Observations on the feeding ecology of impala

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The distribution, habitat preference, and diet of impala in mixed wooded savanna were studied. In the wet season impala were evenly distributed through the different vegetation types and their diet was predominantly grass, but in the dry season they concentrated in areas of *Acacia* savanna and changed to a mainly browsing diet. The amount of grass in the diet was related to plant moisture content and recent effective rainfall. The impala selected succulent food rich in crude protein but preferred grazing to browsing when palatable grass was available. These factors and the presence of fallen *Acacia* pods probably attracted impala to the *Acacia* areas in winter.
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Die verspreiding, habitatsvoorkeur, en dieët van rooibokke in gemengde bossavanne is bestudeer. Gedurende die nat seisoen kom die rooibokke eweredig verspreid in die verskillende plantegroeitipes voor en eet hoofsaaklik gras, maar in die droë seisoen konsentreer hulle in gebiede van *Acacia* savanne en verander na 'n hoofsaaklike blaardieët. Die hoeveelheid gras in die dieët is gekoppel aan plantvoginhoud en onlangse effektiewe reënval. Die rooibokke het sappige voedsel wat ryk was in ruproteïene uitgesoek maar het by voorkeur gewei wanneer smaaklike grasse beskikbaar was. As gevolg hiervan, en die teenwoordigheid van *Acacia* peule, word rooibokke heelwaarskynlik in die winter na *Acacia*-gebiede gelok.
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Impala are found in a wide variety of habitats in both eastern and southern Africa and seem to be particularly versatile feeders, choosing a diet appropriate to local and seasonal conditions. They are invariably mixed feeders taking monocotyledons and dicotyledons, and exhibit reversible structural changes to their stomach linings which enable them to accommodate a considerable variety of foods (Hofmann 1973). The reported mean contribution of dicotyledons to the diet varies from less than 5% (Azavedo & Agnew 1968) to over 95% (Jarman 1971) in different areas, with figures of 35 – 40% being more common (Talbot & Talbot 1962; McAllister & Bornman 1972). Slight or major increases in the use of dicotyledons occur during the dry season (Lamprey 1963; Joubert 1971; Stewart 1971; Mason 1976; Rodgers 1976). The latter suggested that this represented selection for items of the highest nutritional value at a time when general food quality is low. Some relationship between climate, nutrient availability, diet and habitat selection is therefore apparent and this paper examines some of these aspects of impala ecology.

Study area

The observations reported here were made on the Nylsvley Nature Reserve in the northern Transvaal, South Africa (24°40'S 28°43'E) between September 1975 and December 1978. Average annual rainfall in this region is 630 mm, 79% of which falls in the hot summer period from November through March (Huntley & Morris 1978). The study area was situated on gently sloping sandy soils and consisted of about 800 ha of semi-arid, deciduous wooded savanna. The vegetation within this area formed a mosaic of different communities, each with their characteristic species and these have been described by Coetzee, Van der Meulen, Swanziger, Gonsalves and Weisser (1976). In the current paper only the two broad habitat types of most importance to the impala will be briefly described. These were the dominant, but poor quality, *Burkea* savanna and the small areas of *Acacia* community which occurred within the *Burkea* savanna.

The woody component of the *Burkea* savanna consisted of a variety of broad leafed tree and shrub species, notably *Burkea africana, Terminalia sericia, Ochna pulchra, Combretum* spp. and *Grewia flavescens*. The herbaceous layer was dominated by the tall tussock grass *Eragrostis pallens* and the shorter but more palatable *Digitaria eriantha* with *Panicum maximum* being common under trees. This habi-

tat was generally characterized by a great diversity of species and although it could provide reasonable summer forage it offered little in the way of winter grazing for ungulates because by the end of the growing season most of the grasses had become fibrous and unpalatable. In contrast, the patches of *Acacia* savanna were characterized by much lower species diversity but provided better winter grazing. The tree layer in this community consisted almost entirely of the leptophyllous species, *Acacia nilotica, A. tortilis* and *Dichrostachys cinerea* while the herb layer was dominated by two of the more palatable species of *Eragrostis, E. lehmanniana* and *E. rigidior,* with the forb *Solanum panuraeforme* also being abundant. These two plant communities were thus quite different in both structure and species composition and were used in different ways by the impala.

Methods

The distribution of impala was monitored using censuses on 14 occasions during the period of study. These involved 8 — 12 people walking simultaneously through a part of the study area on transects 100 m apart while recording the exact locality of all animals seen. This procedure was repeated until the whole of the study area had been covered. Further data was collected by a single person (R.D. Carr) making daily observations on foot and thus covering the whole area on a monthly basis from September to December 1975 and from April to August 1976. Comparisons of the distribution of impala with vegetation maps gave an index of habitat preference (P = percentage of all impala seen in habitat A, divided by the percentage contribution of habitat A to the total area censused) for different months of the year.

Diet was investigated using three methods described by Monro (1979). The first of these was to microscopically examine the rumen contents of one to four impala shot in unspecified habitats in the study area each month (except March) from February 1975 to February 1976. A sample of the well mixed rumen contents from each impala was physically broken down with a blender and treated with nitric acid and FAA, following Wilson, Hirst and Ellis (1977), before being analysed for species composition under 100X magnification. Epidermal characteristics were used for the identification of 200 fragments in each sample. For the purpose of this paper the results have been arranged into only two plant categories, namely dicotyledons and grasses. The second method was to collect fresh impala dung from the study area on a monthly basis from February 1977 to January 1978 and to analyse this in the same way as the rumen contents. Here, however, single samples were made up of material collected from five to ten separate sites in both *Burkea* and *Acacia* habitats for the purpose of comparing diet in these two savanna types. The third method was to study the feeding of a single, young tame impala ram, kept in a 2 ha enclosure of natural vegetation in the study area. Monthly 24 h behaviour studies were conducted with this individual and during these the distribution of feeding time between different plant species was recorded. These data were converted to specific proportions of dietary intake by measuring biting rates and estimating bite size by hand plucking for each relevant plant species, thus giving an estimate of the dry weight composition of the diet. The crude protein content of the tame impala's simulated diet and of the untreated rumen contents collected from the wild impala was measured using the Kjeldahl method, as recommended by the Association of Official Agricultural Chemists (Horwitz 1965).

Table 1 Preference indices of impala for the *Acacia* and *Burkea* habitats at Nylsvley in different months. n = Total number of impala recorded.
Preference index =
% of all impala seen in habitat A
% contribution of habitat A to total area censused

Month	n	Preference index	
		Acacia	*Burkea*
January	108	0,18	1,22
February	63	0,82	1,17
March	372	1,28	0,69
April	456	4,71	0,51
May	258	3,71	0,54
June	713	3,40	0,67
July	557	5,10	0,48
August	938	1,92	0,63
September	692	4,22	0,34
October	527	2,59	0,40
November	691	1,96	0,82
December	249	2,16	0,88

Table 2 Percentage of dicotyledons in the diet of impala at Nylsvley from analyses of rumen contents and dung collected from *Acacia* and *Burkea* savanna types. n = Number of impala from which rumen contents were taken

Month	n	Rumen contents	*Acacia*	*Burkea*
January	3	28,4	8,5	9,3
February	4	15,3	29,4	10,8
March	—	—	37,7	22,5
April	4	28,3	27,9	13,3
May	2	32,6	34,3	82,9
June	3	40,1	77,4	65,0
July	4	61,5	54,5	69,1
August	2	66,7	66,5	58,1
September	4	35,0	35,6	21,2
October	3	23,2	2,8	11,8
November	1	12,9	—	27,5
December	2	14,8	—	16,4

Results and Discussion

Habitat preference

The preference indices of the impala for the *Acacia* and *Burkea* habitats for each month of the year are shown in Table 1. These figures represent a combination of all the results obtained from the two methods of monitoring distribution. They indicate that although the impala showed some preference for the *Acacia* habitat most of the year, this was especially pronounced during the dry winter months from April to September. In the wetter months they were more evenly distributed through the entire study area.

Diet

Table 2 shows the percentage of dicotyledons found in the rumen contents collected in 1975/76 and in the dung collected in both *Burkea* and *Acacia* savannas in 1977/78 for each month of the year. These results show a change from a predominantly grass diet during the wet summer

months, when the animals were widely dispersed, to a predominantly browse diet at the height of the dry winter season when they were concentrated in the *Acacia* areas. From this one might conclude that the impala moved to the *Acacia* habitat to obtain some desirable browse items which only occurred there, such as fallen *Acacia* or *Dichrostachys* pods, and this may be partly true. However, it is apparent from the results of the faecal analyses that dicotyledons dominated the diet of impala in the *Burkea* savanna a month before they became predominant in the diet in the *Acacia* patches. This indicates that the impala concentrated in the *Acacia* areas because these provided them with palatable grass when the surrounding *Burkea* savanna did not, and that they preferred grazing to browsing if suitable forage was available.

The data in Table 2 also show a difference in the time of peak dicotyledon use in the two years studied. In 1975 the greatest increase in browsing took place between June and July while in 1977 it occurred between April and June. This difference may be attributable to a marked dissimilarity in rainfall in the two years, *viz.* 60 mm in April 1975 and 2 mm in April 1977.

Table 3 shows the proportion of moisture and grass in the simulated diet of the tame impala between April 1977 and February 1978. This table again demonstrates that there was a clear seasonal change from a predominantly grass diet in the wet season to a predominantly browse diet in the dry season and that this appeared to be related to dietary water content. When a power curve was fitted to the data a significant correlation ($p = <0,05$) was found between the percentage of grass in the diet (Y) and dietary moisture content (X).

The equation was

$$Y = 0,30\ X^{1,25}\ (r^2 = 0,83)$$

The moisture content of the diet was also found to be significantly correlated to the previous two months' effective rainfall as defined by Stanley-Price (1977). The percentage of grass in the simulated diet (Y) could also be expressed in terms of this parameter (X = previous two months total precipitation divided by total evapotranspiration for the same period).

The equation relating them was

$$Y = 79,03\ X^{0,23}\ (r^2 = 0,87)$$

A similar significant correlation was not found for the analysed rumen contents or the dung. Nevertheless, it would seem likely that some relationship existed between rainfall and subsequent diet composition.

The percentage of crude protein found in the simulated diet of the tame impala and the rumen contents, used for microscopic analysis, are shown in Table 4. The values for the rumen contents were on average 6,0% higher than those for the simulated diet in corresponding months, but this was probably influenced by the presence of rumen microbiota and recycled urea. The pattern of seasonal change in the two sets of data was also different but both of these differences could have been due to sampling errors in the hand-plucking technique employed. Nevertheless, it is clear that the general level of crude protein in the diet is very high when compared to the level that might be expected in the whole sward or, for instance, to the levels found in the diet of cattle in the same habitat. The latter ranged from 5,7 – 14,1% (Zimmermann 1978). This suggests that the impala were feeding selectively on the high protein components of the available forage.

Table 3 The moisture content (% weight) and proportion of grass (% dry weight) in the simulated diet of the tame impala at Nylsvley

Date	H_2O %	Grass %
5 April 1977	—	68,4
3 May 1977	61,3	54,3
29 May 1977	57,3	30,3
1 July 1977	30,3	12,1
29 July 1977	12,6	9,4
2 September 1977	54,4	73,9
27 September 1977	74,8	65,3
26 October 1977	71,1	63,0
24 November 1977	69,5	57,8
24 January 1978	71,6	79,4
23 February 1978	69,8	68,9

Table 4 Crude protein content (% of organic matter) of the simulated diet of the tame impala and of the rumen contents of wild impala in different months

Month	Tame impala	Rumen contents
January	15,4	24,8
February	15,8	19,8
March	—	—
April	—	25,2
May	13,6	23,6
June	13,1	21,5
July	13,3	18,1
August	10,6	15,9
September	21,3	20,6
October	17,8	22,3
November	16,8	24,8
December	—	28,6

This conclusion is supported by another observation on the feeding habits of the tame impala. During the dry season the diet consisted almost entirely of fallen *Acacia* pods. Of the more abundant species of these *Acacia tortilis* was much preferred to *A. nilotica*. On analysing these pods (without their indigestible seeds) it was found that the former had almost twice the crude protein content of the latter (14,5 cf. 7,3%).

Stanley-Price (1977) showed that crude protein levels in grasses were related to their moisture content and this might account for grasses making up a higher proportion of the impalas' diet during the wet season than during the dry season. However, in terms of crude protein alone the impalas' apparent preference for grazing presents an anomalous situation as dicotyledons generally contain higher levels of nitrogen than grasses. This suggests that the type of crude protein obtained is probably more important than the quantity and that the succulence of grasses is also important, or that other factors are involved.

Conclusions

In the study area impala were found to be mixed feeders whose diet changed from being predominantly grasses in the wet season to predominantly dicotyledons in the dry season. Recent effective rainfall and plant moisture content influenced the timing of this change. They appeared to be selecting succulent food with high levels of crude protein but preferred grazing to browsing when palatable grass was available. These factors, as well as the presence of nutritious seed pods, probably attracted impala to *Acacia* dominated areas of the savanna during the dry season. These observations demonstrate some of the interrelationships between climate, nutrient availability, diet and habitat selection in the ecology of impala.

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