

FOOD PREFERENCES OF BLACK RHINOCEROS IN THE TSAVO NATIONAL PARK

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SUMMARY

Food preferences of the black rhinoceros population in Tsavo National Park, Kenya were studied from 1967 to 1969. Feeding rhinoceros were watched for a period of 1 h, and the plants which they selected and rejected were identified, either as they were feeding or when they had moved on. A technique was used which provided an indication of the relative importance of certain plants in the diet during the wet and dry seasons. A total of 70 h was spent actually watching feeding rhinoceros in six habitat types representative of the changing ecosystem; 3,600 feeding stations were examined. Black rhinoceros were observed eating 102 species from 32 botanical families. In all habitat types the rhinoceros is very selective for herbs and shrubs, and shows a marked preference for legumes. Available grasses are very rarely eaten. Results of food preference studies in other areas of East Africa are compared with the present study. It is suggested that the abundance and distribution of certain kinds of leguminose flora may be the key to an optimum black rhinoceros habitat.

INTRODUCTION

Tsavo National Park, in Kenya, covers an area of some 20,850 km² (8050 sq. miles). Up until about 1950 large areas of the park were covered in *Commiphora* woodland. Sheldrick (1965) stated: "At that time (i.e. 1949) the eastern portion of the park was covered in dense bush consisting for the most part of *Commiphora*, *Delonix*, and *Acacia* with extensive beds of *Sansevieria* growing under the shade of these trees". Under the large-scale destruction by elephant (*Loxodonta africana* (Blumenbach)), the tree-bush complex has been destroyed and thinned in many areas, and has been replaced by bush-grassland and grassland. Annual rainfall varies from 15-76 cm (6-30 in) with a markedly seasonal pattern (Laws, 1967).

During 1967-1969 a study was conducted of the ecology and population dynamics of the black rhinoceros (*Diceros bicornis* (L.)) in Tsavo. Part of the programme was concerned with a study of the food preferences of this mammal in the various habitats of the park. A total of 70 h was spent actually watching feeding rhinoceros in six representative habitat types. Observations were made during both wet and dry seasons.

Destruction by elephant has modified vast areas of Tsavo from woodland to bush-grassland and grassland. Hundreds of thousands of trees have been pushed over and partially eaten or devoured completely. In some parts of the park destruction of the *Commiphora* woodland has been phenomenal (Plate 1a); with the large accumulation of dead and decaying combustible debris present, hot fires sweep through, aided in their spread by the inevitable invasion of the open areas by grasses. These fires retard or destroy regeneration of browse, and these secondary effects are changing the whole ecology of the region.

METHOD

Conventional methods of food-habit determination for large mammals could not be used with this population. The collection of a representative and significant sample of specimens and subsequent analysis of stomach contents is not to be contemplated with the black rhinoceros. Because of the absence of a suitable method of identification of browse items in faecal samples, and the probability of the least-digested browse making up a proportionally greater content

of the faecal bulk, this method was not attempted.

The method used was based on direct observation of feeding rhinoceros, for a unit sample of one complete hour per individual. Data were collected and analysed according to the method described by Goddard (1968). As stressed by that author the method does not give a precise measure of the bulk or volume of each plant species which is consumed, but does provide an indication of the relative importance of the various plant species.

Observations were made from trees, from rocks, from tall termite hills, and on foot using 10×40 binoculars; the plants which the rhinoceros selected were identified either as the animal was feeding or when it had moved on. Because of the myopia of the black rhinoceros the method was practicable. If the wind direction remained favourable, and the animal was not accompanied by red-billed oxpeckers (*Buphagus erythrorhynchus* Stanley), it was sometimes possible to follow behind the feeding rhinoceros at a distance of 35-50 m.

The rhinoceros could usually be kept in sight in most habitat types, but following the animal closely in areas devoid of cover is not advisable. The rhinoceros can detect movement from a considerable distance (<35m) in open areas, and invariably investigates detected movements. The possibility of encountering another rhinoceros concealed from view should also not be overlooked.

HABITAT DESCRIPTION

Pratt *et al.* (1966) show some of the Tsavo vegetation types together with other major vegetation zones of East Africa. Greenway (1969) presents a general description of several major habitat types in the eastern part of the Tsavo National Park. His definitions of three types are as follows:

a. Grassland: land covered with grasses and other herbs generally perennial, sometimes with evergreen or deciduous trees or shrubs, either very scattered or in small isolated groups, in either case not covering more than 10% of the ground.

b. Wooded grassland: land covered usually by perennial grasses and other herbs, with

either evergreen or deciduous, grouped or scattered, armed or unarmed, trees and shrubs that cover less than 50% of the ground. The grasses dominate the aspect, though the trees and shrubs are always conspicuous (Plate 1b). Greenway divided this habitat into three types: grouped-tree grassland, scattered-tree grassland, and shrub or dwarf-tree grassland.

c. Bushland: land covered with more than 50% cover of shrubs or small trees growing densely together. The trees or bushes may be evergreen or deciduous, armed or unarmed. The bushes have no clearly defined boles and may be 2-5 m tall, rarely more. Tall trees are present, occasionally in clumps, but more often as widely scattered individuals.

In this study, habitat 1 is grassland as defined above. Habitats 2, 3, 5 are "wooded grassland", especially "shrub or dwarf-tree grassland"; small parts of these habitats, however, are "bushland". Habitat 4 is mainly "bushland", but has considerable areas of "wooded grassland". Habitat 6 is mainly "bushland".

The location of the habitat types in which observations were made is shown in Figure 1. A description of each type, and the dominant flora available to the feeding rhinoceros, is presented below. Description of the habitat types refers to the floral composition during 1968; densities of black rhinoceros were taken from Goddard (1969).

1. Grassland habitat: Aruba-Buchuma grasslands. Observations were made in the entire area of Tsavo East south of the Voi river. *Commiphora* destruction almost complete; but patches of *Commiphora* scrub present in the south-eastern corner. Essentially open grassland dominated by *Chloris roxburghiana* Schult. Ground herbs are sparse with *Heliotropium* sp. locally common. *Sericocomopsis pallida* (authorities not mentioned in the text are given in the Tables) is locally common. Other shrub growth is scattered and sparse and dominated by *Cordia gharaf*, *Grewia* sp. and *Anisotes parvifolius*. Tree cover is extremely sparse with *Platycelyphium voense*, *Melia volkensii* Guerke and *Delonix elata* (L.) Gamble scattered throughout. Regeneration of *Boscia* sp. is locally common. The area is frequently burnt by fires started from the railway; this factor continually retards re-generation of *Commiphora* and certain browse species. Densities of

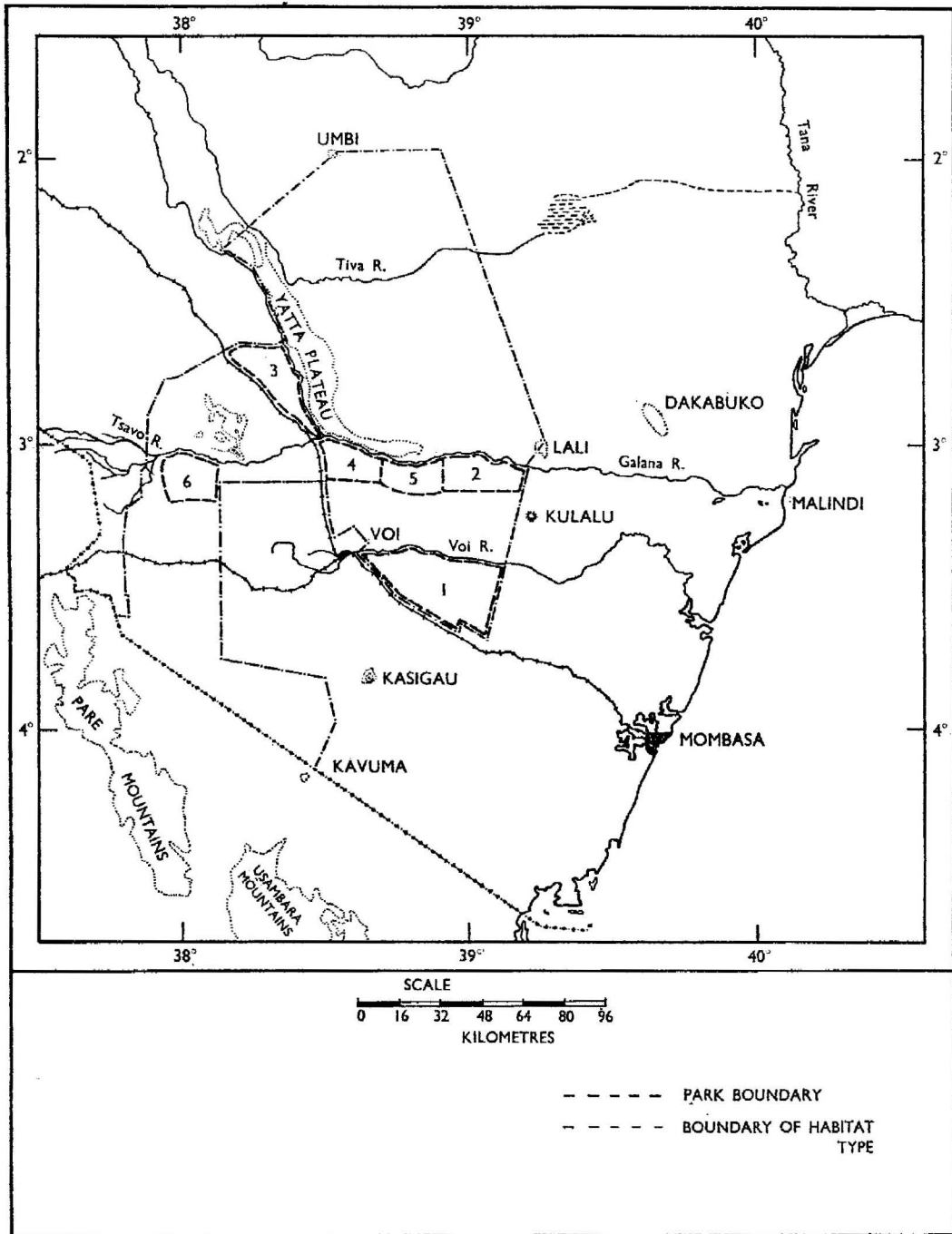


Figure 1
Tsavo National Park showing position of habitat types.

black rhinoceros vary from 1 animal per 6.5 km² to 1/26 km². Distribution of rhinoceros is sometimes clumped; concentrations sometimes occur in the vicinity of flood plains, especially during the dry season.

2. Bush-grassland habitat: Open habitat with *Chloris* sp. locally common. Destruction of mature *Commiphora* complete, and very sparse regeneration of this genus. *Indigofera spinosa* and *Blepharis linearifolia* form an ubiquitous mat, together with *Pupalia lappacea* and *Indigofera schimperi* scattered throughout. *Grewia* sp., *Cordia* sp., *Caucanthus albidus* and *Dirichletia glaucescens* widely scattered with *Sericocomopsis pallida* locally common in some areas. Tree cover extremely sparse with *Dobera glabra* and *Boscia coriacea* scattered throughout. *Lawsonia inermis* locally common on bank fringes of seasonal stream beds. Mean density of black rhinoceros 1/2.4 km².

3. Scrub-bush-grassland habitat: Destruction of mature *Commiphora* complete in southern part, and very little regeneration of this genus. Grasses such as *Schmidtia pappophoroides* Steud. and *Hyparrhenia* sp. very common in open areas. *Indigofera spinosa* and several species of *Tephrosia* abundant. Both species of *Sericocomopsis* present but not common. *Indigofera vohemarensis* very common in sand ravines with *Lawsonia inermis* forming a bank fringe. *Grewia forbesii*, *Grewia lilacina*, *Grewia villosa*, *Hemizygia fischeri*, and *Caesalpinia trothae* scattered throughout. *Boswellia hildebrandtii* regeneration locally common. Tree cover sparse with *Boscia coriacea* common, and *Acacia* and *Delonix elata* scattered throughout. Mean density of black rhinoceros 1/1.1 km².

4. Bush-scrub habitat: Approximately 90% of *Commiphora* is totally destroyed. *Indigofera spinosa* forms an ubiquitous mat throughout, interspersed with *Pupalia lappacea*. *Tephrosia villosa* and other *Tephrosia* spp. are common with *Helinus integrifolius* scattered throughout. *Bauhinia taitensis*, *Dirichletia glaucescens* and *Grewia villosa* are common shrubs with *Grewia forbesii*, *Grewia lilacina*, and *Premna resinosa* locally common. *Indigofera vohemarensis* common in sand ravines. *Schmidtia pappophoroides* colonizing open areas, with *Hemizygia fischeri* locally common. Common trees are *Boscia coriacea* with *Acacia tortilis* and *A. mellifera* scattered throughout. *Lawsonia inermis* common on bank fringes of dry

stream beds. Mean density of black rhinoceros 1/1.1 km².

5. Bush-grassland habitat: Open bush-grassland characterized by *Hyparrhenia* and *Schmidtia pappophoroides*. Destruction of mature *Commiphora* is almost complete, and very little regeneration of this genus. *Indigofera spinosa* is very common, forming an ubiquitous mat throughout, with *Indigofera schimperi* locally common. *Caucanthus albidus*, *Premna resinosa* and *Sericocomopsis pallida* are common shrubs with *Dirichletia glaucescens*, *Caesalpinia trothae* and *Bauhinia taitensis* scattered throughout. *Boscia coriacea* and *Salvadora persica* L. are common trees, with some regeneration of *Acacia*. *Lawsonia inermis* is common on bank fringes of dry stream beds. Mean density of black rhinoceros 1/1.1 km².

6. Bush-woodland habitat: Large areas of climax *Commiphora* woodland. In some areas damage to *Commiphora* and *Sterculia* considerable, and regeneration of former is abundant in open areas. *Grewia lilacina*, *Premna resinosa*, *Grewia* sp. and *Cordia* sp. are common. *Blepharis linearifolia* forms an ubiquitous mat, with an abundance of *Tephrosia villosa* and small patches of *Indigofera arrecta* scattered throughout. *Indigofera vohemarensis* common in sand ravines. In addition to *Commiphora*, *Boscia coriacea* and *Acacia tortilis* are common trees. Mean black rhinoceros density 1/1.1 km².

RESULTS

Tables 1-6 show the food preferences of the black rhinoceros in Tsavo, firstly according to 'h' (the proportional number of hours spent feeding on a plant species) and secondly according to the number of stations at which the species was selected (Goddard, 1968). A station is a hypothetical semicircle in front of the feeding animal in which it can reach the plants available without moving its front feet. No significant differences in the diet were noted according to sex or age, so all observations were combined in this paper. Diets of calves (animals <1 y old) have not been considered in this paper. Observations were made in six habitats during the wet (December-May) season and five during the dry (June-November) season.

TABLE 1

Food preferences of the black rhinoceros in Tsavo (habitat I)

	WET SEASON					DRY SEASON				
	h**	% of total	Stat.	% of total	Part eaten*	h**	% of total	Stat.	% of total	Part eaten*
Acanthaceae										
<i>Anisotes parvifolius</i> Oliv.	0.08	2.0	4	2.8	SL					
<i>Justicia fischeri</i> Lindau	0.88	22.0	44	31.5	A					
Compositae										
<i>Vernonia aemulans</i> Vatke	1.32	33.0	36	25.8	A					
Convolvulaceae										
<i>Ipomoea mombassana</i> Vatke	0.83	20.8	19	13.6	A					
Euphorbiaceae										
<i>Phyllanthus maderaspatensis</i> L.	0.18	4.5	6	4.3	A					
Malvaceae										
<i>Abutilon fruticosum</i> Guill. and Perr.	0.16	4.0	8	5.6	T					
Papilionaceae										
<i>Indigofera arrecta</i> A. Rich.	0.90	45.0	36	45.0	T					
<i>Tephrosia villosa</i> (L.) Pers.	0.98	49.0	39	48.7	A					
<i>Platycelyphium voense</i> (Engl.) Wild	0.02	1.0	1	1.3	T					
Rhamnaceae										
<i>Helinus integrifolius</i> (Lam.) Kuntze	0.08	2.0	4	2.8	A					
Tiliaceae										
<i>Grewia lilacina</i> K. Schum.	0.10	5.0	4	5.0	T					
<i>Grewia</i> sp.	0.18	4.5	6	4.3	T					
Total:	2.00	100	80	100		4.00	100	140	100	

** Proportional number of hours spent feeding on the plant species

* Part of plant eaten:

A = stems, leaves, and inflorescence

I = inflorescence only

L = leaves only

S = stems only

T = tips of shoots

TABLE 2

Food preferences of the black rhinoceros in Tsavo (habitat 2)

	WET SEASON					DRY SEASON				
	h**	% of total	Stat.	% of total	Part eaten*	h**	% of total	Stat.	% of total	Part eaten*
Acanthaceae										
<i>Blepharis linearifolia</i> Pers.						0.31	7.8	8	5.5	A
<i>Justicia fischeri</i> Lindau						0.06	1.5	2	1.3	A
Amaranthaceae										
<i>Aerva persica</i> (Burm. f.) Merr.						0.03	0.8	2	1.3	A
<i>Pupalia lappacea</i> (L.) Juss.	0.05	1.7	4	1.8	A					
<i>Sericocomopsis pallida</i> (S. Moore) Schinz	0.07	2.3	4	1.8	T	0.11	2.7	7	4.8	T
Boraginaceae										
<i>Ehretia teitensis</i> Guerke						0.06	1.5	4	2.7	T
Caesalpiniaceae										
<i>Caesalpinia trothae</i> Harms	0.02	0.7	2	0.9	A	0.70	17.5	28	19.2	A
<i>Cassia longiracemosa</i> Vatke	0.01	0.3	1	0.4	T					
Convolvulaceae										
<i>Ipomoea mombassana</i> Vatke						0.08	2.0	2	1.3	A
Euphorbiaceae										
<i>Euphorbia</i> sp.						0.04	1.0	1	0.7	S
Labiatae										
<i>Leucas</i> sp.	0.02	0.7	1	0.4	A					
Malpighiaceae										
<i>Caucanthus albidus</i> (Nied.) Nied.	0.13	4.3	11	4.9	T					
Malvaceae										
<i>Abutilon fruticosum</i> Guill. & Perr.	0.13	4.3	8	3.5	T					
<i>Hibiscus micranthus</i> L.f.	0.46	15.3	38	16.8	A					
<i>Hibiscus</i> sp.	0.01	0.3	1	0.4	A	0.38	9.5	9	6.1	A
<i>Pavonia zeylanica</i> (L.) Cav.						0.03	0.8	2	1.4	A
Nyctaginaceae										
<i>Commicarpus pedunculatus</i> (A. Rich.) Cuf.						0.11	2.7	3	2.0	A
Papilionaceae										
<i>Indigofera schimperi</i> Jaub. & Spach	0.25	8.3	20	8.9	T	0.03	0.8	2	1.4	T
<i>Indigofera spinosa</i> Forsk.	1.14	38.0	79	35.0	A	1.53	38.2	58	39.7	A
<i>Indigofera vohemarensis</i> Baill.						0.11	2.7	3	2.0	T
<i>Tephrosia villosa</i> (L.) Pers.	0.11	3.7	6	2.6	A	0.21	5.3	5	3.3	A
Rhamnaceae										
<i>Helinus integrifolius</i> (Lam.) Kuntze	0.09	3.0	7	3.1	A					
Rubiaceae										
<i>Dirichletia glaucescens</i> Hiern	0.28	9.3	21	9.3	T					
Solanaceae										
<i>Lycium europaeum</i> L.	0.02	0.7	1	0.4	A	0.06	1.5	2	1.3	A
Sterculiaceae										
<i>Melhania ferruginea</i> A. Rich.						0.01	0.3	1	0.7	A
Tiliaceae										
<i>Grewia forbesii</i> Mast.	0.02	0.7	2	0.9	T					
<i>Grewia lilacina</i> K. Schum.	0.02	0.7	2	0.9	T	0.11	2.6	6	4.0	T
<i>Grewia nematopus</i> K. Schum.	0.02	0.7	1	0.4	T					
<i>Grewia villosa</i> Willd.						0.03	0.8	2	1.3	A
Verbenaceae										
<i>Chascanum hildebrandtii</i> (Vatke) Gillett	0.10	3.3	13	5.8	A					
<i>Premna resinosa</i> (Hochst.) Shauer	0.05	1.7	4	1.8	T					
Total:	3.00	100	226	100		4.00	100	147	100	

** and * — see footnote to Table 1

TABLE 3

Food preferences of the black rhinoceros in Tsavo (habitat 3)

	WET SEASON				
	h**	% of total	Stat.	% of total	Part eaten*
Acanthaceae					
<i>Barleria</i> sp.	0.02	0.2	1	0.2	A
<i>Ecobolium revolutum</i> (Lindau) C.B.C1.	0.52	4.2	20	3.5	A
Amaranthaceae					
<i>Sericocomopsis pallida</i> (S. Moore) Schinz	0.18	1.5	7	1.2	T
Balanitaceae					
<i>Balanites</i> sp.	0.08	0.7	3	0.5	T
Boraginaceae					
<i>Cordia ovalis</i> R. Br.	0.03	0.3	2	0.3	A
<i>Cordia</i> sp.	0.03	0.3	1	0.2	T
<i>Ehretia teitensis</i> Guerke	0.10	0.8	4	0.7	T
Burseraceae					
<i>Boswellia hildebrandtii</i> Engl.	0.03	0.3	2	0.3	T
Caesalpiniaceae					
<i>Bauhinia taitensis</i> Taub.	0.10	0.8	3	0.5	T
<i>Caesalpinia trothae</i> Harms	1.45	12.1	76	13.1	A
<i>Cassia longiracemosa</i> Vatke	0.12	1.0	6	1.0	T
Commelinaceae					
<i>Commelina</i> sp.	0.02	0.2	1	0.2	A
Compositae					
<i>Vernonia aemulans</i> Vatke	0.11	0.9	4	0.7	A
Euphorbiaceae					
<i>Euphorbia</i> sp.	0.02	0.2	1	0.2	S
Malvaceae					
<i>Abutilon fruticosum</i> Guill. & Perr.	0.25	2.1	12	2.1	T
<i>Hibiscus micranthus</i> L.f.	0.23	1.9	11	1.9	A
<i>Hibiscus vitifolius</i> L.	0.18	1.5	8	1.4	A
<i>Pavonia arabica</i> Boiss.	0.13	1.1	5	0.8	A
<i>Pavonia patens</i> (Andr.) Chiov.	0.02	0.2	1	0.2	A
<i>Pavonia zeylanica</i> (L.) Cav.	0.02	0.2	1	0.2	A
Mimosaceae					
<i>Acacia tortilis</i> (Forsk.) Hayne	0.49	4.1	22	3.8	T
Papilionaceae					
<i>Indigofera spinosa</i> Forsk.	1.76	14.6	100	17.2	A
<i>Tephrosia</i> sp.	0.03	0.3	2	0.3	A
<i>Tephrosia villosa</i> (L.) Pers.	3.23	26.8	155	26.7	A
<i>Vigna fragrans</i> Bak.f.	0.16	1.3	10	1.7	A
Rubiaceae					
<i>Dirichletia glaucescens</i> Hiern	0.26	2.2	15	2.6	T
Sterculiaceae					
<i>Melhania ferruginea</i> A. Rich.	0.03	0.3	2	0.3	A
Tiliaceae					
<i>Grewia forbesii</i> Mast.	0.16	1.3	7	1.2	T
<i>Grewia lilacina</i> K. Schum.	0.58	4.8	20	3.4	T
<i>Grewia nematopus</i> K. Schum.	0.98	8.2	48	8.3	T
<i>Grewia villosa</i> Willd.	0.51	4.2	22	3.8	A
Verbenaceae					
<i>Premna resinosa</i> (Hochst.) Shauer	0.17	1.4	9	1.5	T
Total:	12.00	100	581	100	

** and * — see footnote to Table 1

TABLE 4

Food preferences of the black rhinoceros in Tsavo (habitat 4)

	WET SEASON					DRY SEASON				
	h**	% of total	Stat.	% of total	Part eaten*	h**	% of total	Stat.	% of total	Part eaten*
Acanthaceae										
<i>Barleria</i> sp.	0.03	0.8	1	0.4	A					
<i>Crossandra mucronata</i> Lindau						0.09	0.7	2	0.2	A
<i>Ecbolium revolutum</i> (Lindau) C.B.Cl.	0.06	1.5	5	1.9	A	0.23	1.9	9	1.1	A
<i>Justicia fischeri</i> Lindau	0.02	0.5	2	0.8	A	0.24	2.0	13	1.6	A
Amaranthaceae										
<i>Sericocomopsis hildebrandtii</i> (C.B.Cl.) Schinz						0.23	1.9	18	2.2	T
<i>Sericocomopsis pallida</i> (S. Moore) Schinz						0.56	4.7	23	2.8	T
Boraginaceae										
<i>Cordia</i> sp.						0.03	0.3	3	0.4	T
<i>Ehretia tettensis</i> Guerke						0.05	0.4	2	0.2	T
Burseraceae										
<i>Boswellia hildebrandtii</i> Engl.	0.02	0.5	1	0.4	T					
<i>Commiphora</i> sp.	0.03	0.8	2	0.8	T					
Caesalpinjiaceae										
<i>Bauhinia taitensis</i> Taub.						0.08	0.7	4	0.5	T
<i>Caesalpinia trothae</i> Harms	0.19	4.8	11	4.2	A	1.27	10.5	66	8.0	A
<i>Cassia longiracemosa</i> Vatke	0.08	2.0	3	1.2	T					
Compositae										
<i>Vernonia aemulans</i> Vatke	0.01	0.2	1	0.4	A					
Cucurbitaceae										
<i>Cucumis</i> sp.						0.03	0.3	3	0.4	A
Euphorbiaceae										
<i>Euphorbia</i> sp.	0.01	0.2	1	0.4	S					
Malpighiaceae										
<i>Caucanthus albidus</i> (Nied.) Nied.						0.38	3.2	22	2.7	T

TABLE 4 (Continued)

Malvaceae										
<i>Abutilon fruticosum</i> Guill. & Perr.	0.01	0.2	1	0.4	T	0.18	1.5	7	0.8	T
<i>Hibiscus micranthus</i> L.f.	0.32	8.0	18	6.7	A					
<i>Pavonia zeylanica</i> (L.) Cav.						0.34	2.8	34	4.1	A
Papilionaceae										
<i>Crotalaria laburnifolia</i> L.						0.09	0.7	2	0.2	A
<i>Indigofera schimperi</i> Jaub. & Spach	0.04	1.0	2	0.8	T	0.06	0.5	2	0.2	T
<i>Indigofera spinosa</i> Forsk.	1.13	28.2	92	35.1	A	2.04	17.0	134	16.4	A
<i>Indigofera vohemarensis</i> Baill.	0.16	4.0	7	2.7	T					
<i>Tephrosia villosa</i> (L.) Pers.	0.69	17.2	41	15.6	A	2.21	18.4	225	27.5	A
Portulacaceae										
<i>Talinum</i> sp.	0.04	1.0	4	1.5	A					
Rhamnaceae										
<i>Helinus integrifolius</i> (Lam.) Kuntze	0.09	2.3	6	2.3	A	0.38	3.2	25	3.0	A
Rubiaceae										
<i>Dirichletia glaucescens</i> Hiern	0.14	3.5	8	3.0	T	1.05	8.7	70	8.6	T
Solanaceae										
<i>Lycium europaeum</i> L.	0.09	2.3	6	2.3	A	0.69	5.7	39	4.8	A
Tiliaceae										
<i>Grewia forbesii</i> Mast.	0.18	4.5	11	4.2	T					
<i>Grewia lilacina</i> K. Schum.	0.14	3.5	10	3.8	T	0.23	2.0	12	1.5	T
<i>Grewia nematopus</i> K. Schum.	0.09	2.3	9	3.4	T	0.27	2.3	12	1.5	T
<i>Grewia</i> sp.	0.09	2.3	5	1.9	T	0.78	6.5	59	7.2	T
<i>Grewia villosa</i> Willd.	0.01	0.2	2	0.8	A	0.37	3.1	30	3.7	A
Verbenaceae										
<i>Premna oligotricha</i> Bak.						0.03	0.3	2	0.2	T
<i>Premna resinosa</i> (Hochst.) Shauer	0.32	8.0	12	4.6	T	0.09	0.7	2	0.2	T
Zygophyllaceae										
<i>Tribulus terrestris</i> L.	0.01	0.2	1	0.4	A					
Total:	4.00	100	262	100		12.00	100	820	100	

** and * — see footnote to Table 1

TABLE 5

Food preferences of the black rhinoceros in Tsavo (habitat 5)

	WET SEASON					DRY SEASON				
	h**	% of total	Stat.	% of total	Part eaten*	h**	% of total	Stat.	% of total	Part eaten*
Acanthaceae										
<i>Anisotes parvifolius</i> Oliv.	0.11	0.8	4	0.5	SL					
<i>Barleria</i> sp.	0.06	0.4	4	0.5	A					
<i>Ecbolium revolutum</i> (Lindau) C.B.C1.	0.56	4.0	28	3.6	A	0.15	1.4	5	1.4	A
<i>Justicia fischeri</i> Lindau	0.04	0.3	3	0.4	A	0.18	1.7	3	0.8	A
<i>Justicia striata</i> (K1.) Bullock	0.05	0.4	2	0.2	A					
Amaranthaceae										
<i>Aerva persica</i> (Burm. f.) Merr.						0.17	1.5	2	0.6	A
<i>Amaranthus</i> sp.	0.45	3.2	14	1.9	A					
<i>Pupalia lappacea</i> (L.) Juss.	0.06	0.4	3	0.3	A					
<i>Sericocomopsis hildebrandtii</i> (C.B.C1.) Schinz	0.22	1.6	13	1.7	T					
<i>Sericocomopsis pallida</i> (S. Moore) Schinz	0.48	3.4	21	2.7	T	0.16	1.4	6	1.7	T
Boraginaceae										
<i>Cordia ovalis</i> R.Br.						0.02	0.2	1	0.3	A
Burseraceae										
<i>Boswellia hildebrandtii</i> Engl.	0.02	0.1	1	0.1	T					
<i>Commiphora</i> sp. (regen.)	0.11	0.8	10	1.3	T					
Caesalpiniaceae										
<i>Cassia longiracemosa</i> Vatke						0.06	0.5	1	0.3	T
<i>Caesalpinia trochae</i> Harms	0.80	5.7	36	4.7	A	1.80	16.4	59	16.8	A
Compositae										
<i>Vernonia aemulans</i> Vatke	0.05	0.4	3	0.4	A					
Euphorbiaceae										
<i>Euphorbia espinosa</i> Pax						0.37	3.4	9	2.5	A
<i>Euphorbia</i> sp.	0.02	0.1	1	0.1	S	0.02	0.2	1	0.3	S
Labiatae										
<i>Leucas</i> sp.	0.01	t	1	0.1	A					
Liliaceae										
<i>Asparagus</i> sp.	0.07	0.5	4	0.5	A	0.02	0.2	1	0.3	A
Malpighiaceae										
<i>Caucanthus albidus</i> (Nied.) Nied.	0.31	2.2	17	2.2	T	0.15	1.4	6	1.7	T
Malvaceae										
<i>Abutilon fruticosum</i> Guill. & Perr.	0.19	1.3	13	1.7	T	0.20	1.8	6	1.7	T
<i>Hibiscus micranthus</i> L.f.	0.71	5.1	37	4.9	A	0.13	1.2	2	0.6	A
<i>Hibiscus vitifolius</i> L.	0.10	0.7	3	0.4	A					
<i>Pavonia patens</i> (Andr.) Chiov.	0.02	0.1	1	0.1	A					
<i>Pavonia zeylanica</i> (L.) Cav.						0.19	1.7	7	2.0	A

TABLE 5 (Continued)

Mimosaceae											
<i>Acacia tortilis</i> (Forsk.) Hayne	0.04	0.3	2	0.2	T	0.08	0.7	2	0.6	T	
Papilionaceae											
<i>Indigofera schimperii</i> Jaub. & Spach	1.21	8.8	54	7.0	T	0.20	1.8	7	2.0	T	
<i>Indigofera spinosa</i> Forsk.	4.73	33.9	285	36.8	A	3.55	32.3	107	30.4	A	
<i>Tephrosia pumila</i> (Lam.) Pers.	0.65	4.6	32	4.1	A						
<i>Tephrosia villosa</i> (L.) Pers.	0.16	1.1	6	0.8	A	0.73	6.6	32	9.1	A	
Portulacaceae											
<i>Talinum</i> sp.						0.04	0.4	2	0.6	A	
Rhamnaceae											
<i>Helinus integrifolius</i> (Lam.) Kuntze	0.06	0.4	4	0.5	A	0.38	3.4	10	2.8	A	
Rubiaceae											
<i>Dirichletia glaucescens</i> Hiern	1.54	11.1	93	12.1	T	0.48	4.4	20	5.7	T	
Solanaceae											
<i>Lycium europaeum</i> L.	0.11	0.8	9	1.2	A	0.64	5.8	16	4.5	A	
<i>Solanum incanum</i> L.	0.05	0.4	2	0.2	A						
Sterculiaceae											
<i>Sterculia</i> sp.	0.04	0.3	2	0.2	T						
Tiliaceae											
<i>Grewia bicolor</i> Juss.	0.09	0.6	4	0.5	T	0.06	0.5	1	0.3	T	
<i>Grewia forbesii</i> Mast.	0.27	1.9	20	2.6	T	0.06	0.5	3	0.8	T	
<i>Grewia lilacina</i> K. Schum.	0.15	1.1	9	1.2	T	0.67	6.1	24	6.8	T	
<i>Grewia nematopus</i> K. Schum.	0.09	0.6	6	0.8	T	0.22	2.0	10	2.8	T	
<i>Grewia</i> sp.	0.05	0.4	3	0.4	T						
<i>Grewia villosa</i> Willd.	0.04	0.3	2	0.2	A	0.14	1.3	6	1.7	A	
Verbenaceae											
<i>Premna resinosa</i> (Hochst.) Shauer	0.24	1.7	21	2.7	T	0.11	1.0	2	0.6	T	
<i>Premna oligotricha</i> Bak.						0.02	0.2	1	0.3	T	
Vitaceae											
<i>Cissus quadrangularis</i> L.	0.02	0.1	1	0.1	S						
Zygophyllaceae											
<i>Tribulus terrestris</i> L.	0.02	0.1	1	0.1	A						
Total:	14.00	100	775	100		11.00	100	352	100		

** and * — see footnote to Table 1

TABLE 6

Food preferences of the black rhinoceros in Tsavo (habitat 6)

	WET SEASON					DRY SEASON				
	h**	% of total	Stat.	% of total	Part caten*	h**	% of total	Stat.	% of total	Part caten*
Boraginaceae <i>Cordia</i> sp.	0.10	5.0	5	4.2	A					
Malvaceae <i>Abutilon fruticosum</i> Guill. & Perr.						0.10	5.0	5	5.0	T
Mimosaceae <i>Acacia mellifera</i> (Vahl) Benth.						0.10	5.0	5	5.0	T
<i>Acacia tortilis</i> (Forsk.) Hayne						0.10	5.0	5	5.0	T
Papilionaceae <i>Indigofera arrecta</i> A. Rich.	1.05	52.5	57	48.3	T	0.84	42.0	42	42.0	T
<i>Tephrosia villosa</i> (L.) Pers.	0.20	10.0	14	11.9	A	0.44	22.0	22	22.0	A
Tiliaceae <i>Grewia lilacina</i> K. Schum.	0.10	5.0	5	4.2	T					
<i>Grewia</i> sp.	0.30	15.0	20	17.0	T	0.20	10.0	10	10.0	T
Verbenaceae <i>Premna resinosa</i> (Hochst.) Shauer	0.25	12.5	17	14.4	T	0.22	11.0	11	11.0	T
Total:	2.00	100	118	100		2.00	100	100	100	

** and * — see footnote to Table 1

An attempt was made to observe animals feeding in locations which were representative of each habitat type. Rhinoceros feeding on the edge of river banks, near the edge of roads, on rock outcrops or in other atypical locations of the habitat were observed but the results were not included in the analysis. For example, rhinoceros were sometimes observed feeding among the *Suaeda monoica* J. F. Gmel. fringe on the banks of the Galana river. Results of these observations were recorded, but not included in the calculations of relative importance (Tables 1-6).

There is a definite possibility that the data may be biased toward habitat types where topography and cover facilitated observations, i.e. it is far easier to watch a rhinoceros feeding in a semi-open area than in thick cover. In addition, when one is initially searching for a feeding rhinoceros from a distant viewpoint, the chance of detecting an animal feeding in the open is greater than the chance of detecting one feeding in thick cover. However, in Tsavo most habitat types studied were fairly homogeneous, so that I consider that this form of bias did not significantly affect the major conclusions.

Table 1 shows the food preferences of the black rhinoceros in the grassland habitat of Tsavo. This is a low carrying-capacity area for black rhinoceros. In the wet season a very large percentage of the diet was made up of ground legumes; in the dry season a preference for the green herbs *Justicia fischeri*, *Vernonia aemulans*, and *Ipomoea mombasana* was noted. The common shrub *Sericocomopsis pallida* (Plate 2a) was not observed to be eaten; signs of black rhinoceros browsing on this shrub were noted but in relation to its abundance it did not seem to be an important source of food; it might however be important during dry periods. Grasses were not eaten.

Food preferences in one of the bush-grassland habitats of Tsavo are shown in Table 2. Nearly 40% of the diet was made up of the dominant ground legume *Indigofera spinosa* during both seasons of the year. The uncommon legume *Caesalpinia trothae* made up nearly 20% of the diet during the dry season, but less than 1% during the wet season. *Blepharis linearifolia*, a very common constituent of the "mat" complex, made up a very small part of the diet; only green specimens of this plant were selected. Shrubs such

as *Sericocomopsis pallida*, *Caucanthus albidus* and several species of *Grewia* make up a relatively small part of the diet. *Dirichletia glaucescens* appears to be particularly palatable when it is flowering. Grasses were not eaten.

Table 3 shows food preferences of the rhinoceros in the scrub-bush-grassland habitat. No observations were made during the dry season. Leguminose flora constituted 60% of the diet. The abundant *Indigofera spinosa* made up c. 15% of the diet, and a marked preference for the green succulent legume *Tephrosia villosa* was noted. The relatively uncommon *Caesalpinia trothae* made up c. 12% of the diet. Four species of *Grewia* constituted nearly 20% of the diet.

Food preferences in the bush-scrub habitat are shown in Table 4. Nearly 60% of the diet consisted of legumes during the wet season, and c. 50% during the dry season. The common *Indigofera spinosa* made up a large part of the diet. Several species of *Grewia* made up c. 13% of the diet during both seasons of the year. *Hibiscus micranthus* and *Premna resinosa* made up a significant part of the diet during the wet season; the former was not eaten during the dry season and the latter is invariably ignored during this period of the year. Grasses were not eaten.

Table 5 shows food preferences in another bush-grassland habitat. The very common *Indigofera spinosa* constituted approximately one-third of the diet during both seasons of the year. Legumes constituted nearly 60% of the diet during the dry season, and >50% during the wet season. The uncommon legume *Caesalpinia trothae* made up nearly 17% of the diet during the dry season and c. 5% during the wet season. Common shrubs made up a relatively small percentage of the diet. Grasses were not eaten.

Food preferences in the bush-woodland habitat are shown in Table 6. *Commiphora* was not observed to be eaten. In addition, the ubiquitous *Blepharis linearifolia* was not eaten during the recorded observations; one rhinoceros, however, was observed eating this plant on the edge of a road. The animal selected only green specimens from an extensive dry "mat" made up entirely of this species. Over 60% of the diet consisted of legumes during the wet season, and nearly 75% during the dry season. A very

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marked preference for *Indigofera arrecta* was noted.

Table 7 shows a list of 33 additional species eaten by black rhinoceros in Tsavo

TABLE 7

Additional list of plants eaten by black rhinoceros in Tsavo

	Part eaten*
Acanthaceae	
<i>Anisotes ukambensis</i> Oliv.	SL
<i>Barleria stuhlmannii</i> Lindau	A
<i>Blepharis</i> sp.	A
<i>Barleria submollis</i> Lindau	A
<i>Thunbergia alata</i> Sims	A
<i>Thunbergia guerkeana</i> Lindau	A
Amaranthaceae	
<i>Achyranthes aspera</i> L.	A
<i>Digera mucronata</i> (L.) Mast.	A
Boraginaceae	
<i>Cordia gharaf</i> (Forsk.) Aschers.	T
<i>Heliotropium steudneri</i> Vatke	A
Caesalpinaceae	
<i>Cassia</i> sp.	T
<i>Cassia mimosoides</i> L.	A
Chenopodiaceae	
<i>Suaeda monoica</i> J. F. Gmel.	T
Combretaceae	
<i>Combretum aculeatum</i> Vent.	T
Commelinaceae	
<i>Commelina imberbis</i> Hassk.	A
Compositae	
<i>Aspilia</i> sp.	T
Euphorbiaceae	
<i>Croton</i> sp.	A
<i>Euphorbia heterochroma</i> Pax	S
<i>Euphorbia kibwezensis</i> N.E. Br.	S
Gramineae	
<i>Dactyloctenium aegyptium</i> (L.) Beauv.	I
Labiatae	
<i>Coleus lasianthus</i> Guerke	A
<i>Erythrochlamys spectabilis</i> Guerke	T
Loganiaceae	
<i>Strychnos decussata</i> (Pappe) Gilg	T
Lythraceae	
<i>Lawsonia inermis</i> L.	T
Mimosaceae	
<i>Acacia ataxacantha</i> D.C.	T
Papilionaceae	
<i>Crotalaria ukambensis</i> Vatke	A
<i>Indigofera costata</i> Guill. & Perr.	A
<i>Tephrosia noctiflora</i> Bak.	A
<i>Tephrosia subtriflora</i> Bak.	A
Rhamnaceae	
<i>Helinus mystacinus</i> (Lam.) Kuntze	A
Rubiaceae	
<i>Hymenodictyon parvifolium</i> Oliv.	A
Solanaceae	
<i>Solanum dubium</i> Fres.	A
Verbenaceae	
<i>Lantana</i> sp.	T

* — see footnote to Table 1

which are not recorded in Tables 1-6. These were collected from three sources: (a) casual observations; (b) records collected during an uncompleted observation period; (c) observations made in atypical locations of each habitat type (see above).

Plant species which were available but consistently rejected by feeding rhinoceros are shown in Table 8. The small trees *Boscia coriacea* and *Dobera glabra* had remained almost untouched by elephants up to the

TABLE 8

Plants rejected by feeding black rhinoceros

Capparaceae
<i>Boscia coriacea</i> Pax
Labiatae
<i>Hemizygia fischeri</i> (Guerke) Greenway
Salvadoraceae
<i>Dobera glabra</i> (Forsk.) Poir.

end of 1968. Black rhinoceros frequently use them as a source of shade, and for "rubbing", but apparently very rarely, if ever, as a source of food.

DISCUSSION

Black rhinoceros in Tsavo were observed eating 102 species from 32 botanical families. The animal is very selective for herbs and shrubs, and shows a marked preference for legumes. It is interesting to note the preference for leguminose flora by black rhinoceros documented in two other areas of East Africa (Goddard, 1968).

In all habitat types studied in Tsavo black rhinoceros were predominantly "ground" feeders, concentrating between 60 and 80% of their feeding time on relatively small herbs and shrubs. Prominent bushes of the ecosystem such as *Ehretia*, *Bauhinia*, *Premna* and some *Grewia* were eaten but did not appear to be preferred foods, even when available in quantity. The uncommon legume *Caesalpinia trothae* was extremely palatable (Plate 2 b) and eaten in large quantities.

At certain periods of the year, especially during the height of the dry season, rhinoceros were very selective, and only certain specimens of a particular plant species were eaten. Green specimens of a plant species were nearly always selected in preference to dry withered specimens. The legume *Indigofera spinosa*, for example, constitutes a considerable part of the diet in four

habitat types. On many occasions rhinoceros were observed feeding actively in a "mat" of this species, but selecting only the green flowering specimens. This feeding behaviour is particularly noticeable in October, when a large percentage of this plant "mat" has dried and withered. The same behaviour was noted when rhinoceros were observed feeding in an abundant growth of *Blepharis linearifolia*.

As was also noted in two study areas in Tanzania (Goddard, 1968) several species in Tsavo made up a significant part of the diet during the wet season, but only a relatively small part of the diet during the dry season, either because they are unavailable or because they are dry and sterile. In this study, for example, the herb *Hibiscus micranthus* constituted a significant part of the diet during the wet season in three habitat types; during the dry season this plant is invariably rejected. The shrubs *Caucanthus albidus* and *Dirichletia glaucescens* are invariably selected only when in leaf. However, several species of *Grewia* appeared to be eaten to a similar extent during both seasons of the year. *Sericocomopsis pallida*, a locally common shrub of open areas in four habitat types, made up a relatively small part of the diet during both seasons of the year.

Feeding rhinoceros sometimes made frequent use of plants which were regenerating from rhinoceros dung-piles which were situated along well used trails. *Cassia longiracemosa* commonly regenerates from these piles, presumably from viable seeds which passed through the alimentary tract of the animal. This shrub was sometimes heavily utilised by rhinoceros in these locations.

Although black rhinoceros select a very wide variety of herbs and shrubs, their preference for leguminose flora has been recorded in three areas of East Africa under natural conditions. Relatively high densities of black rhinoceros in Tsavo were observed in areas where legumes were relatively abundant. Rhinoceros are present in many areas of Tsavo where leguminose flora are sparse and widely scattered, but in relatively low densities. The fact that the black rhinoceros show a preference for this kind of flora, and that there are high densities of rhinoceros on the soil types (e.g. the lithosols and regosols adjacent to the Athi-Galana river) supporting abundant legumes,

suggests a relationship. It is suggested that the relative abundance and availability of certain legumes may well be the key to an optimum black rhinoceros habitat. Large areas of Tsavo are particularly rich in leguminose flora; Greenway (1969) recorded at least 35 genera and 101 species available in the park.

It must be stressed that interpretation of the data is affected by factors such as plant availability, stage of growth, plant condition, part eaten, and method of feeding. Goddard (1968) discusses these aspects.

Thus on one occasion a feeding rhinoceros visited 94 stations during a 1 h period. The entire diet consisted of legumes; at 92 stations the animal selected *Indigofera spinosa*; in this particular case only terminal shoots were eaten. At the other two stations the rhinoceros totally devoured several branches of two *Caesalpinia trothae* bushes. Calculated on a station basis *Indigofera spinosa* clearly formed the predominant part of the diet; by actual bulk, however, *Caesalpinia trothae* would probably have constituted a larger proportion.

The problem is further complicated by the fact that the rhinoceros may consume a greater percentage of a preferred plant than a non-preferred species. On one occasion, for example, a rhinoceros approached a *Dirichletia glaucescens* and a regenerating *Acacia tortilis* growing in close proximity to one another. After sniffing the entire *Dirichletia* it selected one terminal shoot. It then proceeded to the small *Acacia tortilis* and devoured most of the tree. These examples illustrate several facets of feeding behaviour which should be considered when interpreting the data shown in the Tables. The part of the plant eaten is an important consideration.

The interrelationship of elephant and rhinoceros is a most important and interesting aspect of the ecology of the Tsavo National Park. Buss (1961), Napier Bax *et al.* (1963), and Laws *et al.* (1968) all record high proportions of grass in the diet of the African elephant. With the possible exception of Buss (1961), it is not clear from these studies whether grass was actually selected, or whether it formed a large proportion of the diet simply because of its high availability. Buss (1961) concluded that in the Murchison Falls National Park region grass was the preferred diet even where woody vegetation was

available. Wing and Buss (1970) repeatedly emphasize that grass was the preferred diet in several areas of Uganda. However, Laws *et al.* (1968) postulate that stable elephant populations can only be supported in areas with extensive browse and woody vegetation.

If the latter is correct the overlap in diet between elephant and black rhinoceros, which is already apparent at certain seasons in Tsavo, will increase in drier years when the grasses reach the nutritive value of a poor-quality standing hay, or wither, or are burnt off. Under these circumstances more and more browse will be consumed by the elephant; the black rhinoceros, which as this and other studies clearly show, eats little or no grass, may then suffer severely from competition. In addition, the concentration of both species near permanent water in times of drought exacerbates the situation: this happened in 1961 (Napier Bax *et al.*, 1963) when large-scale habitat destruction occurred in Tsavo and extensive mortality of rhinoceros took place (at least 282 animals died along a 64-km section of the Athi River)—these animals were shown to have died from the effects of nutritional anaemia (Tremlett, 1961). The extent to which food competition from the elephant influenced this mortality still remains a matter of subjective debate.

Although Agnew (1968) considers that destruction of the woody vegetation has "apparently now ceased and regeneration is in progress", this regeneration has probably resulted at least in part from the atypically heavy rainfall during the last few years. In addition, habitat destruction continued in early 1969 when elephant, which previously concentrated on *Commiphora*, *Acacia* and *Sterculia*, began to destroy *Delonix elata* and *Platycelyphium voense*, trees which they formerly left almost untouched. This was at the time of a relatively dry period, and may well be the preliminary phase of a second stage of destruction.

Goddard (1970) considers that the Tsavo rhinoceros population was stable during the 1960's despite the destruction of the *Commiphora* woodland and that the species could perhaps survive in the present bush-grassland or even grassland, by utilising the legumes or certain shrubs. However, if the present numbers of elephant concentrate along permanent water when another drought occurs they are likely to reduce

the browse and leguminous herbs to the point where the rhinoceros population will again be severely affected. In the absence of population management or emigration of the elephants, and the rigid control of fire, it seems probable that during another severe drought, another spectacular mortality of rhinoceros may be expected.

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Plate 1a

25th October, 1968. Looking due north-east from 2°54'10" S., 38°37'20" E. in Tsavo East. Large-scale destruction of Commiphora woodland by elephant. Surviving trees are Boscia coriacea, Platycelyphium voense and Delonix elata.

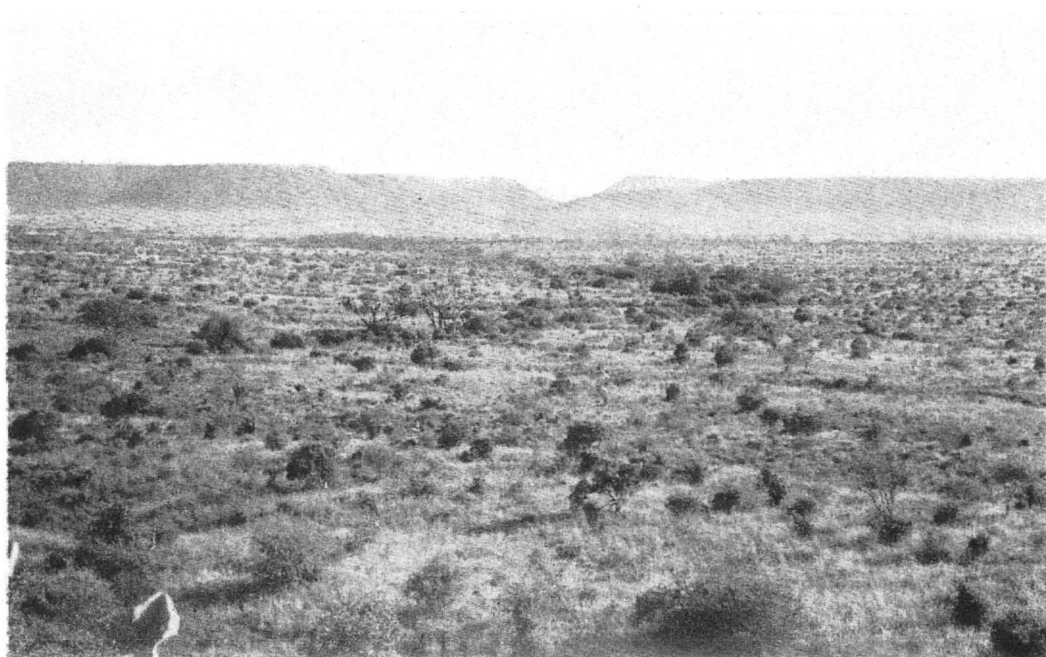


Plate 1b

Habitat 5: 14th March 1969. Looking toward Mopea Gap (3°00'40" S., 38°40'25" E.) from Euphorbia Rock (3°02'50" S., 38°40'10" E.). Typical "shrub or dwarf-tree grassland", with Lawsonia inermis forming a bank fringe on seasonal stream bed.

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Plate 2a

17th April 1969. Looking east from $3^{\circ}18'07''$ S., $38^{\circ}37'10''$ E. in Tsavo East. Luxuriant growth of *Sericocomopsis pallida* colonizing open areas in a zone which was formerly *Commiphora* woodland. Although a common shrub in open areas it did not appear to be highly palatable to black rhinoceros.



Plate 2b

March, 1969. *Caesalpinia trochae* browsed by a feeding black rhinoceros.