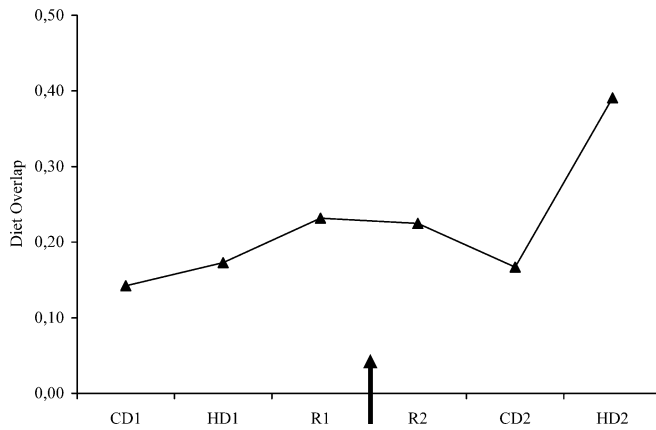
constant according to season, except for LD bushes which were preferred during the cool dry season and less during the rainy season.

Diet overlap between impala and kudu was low, although the decrease in the selectivity of kudu during the rainy season (stopping at a higher proportion at medium and small bushes) resulted in an increase in diet overlap during this period (Fig. 4).

Fig. 2 Selectivity of kudu (*filled bars*) and impala (*open bars*) for *A. nilotica* and *D. cinerea*: seasonal variations and response to manipulation of bush availability in the experimental field. The *arrow* marks the date (18 March 1998) of the modification of the bush availability (see text for details). *CD1* 1st cool dry season (May–July 1997), *HD1* 1st hot dry season (August–October 1997), *R1* rainy season phase 1 (November 1997–March 1998), *R2* rainy season phase 2 (March–April 1998), *CD2* cool dry season phase 2 (May–July 1998), *HD2* 2nd hot dry season (August–October 1998)

Fig. 3 Seasonal variations of the preference of impala and kudu (221 individual trees browsed for 186 impala paths; 70 trees for 79 kudu paths) for the larger bush categories (**a** LD; **b** LA; **c** MD). The *arrow* marks the date (18 March 1998) of the modification of the bush availability (see text for details). For abbreviations, see Fig. 2

Table 3 Number of trees browsed by impala and kudu in each bush category compared with their availability in the study area (see Table 1 for abbreviation of bush category, Fig. 2 for abbreviations of season, and text for results of χ^2). *n* indicates the total no. of individual pathways and the number *in parentheses* the total number of bushes available in the Acacia field

Bush class	Impala						Kudu					
	CD1	HD1	R1	R2	CD2	HD2	CD1	HD1	R1	R2	CD2	HD2
	n=27	n=40	n=39	n=14	n=27	n=39	n=12	n=6	n=24	n=8	n=14	n=15
LD	2 (2)	1 (2)	3 (3)	3 (2)	2 (2)	1 (2)	5 (2)	1 (2)	14 (3)	2 (2)	0 (2)	2 (2)
MD	7 (17)	14 (17)	35 (23)	12 (23)	8 (23)	23 (23)	0 (17)	0 (17)	6 (23)	2 (23)	0 (23)	5 (23)
SD	7 (17)	10 (17)	6 (18)	1 (18)	2 (18)	3 (18)	1 (17)	0 (17)	1 (18)	0 (18)	0 (18)	0 (18)
miD	1 (25)	2 (25)	1 (24)	2 (24)	2 (24)	2 (24)	0 (25)	0 (25)	0 (24)	0 (24)	0 (24)	0 (24)
LA	4 (6)	9 (6)	13 (6)	3 (3)	5 (3)	7 (3)	1 (6)	2 (6)	13 (6)	2 (3)	9 (3)	2 (3)
MA	3 (5)	5 (5)	4 (6)	4 (6)	8 (6)	6 (6)	0 (5)	0 (5)	1 (6)	0 (6)	0 (6)	1 (6)

Fig. 4 Diet overlap between kudu and impala for *A. nilotica* and *D. cinerea* bushes: seasonal variations and response to manipulation of bush availability in the experimental field. The *arrow* marks the date (18 March 1998) of the modification of the bush availability (see text for details). For abbreviations, see Fig. 2

Probability of browsing along foraging pathways

For both kudu and impala, the consumption of larger bush categories (LD and LA) was dependent on the proportion of LD and LA bushes along the foraging pathways (positive values for the parameters estimates) (Table 4). Similarly, for the small or infrequent bush categories (SD, miD and MA) the consumption seems to be either unpredictable (only constant retained in the final models) or essentially linked to the proportion of small bush encountered (%SD). However, the probability of consumption of MD differs markedly between kudu and impala. For kudu, this probability increases when the proportions of large bushes (LA and LD) encountered along the pathways was low, whereas for impala, the probability was dependent on the proportions of MD and LA encountered (increases with %MD but decreases with %LA), as well as on the season (higher probability of consuming MD during the rainy season) and group size (the probability is maximum for a medium group size between two and five individuals).

Encounter rates with bush categories

The proportion of larger bushes encountered by kudu (LD, 6.6%±1.6; LA, 14.2%±2.8) was significantly higher (Mann-Whitney or Student *t*-test, 1 *df*, $P<0.001$ and $P<0.05$, respectively for LD and LA) than for impala (LD, 1.8%±0.3; LA, 8.4%±1.1) (Table 5). In contrast, the proportion of MA encountered by impala was significantly higher than for kudu (Student *t*-test, 1 *df*, $P<0.05$).

Effects of the manipulation of bush availability

The manipulation of trees availability between phases 1 and 2 consisted of the removal of several of the bigger bushes (one LD and three LA) from the experimental Acacia field. This manipulation had little effect on impala foraging choices and pathway characteristics; the proportion of each bush category attacked (Table 3) and the overall selectivity of impala (Fig. 2) were similar during phases 1 and 2.

For kudu, the effects of the manipulation of bush availability varied according to season; during the rainy season of phase 2 the results on bush selection were not conclusive (Table 3) as only six trees were browsed during the rainy season of phase 2 (including two MD). During the following cool dry season, all trees browsed were LA (9/9) indicating a switch in preference between LD and LA (Fig. 3), but a significant number (6/10) of medium bushes (MD and MA) were also browsed during the hot dry season (Table 3). The selectivity of kudu was thus similar between phases 1 and 2 during the rainy season and the cool dry season, but there was a significant decrease in selectivity during the hot dry season of phase 2 (Fig. 2).

Discussion

The ungulate species studied compete for the browse resources, which are important components of their diets especially during the dry season (Dunham 1982; Owen-Smith and Cooper 1987b; Fritz and de Garine-Wichatitsky 1996). For browsers, size of food item is likely to be the limiting factor in large species (Belovsky 1984) and models predict that small browsers and highly selective grazers could exclude large animals because they are able to meet their metabolic requirements on smaller food items (Gordon and Illius 1989, 1996). Impala are more efficient than kudu when feeding on thorny bushes with small leaves (e.g. *A. nilotica* and *D. cinerea*) because their smaller mouth allows them to feed at a higher bite rate (Cooper and Owen-Smith 1986). This is in accordance with what we found during our study, as impala took smaller bites than did kudu on both *A. nilotica* and *D. cinerea*. The depletion of leaves caused by impala feeding on the bushes below 1.75 may force the kudu to lower its use of the most abundant bush category (MD) offering the greatest number of available twigs. On the other hand, kudu had access to a number of bites which were inaccessible to impala because their larger body size allows them to feed in higher strata on the bushes (Owen-Smith and Cooper 1987b), and hence may simply choose large bushes to be able to use this browse stratum. It could also be that the upper branches of the bushes were more profitable because of a higher biomass of leaves per twig (Woolnough and du Toit 1991). However, by efficiently removing the leaves from the lower branches, impala could increase the wood/leaf ratio in the remaining kudu size twigs at lower levels, which would make the upper branches more nutritionally attractive for the kudu (as shown for the giraffe in the Kruger National Park, Cameron and du Toit, unpublished manuscript). When feeding on small twigs as well as leaves, impala would then increase the depletion of potential resources at the

Table 4 Summary results of logistic regression analysis of impala and kudu consumption of each bush category (see legend Table 1 for abbreviations). Models selected following forward selection using Wald statistic (Hosmer-Lemeshow Goodness-of fit and Nagelkerke R^2 are indicated). The value (B) of each parameter (SE in parenthesis below each B-value) is given for the continuous explanatory variable (proportion of each bush category seen along the path, arcsine transformation). Categorical explanatory variables have been recorded and contrasted to reference values (for group size, *0* 1 individual, *1* 2–5 individuals, *2* >5 individuals; for season, *0* cool dry season, *1* hot dry season, *2* rainy season)

Ungulate species	Bush consumed	Goodness of fit				Constant	Parameters estimates (SE)						
		χ^2	df	P	R^2		%LD	%LA	%MD	%MA	%SD	Group size	Season
Impala	LD	0.0485	5	1.0000	0.694	−10.6473* (3.5135)	30.0868* (10.0512)	7.8246* (3.7340)					
	LA	4.4926	5	0.4809	0.578	−4.1223*** (0.7734)	5.1064* (2.2790)	10.3964*** (1.9111)					
	MD	9.4516	8	0.3056	0.427	0.0424 (1.1170)		−4.2708*** (1.0683)	4.5956* (1.6936)			(0)* (1) 1.1407 (2) −0.7311	(0)* (1) −2.2354* (2) −1.1574*
	MA	10.8559	6	0.0929	0.164	−2.7087*** (0.5055)				4.4463** (1.3055)			
	SD	5.2966	8	0.7255	0.216	−4.6583*** (1.1520)	4.2639* (1.6528)				5.4942* (1.9159)		
	miD	–	–	–	0.000	−2.4680*** (0.3293)							
Kudu	LD	0.0000	7	1.0000	0.979	−39.3295 (542.5978)	195.3213 (2,694.6739)	−29.3961 (694.7006)					
	LA	1.3364	7	0.9874	0.920	20.0998 (11.7643)	−34.7944 (17.9600)	22.0064 (11.7446)	−36.9396 (21.3057)				
	MD	7.2199	8	0.5131	0.546	2.3659 (1.3031)	−10.5095* (4.4546)	−12.4803* (4.2848)					
	MA	–	–	–	0.000	−3.1570*** (0.7220)							
	SD	–	–	–	0.000	−3.1570*** (0.7220)							

*$P<0.05$, **$P<0.001$, ***$P<0.0001$ (according to Wald statistic)

Table 5 Proportion of each bush category (mean and SE of mean) visited by kudu and impala during foraging pathways. All trees located in a buffer 1 m wide each side of a foraging pathway (total length >15 m and one or more trees browsed) included. Results of t test or Mann-Whitney U-test performed on the data after arcsine transformation, n indicates the number of paths

	n	LD		MD		SD		LA		MA	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Impala	128	0.018	0.003	0.307	0.012	0.250	0.012	0.084	0.011	0.093	0.009
Kudu	48	0.066	0.016	0.289	0.018	0.209	0.016	0.142	0.028	0.064	0.008
Student t	t			0.800	NS	1.900	NS	−2.283*		2.061*	
Mann–Whitney U	U	−2.991**									

*$P<0.05$, **$P<0.001$, NS $P>0.05$

low and medium browse heights. This would then imply a short-term depletion competition process progressively excluding the kudu.

Kudu showed a consistent, strong preference for the larger *D. cinerea* and *A. nilotica*, and the decision to browse on bushes along foraging pathways was strongly dependent upon the frequency of encounter of these preferred food items. For impala, the decision was more complex, and apparently dependent on the proportions of the various bush categories encountered but also on the season and the size of the foraging group. Fritz and de Garine-Wichatitsky (1996) demonstrated that the number of individuals foraging together influenced foraging choices by impala. This was in part confirmed by the increased probability of stopping at medium bushes when the groups of impala were of intermediate size (two to five individuals), but our recording procedure, using tracks, may result in an underestimation of large groups (see remarks in Results). The foraging decisions of kudu were apparently unaffected by group size, which is not surprising as this antelope usually forages in small groups (average four individuals per group for kudu vs. 10–23 individuals per group for impala depending on resource abundance; Skinner and Smithers 1990).

The comparison of foraging pathways of the two co-existing ungulates, provides evidence that kudu and impala used, and probably perceived, the browse resources in the experimental field in a different manner (Wiens et al. 1995). Etzenhouser et al. (1998) suggested that white-tailed deer (*Odocoileus virginianus*) foraging in an heterogeneous environment increased the proportion of their preferred food item in the foraging path by selecting movement patterns favouring encounters with these bush categories. Our results suggest that kudu did the same, as they had a higher encounter rate with large bushes than did impala, and we speculate that they detected the larger trees (LA and LD) and orientated their movement towards them.

Following the manipulation of the availability of large bushes, we expected little effect on impala foraging choices and pathway characteristics, because the manipulation of bush availability only resulted in a slight change in the proportion of their preferred food item (MD). Accordingly, the proportion of each bush category (Table 3) and the overall selectivity (Fig. 2) were similar for impala during phases 1 and 2 of the study. For kudu,

however, the bush manipulation resulted in a significant reduction of habitat quality (the number of preferred LD and LA was divided by two), which according to the model of Aström et al. (1990) would result in a decrease in the proportion of unbrowsed small trees. As a consequence of the manipulation of the availability of the large bushes in the study area, we expected that kudu would either keep foraging in the area and include more medium bushes in their diet, or leave the area. At first, we observed little change in preference, as kudu selected large and medium bushes (LD, LA, MD), and a shift in preference towards the remaining large *A. nilotica*, which was in accordance with our predictions. However, during the hot dry season when the resources were scarce, the selectivity of kudu decreased and they incorporated some smaller bush categories (MD and MA) in their diet, which is in accordance with theoretical predictions (Aström et al. 1990; Gordon and Illius 1989; Owen-Smith and Novellie 1982).

The niche differentiation between sympatric African browsers, which is likely to reduce the impact of competition, involves differences in preferences for habitats, plant species, plant parts and feeding height (McNaughton and Georgiadis 1986). That feeding height stratification among browsing ungulates allows the coexistence of African browsers has been questioned by du Toit (1990), who found considerable overlap in the feeding height range of the browsers, including kudu and impala. In our case, both plant species (*A. nilotica* and *D. cinerea*) are preferred by both impala and kudu (see also Owen-Smith and Cooper 1987b; Fritz and de Garine-Wichatitsky 1996; Fritz et al. 1996), especially during the dry season. Our results suggest that both impala and kudu select the bushes based on the potential number of bites that they can take from each bush category, as suggested by Fritz and de Garine-Wichatitsky (1996) for impala, but this results in different foraging strategies. Kudu show a strong preference for large bushes, on which they can feed at a higher level than impala and which may also have larger leaves, and tend to orientate their movements to increase encounter rate with these food items. We speculate that an analysis of browsing height between kudu and impala might lead to the conclusion that the overlap is limited, if season and bush height on which bites are made are taken in consideration. Kudu might well browse on *A. nilotica* and *D. cinerea* at levels also accessible to impala, but they

might do so on large bushes, which also provide a number of bites which are out of reach of impala, mainly during periods of low resource abundance. A study of the dynamics of twig selection and browse height on medium and large bushes, and across seasons, may allow for firmer conclusions about this competition process. Our study was conducted on a specific habitat and in a restricted place, whereas the ecological segregation of these two species may in fact be the result of selection processes at other spatial scales (e.g. habitat); however, our results illustrate some of the foraging mechanisms that may allow the coexistence of these two sympatric browser species.

References

Aström M, Lundberg P, Danell K (1990) Partial prey consumption by browsers: trees as patches. J Anim Ecol 59:287–300

Belovsky GE (1984) Moose and snowshoe hare competition and a mechanistic explanation for foraging theory. Oecologia 64:150–159

Cahill JF, Castelli J, Casper B (2001) The herbivory uncertainty principle: visiting plants can alter herbivory. Ecology 82:307–312

Cooper SM, Owen-Smith N (1986) Effects of plant spinescence on large mammalian herbivores. Oecologia 68:446–455

du Toit JT (1990) Feeding-height stratification among African browsing ruminants. Afr J Ecol 28:55–61

Duncan P (1983) Determinants of the use of habitat by horses in a Mediterranean wetland. J Anim Ecol 52:93–109

Dunham KM (1982) The foraging behaviour of impala Aepyceros melampus. S Afr J Wildl Res 12:36–40

Etzenhouser M, Owens MK, Spalinger DE, Murden SB (1998) Foraging behavior of browsing ruminants in a heterogeneous landscape. Landscape Ecol 13:55–64

Fritz H, de Garine-Wichatitsky M (1996) Foraging in a social antelope: effects of group size on foraging choices and resource perception in impala. J Anim Ecol 65:736–742

Fritz H, de Garine-Wichatitsky M, Letessier G, Ducornez S, Chiparo E (1995) The importance of browse for cattle. In: Hofmann RR, Schwartz HJ (eds) Proceedings of the international symposium on wild and domestic ruminants in extensive land use systems. Humboldt University, Berlin, pp 177–184

Fritz H, de Garine-Wichatitsky M, Letessier G (1996) Habitat use by sympatric wild and domestic herbivores in an African savanna woodland: the influence of cattle spatial behaviour. J Appl Ecol 33:589–598

Gordon IJ, Illius AW (1988) Incisor arcade structure and diet selection in ruminants. Funct Ecol 2:15–22

Gordon IJ, Illius AW (1989) Resource partitioning by the ungulates on the Isle of Rhum. Oecologia 79:383–389

Gordon IJ, Illius AW (1996) The nutritional ecology of African ruminants: a reinterpretation. J Anim Ecol 65:18–28

Hofmann RR (1989) Evolutionary steps of ecophysiological adaptations and diversification of ruminants: a comparative view of their digestive systems. Oecologia 78:443–457

Hofmann RR, Stewart DRM (1972) Grazer or browser: a classification based on the stomach structure of and feeding habits of Eastern African ruminants. Mammalia 36:226–240

Hosmer DW, Lemeshow S (1989) Applied logistic regression. Wiley, New York

Hunter RF (1962) Hill sheep and their pasture: a study of sheep grazing in South East Scotland. J Ecol 50:651–680

Illius AW, Fitzgibbon C (1994) Costs of vigilance in foraging ungulates. Anim Behav 47:481–484

Illius AW, Gordon IJ (1987) The allometry of food intake in grazing ruminants. J Anim Ecol 56:989–999

Illius AW, Gordon IJ (1992) Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. Oecologia 89:428–434

Jarman PJ (1972) Seasonal distribution of the large mammals populations in the unflooded middle Zambezi valley. J Appl Ecol 9:283–2299

Lamprey HF (1963) Ecological separation of the large species in the Tarangire Game Reserve, Tanganyika. East Afr Wildl J 1:63–92

Leuthold W (1978) Ecological separation among browsing ungulates in Tsavo East National Park, Kenya. Oecologia 35:241–252

McNaughton SJ, Georgiadis NJ (1986) Ecology of African grazing and browsing mammals. Annu Rev Ecol Syst 17:39–65

Owen-Smith N, Cooper SM (1987a) Assessing food preferences of ungulates by acceptability indices. J Wildl Manage 51:372–378

Owen-Smith N, Cooper SM (1987b) Palatability of woody plants to browsing ruminants in a South African savanna. Ecology 68:319–331

Owen-Smith N, Novellie P (1982) What should a clever ungulate eat? Am Nat 119:151–178

Perry G, Pianka ER (1997) Animal foraging: past present and future. Trends Ecol Evol 12:360–364

Pianka ER (1973) The structure of lizard communities. Annu Rev Ecol Syst 4:53–74

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

Skinner JD, Smithers RHN (1990) The mammals of the Southern African subregion, 2nd edn. University of Pretoria, Pretoria

Sokal RR, Rohlf FJ (1998) Biometry: the principles and practice of statistics in biological research, 3rd edn. Freeman, New York

SPSS (1999) SPSS version 9.0. SPSS, Chicago, Ill.

Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton, N.J.

Wiens JA, Crist TO, With KA, Milne BT (1995) Fractal patterns of insect movement in microlandscape mosaics. Ecology 76:663–666

Woolnough AP, du Toit JT (2001) Vertical zonation of browse quality in tree canopies exposed to a size-structured guild of African browsing ungulates. Oecologia 129:585–590