Aspects of the feeding ecology of a browsing ruminant: the kudu

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Forbs form the preferred dietary component of the kudu *(Tragelaphus strepsiceros)*. This preference was associated with the high nutrient content of their leaves and less fibrous stem material relative to trees and shrubs. Woody browse was most sought after during the early growing season when their new shoots are softest and forbs are least available. Kudus are able to maintain foraging efficiency for most of the year by substituting alternative food species as availability of preferred species declines. Woody species armed with structural defences are preferred during the growing season owing to higher nutrient content in their leaves than in unarmed species. During the dry season when food availability becomes limiting, the preference shifts in favour of species offering highest eating rates. Certain species were consistently rejected despite adequate nutrient levels presumably because of the presence of unidentified chemical deterrents in their leaves.

Forbe is die voorkeur dieetkomponent van die koedoe *(Tragelaphus strepsiceros)*. Hierdie voorkeur spruit uit die hoë voedingswaarde van hul blare en die feit dat hul minder veselrige stammateriaal het in vergelyking met bome en struike. Houtagtige takvoer was die gewildste tydens die vroeë groeiseisoen wanneer die jong lote die sagste is en forbe die minste beskikbaar. Koedoes is in staat om die grootste gedeelte van die jaar effektief te wei deur van alternatiewe voedselspesies gebruik te maak soos die beskikbaarheid van die voorkeur species afneem. Houtagtige spesies bewapen met strukturele beskerming word verkies tydens die groeiseisoen omdat hul blare meer voedingswaarde het as dié van die onbewapende spesies. Tydens die droë seisoen wanneer die beskikbaarheid van kos beperk raak, verskuif die voorkeur na spesies wat die vinnigste vreettempo toelaat. Sekere spesies is voortdurend verwerp ten spyte van voldoende voedingstof vlakke, waarskynlik omdat daar ongeïdentifiseerde chemiese afweermiddels in hul blare voorkom.

Keywords: Feeding ecology, diet, ruminant, browser, kudu

Introduction

Much work has been done on the feeding behaviour and dietary intake of grazing ruminants, both domestic and wild, but relatively little on browsing ungulates under subtropical conditions. In semi-arid savanna regions wild browsers could potentially supplement cattle by making better use of woody plant foliage and also by suppressing the tendency towards bush encroachment which becomes a mounting problem at high stocking densities of grazers.

The greater kudu *Tragelaphus strepsiceros* is a large (180 – 300 kg) browsing antelope which is widely distributed through Africa, from the Cape in the south to Somalia in the north. The studies reported here have been aimed at answering these questions: (i) what are the components of the available food controlling population performance? (ii) what are the factors governing diet selection?

Methods

Field observations have been carried out in two study areas. In the Tshokwane district of the Kruger National Park (KNP) in the eastern Transvaal, the predominant vegetation types are *Acacia nigrescens* savanna on basaltic flats, and *Combretum apiculatum* savanna on rhyolitic slopes. Continuous observations spanning periods of 5 – 43 min were used to record the foraging behaviour of vehicle-habituated kudus. Dietary composition was calculated in terms of the proportionate feeding time devoted to different plant species or categories. All feeding at ground level in the herb layer was assumed to be on forbs. A measure of foraging efficiency was derived from the relation between the feeding time achieved and the number of steps taken while foraging (Owen-Smith, 1979). Food availability was assessed from the densities of particular woody plant species,

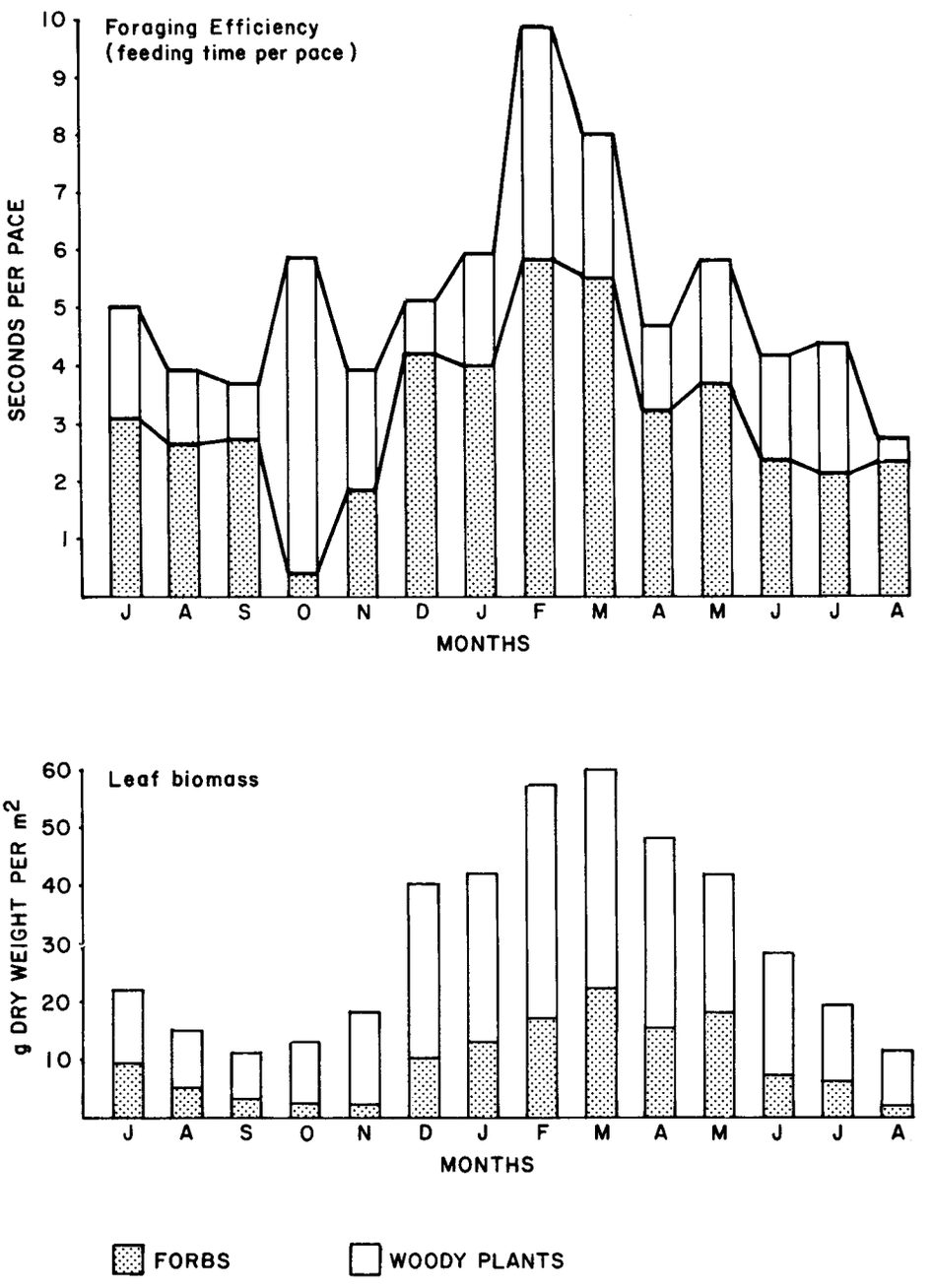

Figure 1 Monthly variations in the foraging efficiency of kudus in the Kruger Park study area in comparison with total leaf biomass for the period July 1976 to August 1977 (from Novellie, in prep).

and from seasonal changes in their leaf mass per unit canopy volume. The standing biomass of forb leaf and terminal stem was measured by harvesting plants from quadrats. Samples of leaves were analysed chemically for their concentrations of crude protein (N × 6,25), phosphorus and calcium at different times of the year.

In the Nylsvley Nature Reserve (NNR) in the northern Transvaal, the vegetation consists of *Burkea africana — Ochna pulchra* savanna on nutrient-poor sands. Hand-reared kudus were observed in a 150 ha enclosure. The feeding sequence of a focal animal was recorded continuously over a period of an hour, while simultaneously, the feeding pathway was marked by a string. Plants accepted and rejected were identified. Biting rates were recorded, and bite sizes estimated. Samples of leaves and terminal stems were collected and are being subjected to chemical analyses for nitrogen, phosphorus, calcium, magnesium, potassium, sodium, cellulose, hemicellulose, lignin and for secondary plant metabolites including tannins, total phenolics, alkaloids, cyanogenic glycosides, saponins and terpenoid resins (still in progress).

Results

Food availability

In the KNP study area, the standing biomass of forb plus woody plant leaves available within the height reach of kudus (2,5 m) varied from a peak of 60 g m^{-2} (dry mass) in March to 11 g m^{-2} at the end of the dry season in September (Figure 1).

Foraging efficiency

The foraging efficiency of kudus varied somewhat less, from about 5 – 10 feeding seconds per step through the wet season and early dry season periods to about 3 – 4 feeding seconds per step at the end of the dry season (Figure 1; see also Owen-Smith, 1979). Seasonal variations in foraging efficiency for the forb component alone were positively correlated with changes in the standing biomass of forb leaf. In contrast, foraging efficiency for woody plant foliage was related not to the abundance of this component, but rather inversely to the quantity of forbs available (Novellie, in prep.).

Diet composition

Forbs formed the principal food category in the KNP study area, but took second place to woody browse in the NNR (Table 1). In the KNP the feeding time devoted to woody plant foliage exceeded that spent feeding in the herb layer only during the early growing season. Grass was eaten in small quantities in the NNR, but in the KNP only when green flush was available following a burn. Fruits, including those of *Sclerocarya caffra* and *Strychnos* spp, and the pods of *Acacia* spp and *Dichrostachys cinerea,* were actively sought when available. At the NNR leaf litter formed a minor dietary addition during the late dry season (Table 1).

A wide variety of forb species was eaten, with creepers such as *Rhynchosia* spp and *Cucumus* spp being most prominent in the KNP. The staple woody species in this area were *Acacia nigrescens* and *Combretum hereroense* during the early wet season, and *C. apiculatum* during the dry season preceding leaf fall. In the NNR *Grewia flavescens* and *Dichrostachys cinerea* were the principal browse species. Evergreen shrubs became important during the late dry season. These included *Euclea divinorum* and *Maytenus heterophylla* in the KNP, and *Strychnos pungens, Euclea undulata* and *E. natalensis* in the NNR. Succulent euphorbias and aloes were also eaten at this time of the year. Certain plant species were rarely eaten despite being commonly available. These included *Pterocarpus rotundifolius* and *Cissus loncerifolia* in the KNP, *Burkea africana* in the NNR, and *Peltophorum africanum, Dombeya rotundifolia* and *Grewia monticola* in both areas.

Table 1 Seasonal changes in diet composition (expressed as percent of feeding time)

	Period							
	Early growing season		Late growing season		Early dormant season		Late dormant season	
	(Oct – Dec)		(Jan – Mar)		(Apr – Jun)		(Jul – Sep)	
Category	KNP	NNR	KNP	NNR	KNP	NNR	KNP	NNR
Woody browse	63	66	30	60	34	53	44	63
Forbs	37	17	60	22	51	21	54	8
Fruits and pods	0	13	10	4	15	20	2	23
Grass	–	4	–	14	–	6	–	0
Leaf litter	–	0	–	0	–	0	–	6

KNP data represents mean of Owen-Smith (1979) and Novellie (in prep.)
NNR data from Cooper & Owen-Smith (in prep.b)

Factors influencing diet selection

The relative acceptance of a plant species was significantly positively correlated with both the crude protein and phosphorus contents of its leaf material during the wet season in the KNP. No correlations between the concentrations of these nutrients and the relative acceptances were found for the dry season (Novellie, in prep.). In the NNR there was a weak positive correlation only with phosphorus contents (Cooper & Owen-Smith, in prep.a).

While structural deterrents such as thorns and spines reduced bite sizes and biting rates to varying degrees, kudus still favoured plants possessing such defences during the wet season. However, the very small-leaved *Acacia tortilis* was eaten relatively little, despite a crude protein content equal to that of the larger-leaved *A. nigrescens.* As the dry season advanced, unarmed plants such as *Combretum* spp became utilized relatively more than the *Acacias* and other prickly species.

No differences in alkaloid contents or in cyanogenic glycosides have been found between accepted and rejected species, with one possible exception: *Grewia monticola* showed a positive response on one alkaloid test, but negative on another. Some of the favoured browse plants such as *Acacia* spp exhibit tannin contents as high as those of rejected species. Work is still in progress to identify other classes of secondary plant metabolite which might influence palatability (Cooper & Owen-Smith, in prep.a).

Conclusions

For kudus, forbs form the preferred dietary component, especially creepers. This seems to be associated both with the relatively high nutrient contents of their leaves, and with the less fibrous nature of their stem material compared with trees and shrubs. Woody browse is most sought after during the early growing season when their new shoots are softest, and also when forbs are least available. Fruits and pods form an important nutrient-rich supplement at certain times of the year. Kudus are able to maintain their foraging efficiency at a high level for most of the year by substituting alternative food species as the availability of preferred species declines. The crucial period in terms of quantitative food abundance spans a two-month period at the end of the dry season, when foraging efficiency drops markedly as a result of leaf fall from deciduous species. Evergreen shrubs, succulents, dry forbs and fallen leaf litter provide important food reserves to carry the animals through this difficult period.

Woody species armed with structural defences are preferred during the growing season because they tend to show higher nutrient contents in their leaves than unarmed species. During the dry season when food availability becomes limiting, kudus shift their preferences in favour of those species offering highest eating rates. At the KNP the dominant woody species in the vegetation were also staple food sources, but this was not so on the nutrient-poor soils of the NNR. Certain species were consistently rejected despite adequate nutrient levels; it is presumed that this rejection is associated with the presence of, as yet, unidentified chemical deterrents in their leaves.

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