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Seasonal variation in the feeding ecology of black rhinoceros (*Diceros bicornis* L.) in Laikipia, Kenya

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Summary

Daily indirect observations were made on the diet and feeding habits of the black rhinoceros (*Diceros bicornis* L.) on Ol Ari Nyiro Ranch, Laikipia, Kenya over a six-month period. Individual rhinos were followed along their feeding tracks, plants consumed by tracked animals were identified and herbivory quantified.

In total, 9665 individual feeding points were recorded at 1967 feeding stations. At least 103 plant species from at least 37 families were identified as rhino food plants. The diet of black rhinos on Ol Ari Nyiro was at least as species-rich as that in bushland habitats in Tsavo National Park and considerably more species-rich than the diet of rhinos in Masai Mara Reserve. Black rhinos ate selectively and showed a marked reference for *Acacia* species and *Phyllanthus fisheri*. They apparently fed less on each plant in the dry season than in the wet season. This may be due to decreased palatability of food plants, and implies that rhinos may travel further per day in the dry season than in the wet season.

Key words: *Acacia*, diet, Kenya, palatability, rhinoceros, selectivity

Résumé

Pendant six mois, on a fait des observations quotidiennes indirectes des habitudes de régime alimentaire et de mode alimentaire du rhinocéros noir (*Diceros bicornis* L.) au ranch d'Ol Ari Nyiro, à Laikipia, au Kenya. On a suivi individuellement les rhinos le long de leurs pistes de nourrissage, on a identifié les plantes consommées par les animaux suivis et on a quantifié cette consommation.

Au total, on a relevé 9665 points de nourrissage individuels, à 1967 stations de nourrissage. On a identifié dans la nourriture des rhinos un minimum de 103 espèces de plantes, appartenant à un minimum de 37 familles. Le régime alimentaire des rhinos noirs de Ol Ari Nyiro était au moins aussi riche en espéces que celui des habitats de brousse du Parc National de Tsavo et considérablement plus riche que celui des rhinos de la Réserve de Masaï Mara. Les Rhinos noirs se montrent sélectifs et montrent une préférence marquée pour les *Acacia* sp. et pour *Phyllanthus fisheri*. Il semble qu'ils mangent moins de chaque plante pendant la saison sèche que pendant la saison des pluies. Ceci doit être dû au goût moins agréable des plantes alimentaires et implique que les rhinos peuvent se déplacer plus chaque jour en saison sèche qu'en saison des pluies.

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Introduction

Black rhinoceros (*Diceros bicornis* L.) are browsers, feeding mainly on woody vegetation, and have an ability to feed on coarser material than most other herbivores. The feeding behaviour and ecology of black rhinoceros in East Africa have been studied in Ngorongoro and Olduvai (Goddard, 1968), Tsavo National Park (Goddard, 1970) and Masai Mara Reserve (Mukinya, 1977). These studies were carried out in relatively open habitats where visibility was good, and involved direct observations of individual animals feeding on particular plant species at a given time and place. The feeding ecology of black rhinos had not been studied previously in the dense bushlands that comprise their preferred habitats.

Rhinoceros species are endangered throughout their range, largely due to heavy poaching pressure. Conservation strategies for black rhinoceros in Kenya include translocations of animals from areas of low rhino density and from unprotected areas to a series of small, protected rhino sanctuaries. At least one of these sanctuaries (Nakuru National Park) has not been historically host to a large resident black rhino population. On-going studies of the suitability of these areas for translocation depends on detailed knowledge of rhino food plants and feeding behaviour in their preferred natural habitats.

Ol Ari Nyiro Ranch is home to Kenya's largest indigenous population of black rhinoceros, estimated at 45–50 animals. Dense vegetation and intensive anti-poaching activities by ranch personnel have helped protect this population. Their continued survival is therefore central to the future of the species in Kenya. Information on the ecology and behaviour of this population is essential for the conservation and management of black rhinoceros.

Study site and methods

Study area

Ol Ari Nyiro Ranch is located on the western edge of Laikipia District, Kenya, between 36°15′ and 36°30′E and between 0°30′ and 0°45′N. Mean annual rainfall is 700 mm. The ranch covers approximately 37,000 hectares, although the rhino population uses only about a third of this area. The major drainage is the Mukutan River, which flows west through a deep gorge into the Rift Valley and Lake Baringo. A series of man-made dams and the springs feeding the Mukutan River provide water for wildlife, domestic stock and ranch employees. The area varies from wooded grasslands and precipitous scrubby gorges on the west to bushlands and open grass plains in the east (Muasya, Young & Okebiro, 1994). The major vegetation types in the study area are as follows (for plant authorities see Tables 1 and 2).

1 *Combretum* wooded grassland

Wooded grassland covers the areas on the top of most ridges and hills. The vegetation is characterized by scattered trees of *Combretum molle* and *Acacia hockii*. Other common plants are *Solanum incanum, Grewia similis, Bersama abyssinica, Indigofera schimperi, Justicia verticillaris* and *J. diclipteroides*.

2 Gorge scrub
The dense scrub vegetation on the steep gorge walls is strikingly different from the wooded grassland on the ridge tops. It is dominated by *Acacia brevispica*, with large numbers of *Euphorbia kibweziensis, E. candelabrum* and other small *Euphorbia* species. Other species include *Phyllanthus fisheri, Plectranthus zatarhendi, Croton dichogamus, Ecbolium revolutum, Tinnea aethiopica, Ruttya fruticosa, Grewia* spp. and *Sanseveria* spp.

3 *Tarconanthus* (leleshwa) bushland
This habitat covers most flat parts of the study area, with a uniformly dense cover of leleshwa (*Tarconanthus camphoratus*). Other species include *Euclea divinorum, Rhus natalensis, Lantana trimera, Lippia javanica, Tephrosia emeroides, Euphorbia crotonoides, Tinnea aethiopica, Ruttya fruticosa* and *Grewia* spp.

4 *Euclea–Carissa* bushland
This vegetation, dominated by *Euclea divinorum* and *Carissa edulis*, was found on level areas not dominated by leleshwa. Other major plant species include *Rhus natalensis, Acacia hockii, Croton dichogamus, Lantana trimera, Lippia javanica, Ferula communis, Tinnea aethiopica* and *Grewia* spp.

5 Riverine woodland
This vegetation is found mainly along drainage lines leading into the Mukutan Gorge and along the river itself. It forms a narrow strip of tall dense cover in most areas, although some parts are open wooded grasslands, dominated by *Acacia xanthophloea. Acacia gerrardii* and *Phyllanthus fisheri* are common. Additional species include *Hibiscus aponeurus, H. lunarifolius, Conyza sumatrensis, Psiadia punctulata* and *Aspilia mossambicensis.*

These vegetation types are interdigitated throughout the study area, and the home ranges of most rhinos encompassed parts of all five of these communities.

Methods

This study was carried out from June 1987 to January 1988. Rainfall records from the ranch headquarters show that the period from April to August 1987 was relatively wet (mean 99·6 mm/month), and the period from September 1987 to January 1988 was relatively dry (mean 32·5 mm/month). The study period was divided into 'wet' from June to August 1987, and 'dry' from September 1987 to January 1988. During the 'dry' period, the conditions were noticeably drier and most of the annual plants died back.

For two reasons, the rhinos on Ol Ari Nyiro were far less visible than in sites of previous feeding studies (Goddard, 1968, 1970; Mukinya, 1977). First, the ranch vegetation was very dense. Second, the rhinos themselves were extremely shy, rarely venturing into the open except at night. Under these conditions it was not possible to use the direct observational techniques of previous studies.

We therefore developed a practical technique of indirect observation that quantified aspects of rhino feeding ecology. This tracking technique was designed to approximate as closely as possible the methods of Goddard (1968, 1970) and Mukinya (1977). An attempt was made to identify individual rhinos by their tracks, which differed in size and wrinkle patterns. Although this helped avoid

confusion when the tracks of different rhinos crossed, it did not always provide an unambiguous method of individual identification (depending on conditions).

The tracks of a rhino were located early in the morning and the path of feeding was followed until the rhino was located, usually sleeping in mid-morning. Rhinos typically feed during the early morning and late afternoon. If rhinos were located before they had stopped to sleep, it was possible to follow them at a distance as closely as 100 m without disturbing them, depending on bush cover and wind direction. Rhinos were followed at distances ranging from 100 m to 1000 m. Other large browsing species in the study area were eland, (*Taurotragus oryx* (Pallas)), giraffe (*Giraffa camelopardalis* Matschie), and elephant (*Loxodonta africana* (Blumenbach)). However, by following closely behind rhinos and considering only fresh herbivory, it was possible to limit observations to rhino feeding. There were no all-day follows. Afternoon tracking was not done; tracks were found in the morning usually after the individual had begun to feed, and it was not always possible to follow a rhino until the end of its morning feeding period. Therefore, we did not attempt to estimate daily ranging distances.

The rhinos browsed vegetation in a very distinct manner, clipping off twigs and shoots cleanly. As rhino feeding tracks were followed, freshly browsed plants were identified along the track. Each place the rhino stopped to feed was called a 'station', forming a rough semicircle in front of the browsing rhino, whose front legs were stationary (after Goddard, 1968).

Feeding on particular plant species was quantified by counting the number of freshly browsed stem tips, called 'cuts'. A given cut stem could be due to a single bite or to several bites, and bite size could not be quantified (as in previous studies). Although this made most interspecific comparisons inappropriate, it did allow broad estimates of relative importance of various food plants and allowed intraspecific comparisons between seasons.

At each station, data were collected on the number of cuts on each species of food plant, the part(s) eaten and the time and date of the observation. Because a detailed vegetation map was not developed until after the completion of this study (Muasya *et al.*, 1994), the proportion of time spent in each vegetation type was not estimated. Food plants were identified on the spot, if possible. Other food plants were collected in plastic bags and later pressed and dried for identification by the Herbarium of the National Museums of Kenya. Several food plants were not found in a reproductive state and not identified by the Herbarium. These species were assigned local (Kimeru) names provided by the experienced trackers that accompanied the observer. Additional food plant species were recorded when encountered outside of normal data collection periods.

Data were analysed separately for wet and dry periods. More stations were sampled in the dry than in the wet period because the dry period covered more months; sampling intensity did not differ between wet and dry periods. Food plant diversity was calculated using the Shannon index. The number of cuts per station was calculated for each species. All 20 food plant species that were represented by four or more stations in both time periods were included in a *t*-test comparing the number of cuts per station between wet and dry periods.

Results

At least 103 plant species from at least 37 families were eaten by black rhinos on Ol Ari Nyiro, either during specific data collection periods (Table 1) or incidentally (Table 2). Latin names were not determined for fourteen of these plants. Families having at least four representatives were: Acanthaceae (9), Papilionaceae (8), Compositae (7), Euphorbiaceae (6), Mimosaceae (4), Verbenaceae (4), Anacardiaceae (4), Rhamnaceae (4). In total, 9665 individual cuts were recorded at 1967 stations. As in previous studies at other sites, *Acacia* species were important food plants, comprising 27% (wet period) and 36% (dry period) of all stations recorded.

Similar numbers of plant species were eaten during the wet ($N=64$) and dry ($N=63$) periods. However, the diversity of food plants eaten was approximately 15% greater during the wet period than during the dry period (Table 3). This was despite the fact that sample sizes were twice as great during the dry period, which would tend to increase measured species richness. There was a more even distribution of commonly eaten plant species during the wet period than during the dry period. In the wet period there were 21 species that each accounted for at least 1% of the diet, but in the dry season only sixteen species. The two plant species most commonly eaten during the wet season (*Acacia hockii* and *A. brevispica*) accounted for 26% of the wet period stations, whereas the two plant species most commonly eaten during the dry period (*Acacia brevispica* and *Phyllanthus fisheri*) accounted for 46% of the dry period stations (Fig. 1).

The relative importance of food plants differed between wet and dry seasons (Table 1 and Fig 1). Eighteen species were eaten only during the wet period, and seventeen species were eaten only during the dry period. Staple plant species eaten commonly during both wet and dry periods were *Acacia brevispica, A. hockii, Phyllanthus fisheri, Carissa edulis, Tinnea aethiopica* and *Euclea divinorum. Phyllanthus fisheri* and *Acacia brevispica* represented much greater proportions of rhino diet during the dry season than during the wet season. *Phyllanthus fisheri* was favoured early in the dry period and *Acacia brevispica* late in the dry period (Fig. 2). During the wet period, several seasonally available plant species were favoured: *Ferula communis, Indigofera schimperi* and *Asparagus buchananii. Ferula communis* was the most eaten plant early in the wet period, but was not eaten at all during the dry period when this species was completely dry (Fig. 2). Herbaceous species (which included some semiwoody herbs) accounted for 18% of the cuts and 27% of the stations in the wet period, but only 10% of the cuts and 13% of the stations in the dry period (cuts: $\chi^2=128{\cdot}0$, $P<0{\cdot}001$; stations: $\chi^2=62.7$, $P<0{\cdot}001$).

Different plant growth forms were not represented equally well. We conducted an intensive botanical survey of one diverse site within the study area. Of the species on that list, 67% (24/36) of the trees and shrubs, 9% (6/64) of the perennial herbs, and 0% (0/15) of the annual herbs were listed as rhino food plants ($\chi^2=33{\cdot}5$, df=2, $P<0{\cdot}001$). Although it is possible that, in general, rhinos do not eat many annuals or herbs, it is more likely that the presence of these plants in the diet is cryptic, with rhinos eating often entire plants and leaving no evidence behind.

Table 1. Food plants eaten by black rhinoceros during wet and dry periods on Ol Ari Nyiro Ranch, Laikipia, Kenya, based on indirect feeding observations. A=all plant parts eaten; S=stems; T=shoot tips; L=leaves; B=bark

Plant family and species	Growth form	Wet season			Dry season		
		No. of cuts	No. of stations	Part eaten	No. of cuts	No. of stations	Part eaten
ACANTHACEAE							
Barleria micrantha C.B.Cl.	Herb	12	3	A	—	—	—
Ecbolium revolutum/(Lindau) C.B.Cl.	Herb	44	7	A	249	55	A
Hypoestes verticillaris (L.f.) Roem. & Schult.	Herb	—	—	—	68	11	A
Justicia cordata (Nees) T. Anders	Shrub	13	9	A	—	—	—
Justicia diclipteroides Lindau	Herb	12	4	A	8	3	A
Ruttya fruticosa Lindau	Shrub	196	9	A	125	32	A
AGAVACEAE							
Sanseveria sp. 1	Herb	—	—	—	3	3	A
AMARANTHACEAE							
Achyranthes aspera L.	Herb	2	1	A	7	2	A
ANACARDIACEAE							
Lannea schimperi (A. Rich) Engl.	Tree	17	2	A	7	4	A
Ozoroa insignis A. & A. Fernandez	Shrub	1	1	A	—	—	—
Rhus natalensis Krauss	Small Tree	52	14	T	18	6	T
APIACEAE							
Ferula communis L.	Herb	139	51	S	—	—	—
APOCYNACEAE							
Carissa edulis (Forssk.) Vahl	Shrub	201	37	A	401	103	A
CAPPARACEAE							
Boscia angustifolia A. Rich.	Tree	—	—	—	15	2	B/L
CELASTRACEAE							
Mystroxylon aethiopicum Loes.	Tree	13	4	A	—	—	—

Table 1. Continued

Plant family and species	Growth form	Wet season			Dry season		
		No. of cuts	No. of stations	Part eaten	No. of cuts	No. of stations	Part eaten
COMBRETACEAE							
Combretum molle G. Don	Tree	—	—	—	9	4	T
COMMELINACEAE							
Commelina benghalensis L.	Herb	10	2	A	—	—	—
COMPOSITAE							
Aspilia mossambicensis (Oliv.) Wild	Shrub	5	2	A	48	9	A
Conyza sumatrensis (Retz) R.H. Walker	Shrub	43	6	T	—	—	—
Gutenbergia boranensis S. Moore	Herb	11	1	A	2	1	A
Psiadia punctulata D.C. Vatke	Shrub	32	7	A	—	—	—
Vernonia brachycalyx O. Hoffm.	Shrub	41	5	A	39	8	A
CONVOVULACEAE							
Ipomoea kituensis Vatke	Climber	12	7	A	2	2	A
EBENACEAE							
Euclea divinorum Hiern.	Tree	275	38	T	232	50	S
EUPHORBIACEAE							
Croton dichogamus L.	Shrub	—	—	—	70	10	A
Euphorbia candelabrum Trem. & Klotsh	Tree	—	—	—	3	1	S
Euphorbia crotonoides Boiss.	Herb	10	4	A	—	—	—
Euphorbia heterochroma Pax	Climber	3	3	A	—	—	—
Phyllanthus fisheri Pax	Shrub	190	20	A	1552	208	S
ICACINACEAE							
Apodytes dimidiata Arn.	Tree	1	1	T	30	6	T
LABIATAE							
Plectranthus spp.	Herb	—	—	—	16	4	A
Tinnea aethiopica Kotschy. & Peyr.	Shrub	417	44	A	244	53	A

LILIACEAE							
Asparagus buchananii Bak.	Herb	32	11	A	34	17	A
MALVACEAE							
Hibiscus aponeurus Sprague & Hutch.	Herb	23	6	A	16?	5	A
Hibiscus lunariifolius Willd.	Shrub	1	1	A	172	38	A
Malva verticillata L.	Herb	5	1	A	—	—	—
MELIACEAE							
Turraea mombassana C.D.C.	Shrub	3	1	A	—	—	—
MELIANTHACEAE							
Bersama abyssinica Fres.	Shrub	8	3	A	46	9	A
MIMOSACEAE							
Acacia brevispica Harms	Bush	366	58	A	1590	430	A
Acacia gerrardii Benth.	Small Tree	—	—	—	6	4	A
Acacia hockii De Wild.	Small Tree	396	93	T	437	81	T
OCHNACEAE							
Ochna ovata F. Hoffm.	Shrub	2	1	A	14	3	A
OLEACEAE							
Jasminum fluminense Vell.	Climber	17	5	A	27	10	A
Olea europea L. spp. *africana* (Mill) P.C. Green	Tree	14	4	A	24	8	A
PAPILIONACEAE							
Indigofera arrecta A. Rich.	Shrub	16	2	T	11	3	T
Indigofera schimperi Jaub. & Spach.	Herb	72	16	T	26	10	T
Indigofera sp.	Shrub	6	3	A	24	5	A
Neonotonia wightii Lackey	Herb	3	4	A	—	—	—
Tephrosia emeroides A. Rich.	Herb	87	10	A	51	9	A
POLYGONACEAE							
Oxygonum sinuatum (Meism.) Dammer	Herb	4	1	A	—	—	—

Table 1. Continued

Plant family and species	Growth form	Wet season			Dry season		
		No. of cuts	No. of stations	Part eaten	No. of cuts	No. of stations	Part eaten
RHAMNACEAE							
Rhamnus staddo A. Rich	Shrub	—	—	—	19	6	T
Scutia myrtina (Burm. f.) Kurz	Small Tree	16	2	A	6	4	A
RUBIACEAE							
Tarrenna graveolens (S. Moore) Benth.	Herb	—	—	—	9	3	A
Vangueria volkensii K. Schum.	Herb	9	2	A	—	—	—
RUTACEAE							
Clausena anisata (Willd.) Benth.	Shrub	1	1	A	—	—	—
Teclea simplicifolia (Engl.) Verdoon	Shrub	3	1	A	19	4	A
SANTALACEAE							
Osyris abyssinica A. Rich.	Shrub	—	—	—	3	1	A
SOLANACEAE							
Datura stramonium L.	Herb	50	11	A	12	3	A
Solanum incanum L.	Herb	37	9	A	49	20	A
STERCULIACEAE							
Dombeya faucicola K. Schum.	Herb	2	1	A	61	14	A
TILIACEAE							
Grewia mollis A. Juss.	Shrub	128	5	A	25	5	A
Grewia similis K. Schum.	Shrub	58	9	A	101	24	A
VERBENACEAE							
Clerodendrum glabrum E. Mey.	Shrub	1	1	T	2	2	T
Clerodendrum myricoides (Hoechst.) Vatke	Shrub	16	2	A	79	15	A
Lantana sp.	Shrub	40	5	T	6	2	T
Lippia javanica (Burm. f.) Spreng.	Shrub	61	8	T	81	24	T

VITACEAE							
Cyphostemma sp.	Climber	2	1	A	—	—	—
Rhoicissus tridentata Wild & Drum.	Shrub	28	3	A	15	7	T
Insufficiently identified species (Meru names)							
Kiberinchi	—	—	—	—	2	1	A
Lobokoko	—	1	1	A	2	2	A
Munkoro	—	10	2	A	119	20	A
Mukena	—	—	—	—	4	4	A
Murema Muthwa	—	6	2	A	23	6	A
Ndaru (*Sarcostemma* sp.?)	Herb	1	1	A	—	—	—
Ndei	—	1	1	A	2	2	A
Nkaba	—	—	—	—	2	1	A
Muthambia	—	—	—	—	2	2	A
Mware Ngatha	—	—	—	—	49	6	A
Mwereki Wakoma	—	25	3	A	31	5	A
Lobit (Turkana name)	Herb	1	1	A	—	—	—
Mutata	Shrub	—	—	—	11	2	A

Table 2. Additional plant species eaten by black rhinoceros on Ol Ari Nyiro

ACANTHACEAE
Barleria volkensii Lindau
Monechma debile (Forssk.) Nees

AGAVACEAE
Sanseveria sp. 2

ANACARDIACEAE
Rhus vulgaris Meikle

APOCYNACEAE
Acokanthera schimperi (A.D.C.) Benth.

ASCLEPIADACEAE
Cynachum tetrapterum (Turz.) R.A. Dyer
Gomphocarpus fruticosus (L.) Ait. f.

COMPOSITAE
Helichrysum glumaceum D.C.
Vernonia sp. C of Agnew

EUPHORBIACEAE
Erythrococca bongensis Pax

OLEACEAE
Schrebera alata (Hoechst.) Welw.

PAPILIONACEAE
Tephrosia lurida Sond.
Vigna membranacea A. Rich.
Vigna vexillata (L.) Verdc.

POACEAE
Cymbopogon pospischilii (K. Schum.) C.E. Hubbard

POLYGALACEAE
Polygala sphenoptera Fresen

RHAMNACEAE
Helinus mystacinus (Ait.) Steud.
Ziziphus mucronata Willd.

RUBIACEAE
Psydrax schimperiana (A. Rich.) Bridson

Goddard (1970) and Mukinya (1977) noted that black rhinoceros ate all parts of individual plants more often than they ate leaves only, stems only or inflorescences only. On Ol Ari Nyiro, a similar pattern was observed. Rhinos usually ate stems, leaves, inflorescences and shoot tips of the same plants, and often in the case of small herbs, the entire plant.

However, there were exceptions where some parts of some plant species were selected more than other parts by rhinos. For example, only the stems of young *Ferula communis* plants were eaten and the feathery leaves rejected. Entire plants of the herbs *Hypoestes verticillaris* and *Justicia cordata* were uprooted, but only the above-ground parts eaten, leaving the roots behind. Rhinos ate the bark of *Boscia angustifolia* during the height of the dry season; in many cases rhinos tore off the bark of trees with their teeth and horns.

In general, rhinos ate the same parts of particular plant species during both wet and dry periods. Exceptions were the shrubs *Euclea divinorum* and

Table 3. Analysis of food plant data for black rhinoceros on Ol Ari Nyiro Ranch during wet and dry periods. Food plant diversity was calculated using the Shannon index, based on the number of cuts. 'Most eaten shared species' includes all twenty species for which data were available at four or more stations in both the wet and the dry periods. 'Cuts per station' numbers are means ± one standard error

Measure	Wet period	Dry period
Species richness of food plants	64	63
Diversity of food plants:		
based on cuts	3·09	2·66
based on stations	3·18	2·78
Number of cuts	3305	6360
Number of stations	571	1396
Cuts per station:		
all species eaten (N=64,63)	5·03 ± 0·55	3·70 ± 0·23
most eaten shared species(N=20,20)	7·60 ± 1·32	4·00 ± 0·30

Phyllanthus fisheri, of which rhinos ate both stems and leaves during the wet period, but only stems during the dry period. *Phyllanthus fisheri* is deciduous and has no leaves during the dry period. In contrast, the leaves of *Euclea divinorum* are present year-round, but are not eaten during the dry period.

The number of cuts per station can be considered an approximate measure of the amount eaten on particular plants. In most cases, the number of cuts counted was apparently equal to the number of stems eaten. However, *Acacia hockii* was unusual in that rhinos often ate plants extensively to down near the ground below where the stems branched, so that the number of cuts remaining was likely to be less than the number of stems eaten.

There were twenty plant species for which there were considerable data (at least four stations) in both the wet and the dry periods. Of these, nineteen had fewer cuts per station during the dry period than during the wet period (Signs test, $P<0·001$). The lone exception was *A. hockii* (see above). Overall, the number of cuts per station among these species was significantly lower (by an average of 30%) during the dry period than during the wet period (Table 3, $t=5·99$, $P<0·001$).

Discussion

Black rhinoceros are browsers with broad diets wherever they have been studied in East Africa. The list of 103 food plant species identified for Ol Ari Nyiro rhinos falls within the range of studies in Masai Mara (70 spp., Mukinya, 1977), Tsavo (102 spp., Goddard, 1970) and Ngorongoro (191 spp., Goddard, 1968). All of these lists are probably incomplete. Rhinos apparently have the ability to eat a wide variety of plants, at least in small quantities.

We did not collect data on the absolute frequencies of plants in the study area and so did not calculate feeding 'preferences'. However, it is striking that leleshwa (*Tarconanthus camphoratus*) was never recorded as a food plant of rhinos during this study, even during the driest conditions, despite being the dominant plant in much of the study area (Young & Francombe, 1991; Muasya *et al.*, 1994). Even cattle will occasionally eat leleshwa (Young & Francombe,

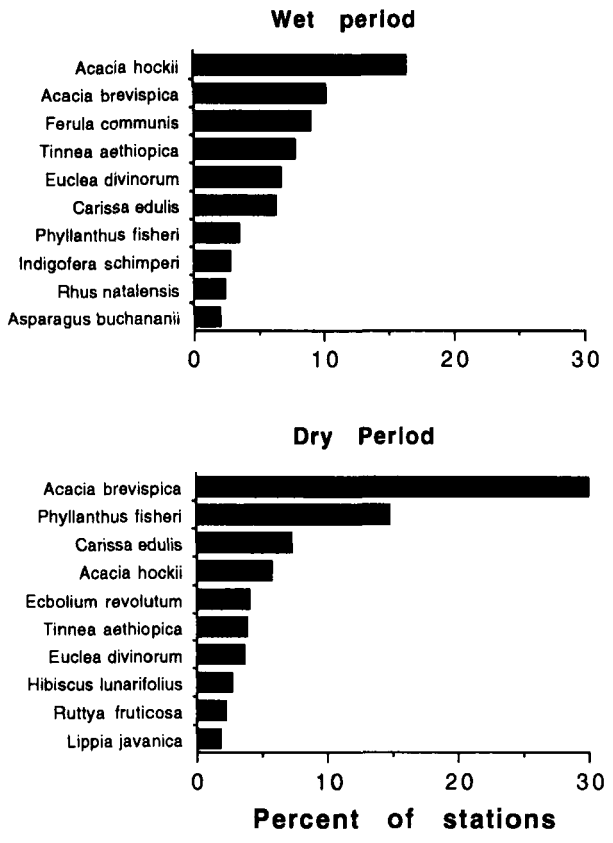

Fig. 1. Percent of stations attributed to each of the ten most commonly eaten plant species during wet and dry periods.

1991). Given the ability of rhinos to feed on species considered 'unpalatable' (at least to cattle), such as *Datura stramonium, Euphorbia* spp., *Sanseveria* spp., and *Euclea divinorum*, the absence of leleshwa from the rhinos' diet is interesting. Leleshwa is rich in aromatic oils such as camphor (P. Waterman, pers. comm.). The ability to leleshwa to form monospecific stands that exclude most other plant species (Young & Francombe, 1991) may be due in part to the competitive advantage provided by their unpalatability to rhinos (and elephants).

Conversely, the availability of particular food plants can effect the movements of rhinos. For example, scattered *Euphorbia candelabrum* trees, although making up a small proportion of the diet, were occasionally highly sought after. Frequently, rhino tracks led straight to individual *E. candelabrum* trees over considerable distances. Similarly, rhinos would make visits to abandoned boma sites where *Datura stramonium* was abundant.

The most common potential competitors of black rhinos in East Africa are probably elephants and giraffes. *Acacia* and *Phyllanthus* spp. are preferred food plants of giraffes (Pellew, 1984; Young & Isbell, 1991), but giraffes tend to avoid dense scrub vegetation favoured by rhinos. Elephants also prefer *Acacia* spp., but eat considerable grass when available (Buss, 1961; Napier & Sheldrick, 1963; Laws & Parker, 1968).

Goddard (1970) suggested that the relative abundance and availability of legume species may be the best indicator of an optimal habitat for black

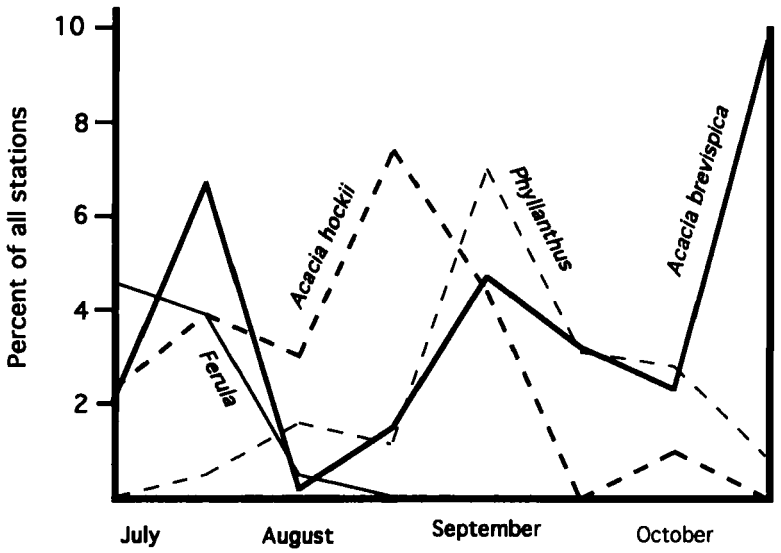

Fig. 2. Change in use of the four most important different food plants over time, as the percent of all feeding stations.

rhinoceros. Similarly, on Ol Ari Nyiro, *Acacia* was the most commonly eaten genus of plants, and rhinos fed most in areas with a high density of low acacias, such as the gorge slopes. Ol Ari Nyiro Ranch has the largest natural population of black rhinoceros in Kenya, and this is apparently due to the occurrence of appropriate food, thick cover and vigorous anti-poaching activity.

There was a tendency in this study for rhinos to feed in the vicinity of water. In the wet period, rhinos fed close to wallow sites and seasonal streams and waterholes. These feeding areas were mainly on the tops and sides of the gorges. In the dry season, when standing water and seasonal streams had dried up, rhinos fed near man-made reservoirs and in the riverine habitat, which retained more water and had a longer persistence of palatable herbs. This led rhinos to be more concentrated during the dry period than during the wet period. These seasonal differences in habitat use may have also influenced observed differences in rhino diet.

Counting cuts and feeding stations cannot measure accurately the absolute amount of material consumed from each plant species (Goddard, 1968, 1970). However, these data do reflect the composition of the diet and allow for comparisons within plant species between wet and dry periods. The indirect method developed here allowed, for the first time, studies of rhino feeding behaviour in the dense scrub that is their preferred habitat.

There are several possible explanations for seasonal changes in rhino diets. First, some food plants are only available during wet periods. These include *Ferula communis, Commelina* spp., *Euphorbia crotonoides, Oxygonum sinuatum* and *Malva verticillata.* As mentioned above, our list of small and annual herbs may well be underestimated relative to woody species. Second, as more favoured plant species become less available during dry periods, rhinos may shift to less palatable species. Third, some species may provide key resources during critical

times, such as succulents during drought. It is difficult to distinguish between the latter two effects.

Lastly, it appears that plants differed in their relative palatability between wet and dry periods (cf Young, 1985). Rhinos ate different plant parts of some plants during different periods. During (wet) periods of plant growth, nutrients may be translocated for development of shoots, leaves, flowers and fruits. In dry periods, nutrients may be translocated to the roots and bark. This may explain the tendency for rhinos to eat the bark of *Boscia angustifolia* and the stems of *Euclea divinorum* during the dry season, and for the leaves of *E. divinorum* to be eaten more during the wet period than during the dry period.

Common rhino food plants exhibited fewer cuts per station during the dry period than during the wet period. This could be due to either fewer palatable plant parts available or to a general decrease in palatability of all parts. If this pattern means that rhinos fed less on each individual plant, it would imply that rhinos travelled farther each day during the dry period and take more time to eat the same amount of food. We did not gather data on ranging distances during this study, so this question must await future research.

Management implications

Although there appears to be no shortage of 'staple' rhino food plants on the ranch, the distribution and seasonal use of particular food plants should be considered in the future management of these rhinos. The movements of rhinos off the ranch into vulnerable areas in time of drought, and the influence that food shortage may have on these movements, are of critical importance to the future of rhinos on Ol Ari Nyiro, and perhaps elsewhere. In 1984, during a severe drought, as many as twenty rhinos wandered off the ranch and were poached (K. Gallmann, C. Francombe, pers. comm.).

Due to the reductions in rhino numbers on the ranch, this wandering in search of food may not be a problem at present, with rhinos occupying only the central third of the ranch. But if continued successful protection of the population and breeding success lead to a larger population, these animals might be under increased pressure to wander in search of sufficient food, particularly during drought. The management may wish to consider providing dry season food around waterholes and salt licks. This could act as lures to reduce the tendency for rhinos to leave the ranch during drought, and could also serve to concentrate the population within the safer centre of the ranch.

The majority of Kenya's rhinos occur on private ranches, which have served as reserves for rhinos removed from vulnerable areas and as sources for introduction programmes. The fates of these rhinos hinge on the ability of these ranches to effectively manage and protect them. Further research into game movements in these areas, and into effective and affordable barriers to these movements, are a vital necessity.

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References

AGNEW, A.D.Q. (1974) *Upland Kenya Wildflowers*. Oxford University Press, Oxford.

BUSS, I.O. (1961) Some observations on food habits and behaviour of the African elephant. *J. Wildl. Manag.* **6**, 75–80.

DALE, I.R. & GREENWAY, P.J. (1961) *Kenya Trees and Shrubs*. Buchanan's Kenya Estates, Nairobi.

GODDARD, J. (1968) Food preferences of two black rhinoceros populations. *E. Afr. Wildl. J.* **6**, 1–18.

GODDARD, J. (1970) Food preferences of the black rhinoceros in Tsavo National Park. *E. Afr. Wildl. J.* **8**, 145–161.

LAWS,. R.M. & PARKER, I.S.C. (1968) Recent studies of elephant populations in East Africa. *Symp. Zool. Soc. Lond.* **21**, 319–359

MUASYA, J.M., YOUNG, T.P. & OKEBIRO, D.N. (1994) Plant checklist and vegetation map of Ol Ari Nyiro and the Mukutan Gorge, Laikipia, Kenya. *J. E. Afr. Nat. Hist.*, in press.

MUKINYA, J.G. (1977) Feeding and drinking habits of the black rhinoceros in Masai Mara Game Reserve. *E. Afr. Wildl. J.* **15**, 125–138.

NAPIER, D. & SHELDRICK, D.L.W. (1963) Some preliminary observations on the food of elephant in the Tsavo Royal National Park (East) of Kenya. *E. Afr. Wildl. J.* **1**, 40–53.

PELLEW, R.A.P. (1984) Food consumption and energy budgets of the giraffe. *J. appl. Ecol.* **21**, 141–159.

YOUNG, T.P. (1985) Herbivory, mortality, and size at reproduction in *Lobelia telekii*: variation with growth rate. *Ecology* **66**, 1879–1883.

YOUNG, T.P. & FRANCOMBE, C. (1991) Growth and yield estimates in natural stands of leleshwa (*Tarconanthus camphoratus*). *For. Ecol. Manage.* **41**, 309–321.

YOUNG, T.P. & ISBELL, L.A. (1991) Sex differences in giraffe feeding ecology: energetic and social constraints. *Ethology* **87**, 79–89.

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