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ECOLOGICAL SEPARATION BY BROWSERS ON THE LEWA WILDLIFE CONSERVANCY, KENYA

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By

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MAGISTER SCIENTIAE (WILDLIFE MANAGEMENT)

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ABSTRACT

This study was conducted on the Lewa Wildlife Conservancy in the northern foothills of Mount Kenya. The vegetation of the area forms a transition from a semi-arid highland to an arid lowland and can be physiognomically described as savanna. Plant communities are described in terms of available browse of the woody vegetation. An evaluation of the structure and condition of the woody vegetation indicates heavy utilisation by game. The dynamics of herbivore-habitat relationships were investigated, with the emphasis on ecological separation of the browsers. The target browsers studied were the black rhinoceros *Diceros bicornis michaeli*, the elephant *Loxodonta africana* and the reticulated giraffe *Giraffa camelopardalis reticulata*. Preference for different habitat types, seasonal variations in these preferences, and the selection for specific environmental parameters contribute to the ecological separation of the browsers. A study of the feeding ecology of the browsers revealed that ecological separation is only partly achieved through food plant selection. The large numbers of browsers on Lewa create an excessive demand for browsable food resources, especially during the dry season. The potential for competition between the browsers therefore becomes eminent. A study of the lack of regeneration of *Acacia xanthophloea* seedlings in the riverine habitats on Lewa revealed that the present stocking rate of browsers is the primary cause for this lack of regeneration.

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CHAPTER 1

INTRODUCTION

GENERAL INTRODUCTION

The practical conservation problems of Kenya's national parks and wildlife areas are two-fold. There are those involving cultural, political and socio-economic factors, and those involving ecological factors. Both are of equal importance. The cultural, political and socio-economic problems involved in wildlife conservation have to be solved before the purely ecological problems can be approached. A management plan should therefore be based on an evaluation of cultural, political and socio-economic factors, as well as on ecological factors. Conservation must be balanced against local human needs in both the short and the long term. The resulting management plan must be acceptable to the rural African. For decades, the national parks have been the mechanism that has forced the rural African from his home. To ensure the future survival of the national parks and protected wildlife areas in Kenya, a system of sustainable utilisation may be the only answer.

A thorough knowledge of the ecology of any game area is vital for the implementation of meaningful management plans. These lead to optimal range utilisation and a stable, resilient range condition (Dekker 1996). Equilibrium between the habitat and resource requirements of ungulate populations is therefore important. Restricted conservation areas harbouring a variety of animal species with diverse habitat preferences necessitate a delicate balance between herbivores and the structural and plant species composition of their respective habitats. Knowledge of the habitat requirements of various animals is especially a prerequisite for the introduction of game onto any area. Habitat suitability also influences the potential ecological capacity of such areas (Fabricius 1994). Habitats are dynamic. Therefore obtaining knowledge of animal-habitat interactions is not an isolated procedure that can be done once or even on odd occasions; it must be an on-going process. As awareness of the importance of various habitats or elements thereof in a wildlife management area is increased, so can management practices be adapted to meet whatever objectives are envisaged.

Any wildlife area should be managed to obtain the desired goals in an economically and ecologically viable manner. In order to achieve an ecologically and economically viable system, it is essential to implement a scientifically based management plan. Any such approach must acknowledge the importance of, and the balance between the ecological capacity and stocking rate. Ecological capacity is a measure of the quality of the environment. It is also a dynamic term when applied to any herbivore population. Stocking rate is often set as a percentage of the ecological capacity (Trollope 1990). Therefore, any increase in natality, mortality, immigration or emigration will affect the ecological capacity and necessitate its periodic revision and adjustments to the stocking rate (Walker 1976b).

Within the ecological limits set by the ecological capacity, it is a personal decision made by a wildlife manager, often with specific economic objectives in mind.

Ecological separation, as defined by Chapman & Reiss (1995), is the division of a resource such as food, among two or more species so that each species has access to a different part of the resource. Herbivores in Africa have developed as an integrated complex whereby the available habitats are fully utilised and competition is limited by ecological separation. Thus, in a well-balanced system with a variety of large herbivores, the potential exists for the available resources to be optimally utilised. Interaction between species can be competitive or beneficial. Exploitative competition occurs when any adverse effects on an individual are brought about by reductions in resource levels caused by other competing individuals. Interference competition occurs when one individual physically excludes another from a portion of habitat and hence from the resources that could be exploited there (Begon, Harper & Townsend 1986). Facilitation is the process by which one animal species benefits from the activities of another. Competition and facilitation can both be manipulated by wildlife management to increase the density of a favoured plant or animal species (Caughley & Sinclair 1994).

THE HISTORY OF THE LEWA WILDLIFE CONSERVANCY

The origins of the Lewa Wildlife Conservancy can be traced back to 1922 when the late Alec Douglas took up land rights on Lewa Downs under the then British government's post-war "Soldier Settler" scheme. He established a cattle ranch there, and the property has remained in the family ever since. Alec Douglas's daughter, Delia, inherited the property and together with her husband, David Craig, ran the ranch for 26 years before handing it over to their eldest son, Ian Craig. Alec Douglas, the pioneer that he was, always sought to manage his ranch in reasonable harmony with the wildlife that occurred there. This tradition has continued through the generations. Consequently, Lewa Downs has always had a rich complement of wildlife.

In 1982, Mrs Anna Merz came to Lewa Downs as a visitor. She subsequently made a simple proposition to the Craig family: if they would lend her the land, she would provide the funds to establish a rhinoceros sanctuary. This was agreed to and in 1983, the Ngare Sergoi Rhinoceros Sanctuary was established on 2 024 ha of Lewa's land.

In 1994, with assistance from concerned individuals and conservation organisations, electrification of the fencing of Lewa Downs and the adjoining Ngare Ndare Forest Reserve was completed. This saw the birth of the Lewa Wildlife Conservancy (for brevity, hereafter referred to as Lewa), which was officially registered in 1995 by the Kenyan Government as a non-profit organisation. Since its inception, Lewa has seen tremendous growth and can now claim its rightful place among the world's most famous conservancies. Conservancies have proved to be highly successful in other parts of the world, but this concept is still in its infancy in Kenya. Consequently Lewa is pioneering the development of the conservancy concept in Kenya.

The aims of the Lewa Wildlife Conservancy can be summarised as follows (Anon 1996):

- To manage and conserve the wildlife resources in close liaison with the Government of Kenya and the Kenya Wildlife Service.
- To minimise conflict between wildlife conservation and human settlement, and to perpetuate a truly pastoral form of land management where man, domestic stock and wildlife can flourish.
- To provide for the protection and encouragement of black and white rhinoceroses, both within Kenya and internationally.
- To develop programmes for the purposes of protection and nurturing endangered endemic plant and animal species.
- To foster and encourage the development of environmentally sensitive tourism.
- To foster and encourage research, alone or in conjunction with other bodies having similar objectives as Lewa.
- To utilise revenue and profits for the maintenance and running of Lewa.
- To make Lewa financially self-supporting.

PAST RESEARCH

Since its early history, there has been an awareness on Lewa of the need for sound management and, consequently, of site specific research. Structured research has, however, been an ongoing activity on Lewa since at least 1983.

A comprehensive study was done on Lewa by Linsen & Giesen (1983) from the University of Nijmegen in the Netherlands. This study comprised a holistic overview of the ranch, including the classification of the vegetation into management units, habitat-suitability surveys, animal-habitat interrelationships, estimation of stocking rates and general management guidelines.

In 1992 Trollope (unpublished) recommended that a controlled burning programme be introduced into the management of Lewa. This recommendation formed part of a continuing investigation into studying the fire ecology of the Central Kenyan Highlands.

In 1995, Ravenhill (pers. comm.)[1] started a study on the competition between the grazers, but principally between the Grevy's zebra *Equus grevyi* and Burchell's zebra *Equus burchellii*, since they form the major component of the grazer population within Lewa. Insight into the level of competition between these two zebra species is necessary in order to manage both populations accordingly, and to the benefit of the Grevy's zebra. This study is due for completion later in 1999.

---

[1] Mr G.A. Ravenhill, Private Bag X4012, Tzaneen, 0850.

In 1995, three veterinary students from Cambridge University in England also spent 6 weeks on Lewa. Their project involved installing a computer programme to analyse range use patterns, interactions between individual animals, and cow/calf relationships in the black rhinoceros population.

Later in 1995, three students from St. Lawrence University in Canton, New York, also visited Lewa and conducted projects which included a range assessment programme, collecting samples for the herbarium, conducting game counts and completing the "Kenyan Wetland Inventory" portion of the Lewa Swamp for the Kenya Wildlife Services.

Botha (1999) completed a study aimed at providing pragmatic solutions to resource management. This study involved a general overview of Lewa, including its location and land-use history, as well as a description of the fundamental ecological characteristics of the study area (climate, geology, geomorphology, soils, impact of range burning on vegetation and impact of large herbivores on vegetation). The existing knowledge of the vegetation and soil classification systems was refined, the ecological status of the herbaceous species was determined and key herbaceous species were selected to provide insight into the current range condition, grazing capacity and grazer stocking rates. The browsing capacity was determined by calculating the available leaf biomass of the woody vegetation. Recommendations and guidelines regarding rangeland, wildlife and general management were proposed in this study.

PRESENT SITUATION

Lewa has had an ongoing research programme with the University of Pretoria in South Africa, in a project that is affiliated to the Kenya Wildlife Service Research Division. This research programme is directed by the Scientific Advisory Committee of Lewa whose principle aim is to establish ecological capacities and hence, optimum stocking rates for Lewa, and in particular to establish the correct balance between the grazers and browsers on Lewa. Active, adaptive management practices are continually being implemented on Lewa in order to comply with their aim of establishing correct grazer-browser stocking rates. The Kenya Wildlife Services has recently completed the translocation of 12 bull elephants from Lewa to Meru National Park. This has reduced the impact of the elephants on the riverine vegetation of Lewa. The translocation of a number of giraffes from Lewa has been the result of an effort to reduce the ever-increasing giraffe population. The Scientific Advisory Committee of Lewa has also advocated a major reduction of the Burchell's zebra to reduce the competition with the Grevy's zebra. Lewa's population of Grevy's zebra is one of only two protected populations in the wild. Therefore the need to manage the grasslands for the benefit of this species is paramount.

One of the other main objectives of Lewa is to ensure the continued survival of both the black and white rhinoceros populations through the promotion of continued population growth. Despite a number of natural deaths, both the rhinoceros populations on Lewa show an increase over time (Anon 1997).

CURRENT STUDY

The current study was aimed at investigating the dynamics of herbivore-habitat interactions on Lewa, with emphasis on the ecological separation of some of the browsers. The target herbivores included the black rhinoceros *Diceros bicornis michaeli*, elephant *Loxodonta africana* and reticulated giraffe *Giraffa camelopardalis reticulata*. According to Riney (1982), mammals are ecologically separated when they share the same geographical area without interspecific competition. Scogings, Theron & Bothma (1990) define ecological separation as a study of the habitat preferences, resource utilisation and potential interspecific competition among animals of an area.

The phytosociological classification of Lewa by Botha (1999) defines 11 plant communities, 10 of which are appropriate to this study. The woody vegetation was first surveyed in order to assess and predict the productivity of the available browse material. This assessment serves to establish a baseline for browse productivity, and acts as a parameter to monitor woody species encroachment or decline. Recommendations regarding the browsing capacity and stocking rates of Lewa are, however, also included in this study.

Habitat selection is a major factor in any ecological study of a species. No meaningful management plan for a conservation area can be compiled without detailed information on the habitat preferences of the major wildlife species inhabiting the area (Penzhorn 1982). The use of road transects made the quantification of animal numbers on Lewa possible. Qualitative vegetation and habitat data were also collected to isolate herbivore-specific habitat elements which were then used to assist in the determination of habitat preferences.

Selection of preferred plant species by animals is important, both in terms of habitat selection and interspecific competition between species selecting for the same food resource. Specific individual animals on Lewa were selected and tracked in order to observe their feeding habits. Qualitative vegetation and habitat data were collected to determine the various elements indicative of plant species and plant part selection.

A noticeable reduction in *Acacia xanthophloea* seedling regeneration and recruitment on the floodplains of Lewa led to an investigation aimed at determining the impact which browsing by the elephant, giraffe and impala populations of Lewa has on the regeneration of *Acacia xanthophloea* seedlings, specifically in the riverine and swamp areas. Exclusion plots were established and subjected to varying degrees of protection from the browser species concerned. The rate of browse production of identified, tagged shoots of *Acacia xanthophloea* seedlings was determined on a monthly basis. Trends in utilisation patterns were observed and used to determine the impact of the elephant, giraffe and impala populations on the regeneration and recruitment of *Acacia xanthophloea* seedlings in the riverine habitats of Lewa.

SPECIFIC OBJECTIVES

The following specific objectives were set for this study:

- The determination of the potential standing biomass of the available browse, to serve as a basis for the calculation of a browsing capacity and hence, optimum stocking rates for Lewa.

- The determination of the distribution and habitat preferences of the black rhinoceros, elephant and giraffe populations relative to each other.

- The determination of the extent to which plant species, plant parts and plant size are selected, in order to establish whether interspecific competition and ecological separation occurs between the black rhinoceros, elephant and giraffe populations on Lewa.

- The determination of the impact of browsing by the elephant, giraffe and impala populations on the regeneration and recruitment of the *Acacia xanthophloea* seedlings in the riverine and swamp areas of Lewa.

CHAPTER 2

THE STUDY AREA

LOCALITY

The Lewa Wildlife Conservancy lies between latitudes 0° 06′ and 0° 17′ North and longitudes 37° 21′ and 37° 32′ East in the northern foothills of Mount Kenya, about 65 km northeast of the town of Nanyuki. Figure 1 shows the position of the study area in Kenya. Lewa is approximately 24 600 ha (246 km^2) in size, with 128 km of boundary fencing. On the northern boundary of Lewa a gap in the fence allows for the migration of some animals. The western border is the Engare Ondare River, one of the streams that drain the northern slopes of Mount Kenya. The eastern border is the Eastern Marania River. In the south, the conservancy borders private land, while the northern boundary fence is also the district boundary between the Meru and Isiolo Districts (Botha 1999).

PHYSIOGRAPHY

Topography

Lewa is located on an altitudinal gradient, varying from 1 450 m above sea level in the north, to 2 300 m above sea level in the south. As a result, the area contains many different topographical and geomorphological units (Botha 1999). The topography of Lewa can be described as broken, with steep valleys in the south, gradual slopes tending to flatter volcanic plains in the central part, and undulating hills with occasional steep river valleys in the north. The differences in altitude and topographical units are less pronounced in an east-west than in a north-south direction. The decrease in altitude from the west (1 780 m above sea level) to the east (1 660 m above sea level) in the study area is gradual. The long, linear ridge that is evident in the southeast of the study area was once an ancient riverbed, filled with fast-flowing lava. Through weathering of the adjacent soils, the original riverbed has been inverted to form the present ridge.

Drainage

Kenya has a simple drainage network. The main rivers radiate either from the central dome formed by the Kenyan Highlands, or from the southern foothills of the Ethiopian Highlands. Lewa borders the northern outskirts of the Kenyan Highlands (Botha 1999). Consequently, Lewa's drainage network forms part of the Ewaso Ngiro River Basin, which is mainly situated north of the study area. Three perennial rivers drain the study area (Figure 2). They are: the Engare Ondare River, the Engare

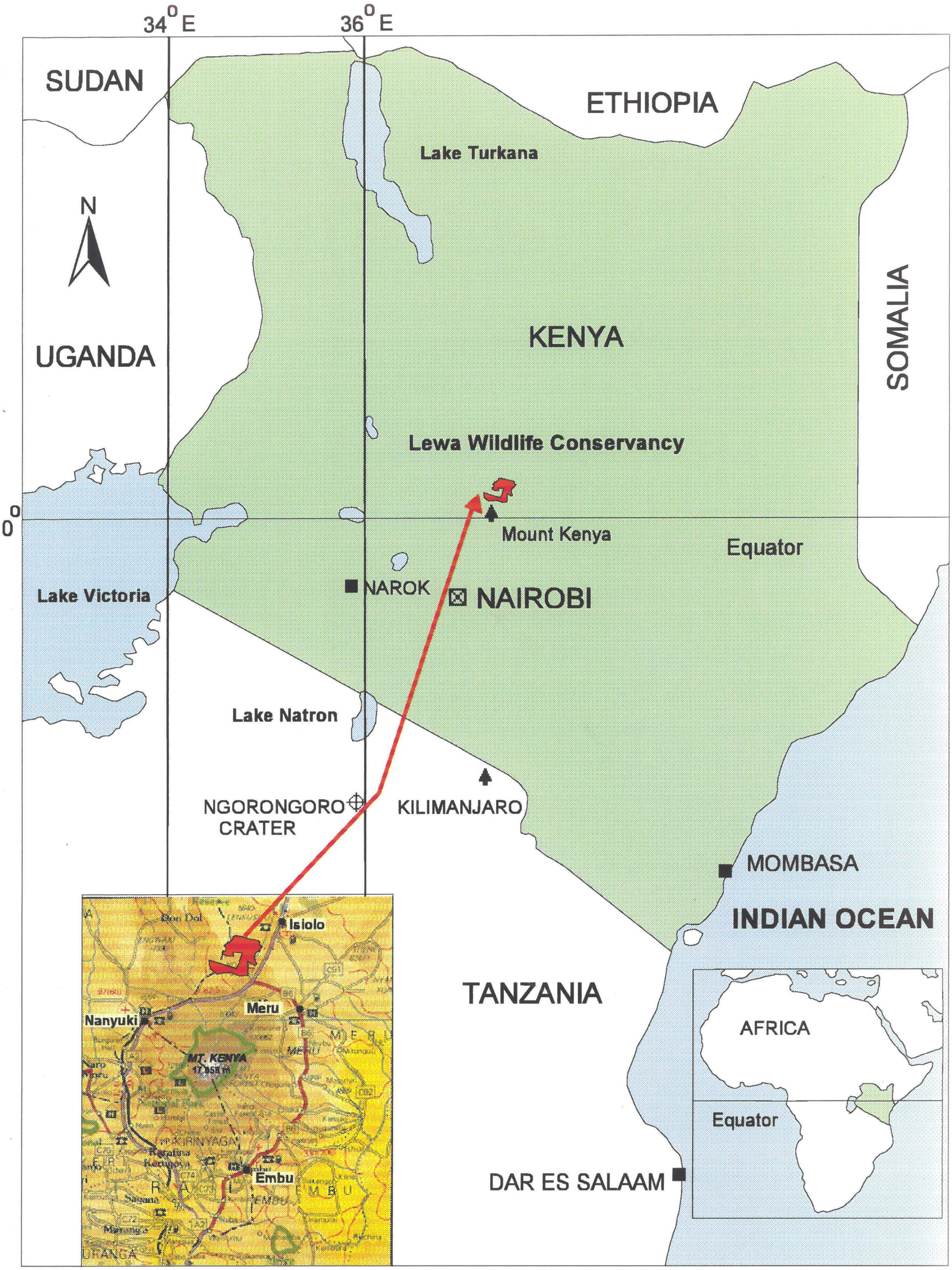

Figure 1 The location of the Lewa Wildlife Conservancy in Kenya, East Africa. Map not to scale.

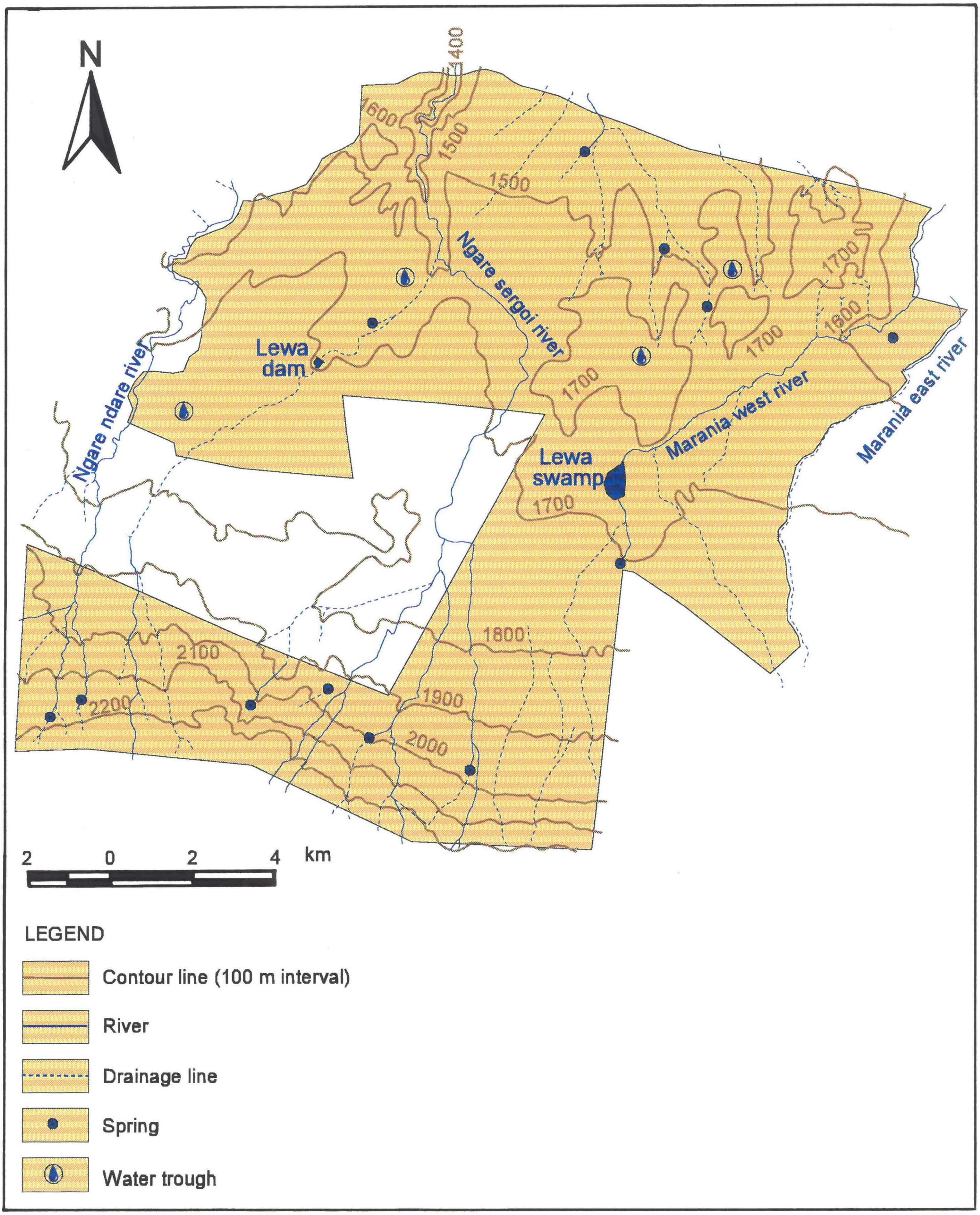

Figure 2 The topography, drainage and water supply on the Lewa Wildlife Conservancy, Kenya.

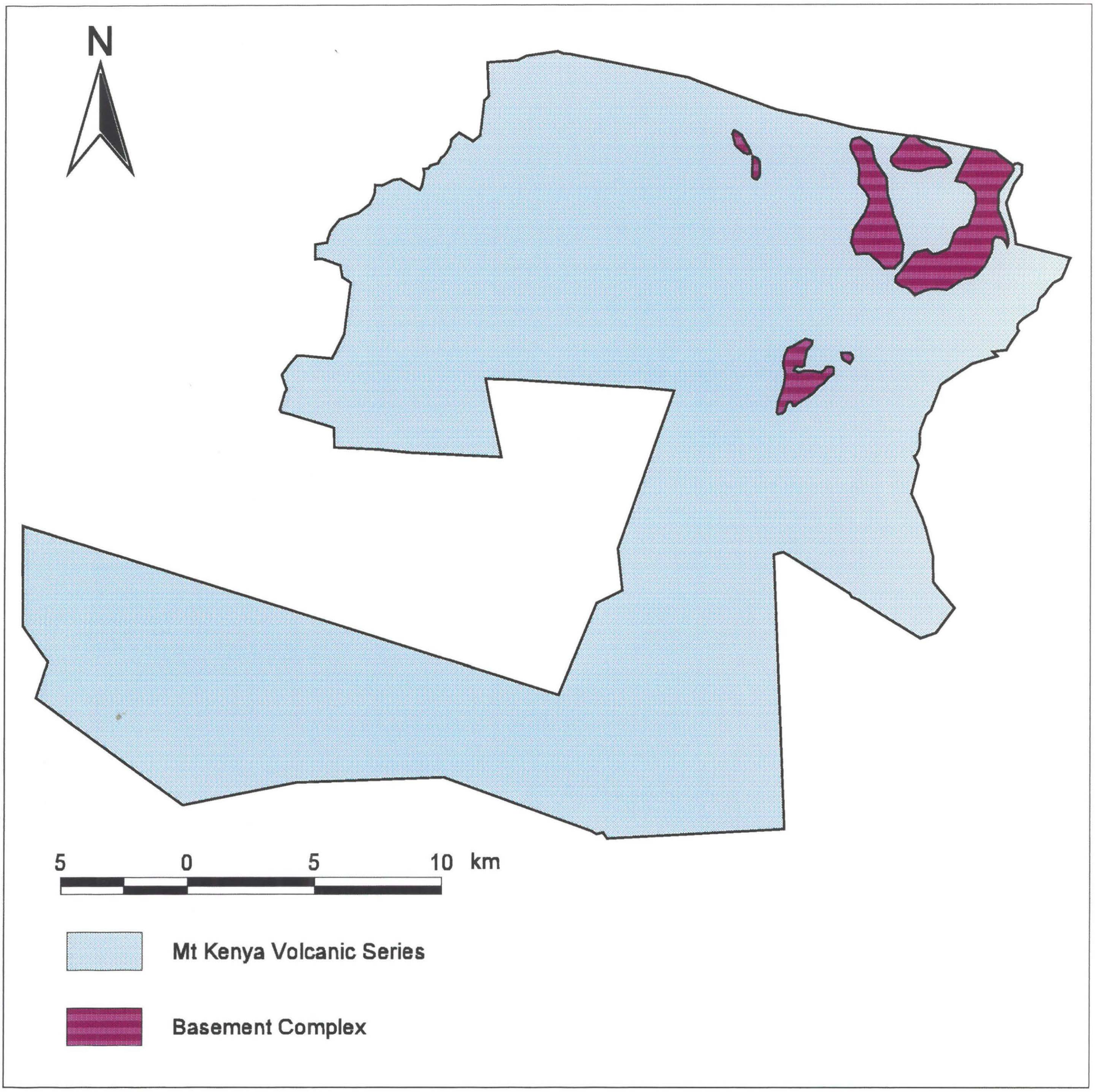

Figure 3 The geology of the Lewa Wildlife Conservancy, Kenya. Source: Botha (1999).

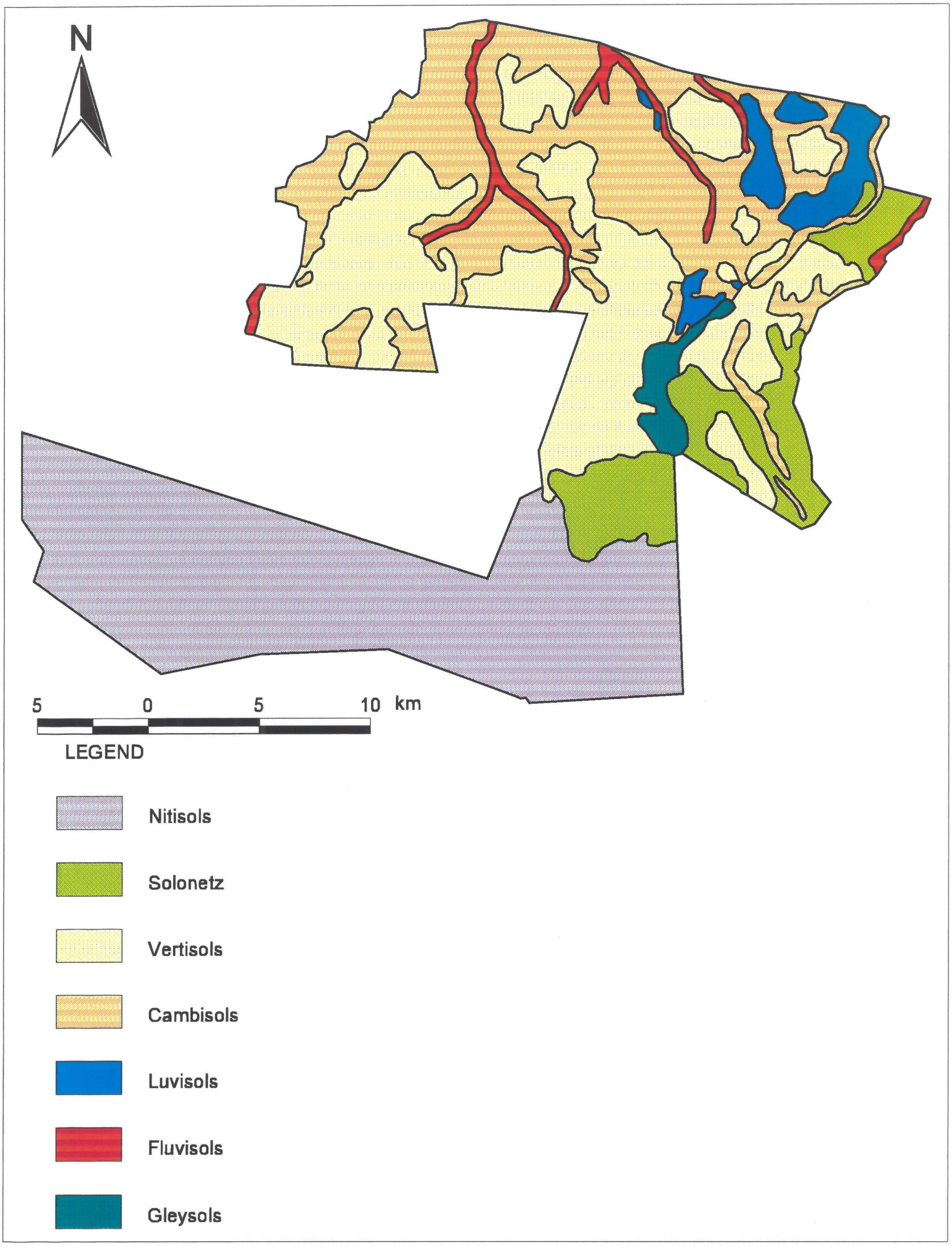

Figure 4 The soil types of the Lewa Wildlife Conservancy, Kenya. Source: Botha (1999).

Sergoi River and the Western Marania River. The latter river originates as a spring on Lewa and flows through the Lewa Swamp, following a northeasterly direction throughout Lewa. The Eastern Marania River has as its source, the Lolmotoni Spring, which occurs in the northeastern corner of Lewa. This river is seasonal over its course within the study area. The Eastern and Western Marania Rivers coalesce at the town of Isiolo to form the Keromet River, which in turn flows into the Ewaso Ngiro River. A single dam, not fed by a river, also occurs on the study area and is reliant on rainfall alone. Four water troughs occur on Lewa, which are used by the domestic stock as well as the game.

GEOLOGY AND SOILS

Geology

Two distinct geological rock formations occur on Lewa (Botha 1999)(Figure 3). They are:

- Basement system rocks: These rocks are sedimentary deposits that form the floor upon which the remaining rocks of the area rest. The system consists of schists, granulites and heterogeneous gneisses. The basement system rocks on Lewa consist of quartz-felspathic gneisses which contain varying proportions of biotite (Linsen & Giesen 1983).

- Volcanic rocks and subordinate sediments of the Mount Kenya volcanic series: The volcanic rocks that occur on Lewa consist of upper basalts, overlying lower basalts of the Mount Kenya volcanic series. Some areas on Lewa are covered by superficial Pleistocene deposits which are chiefly volcanic ash or basement system gneisses.

Soils

Botha (1999) conducted a thorough survey on the soils of Lewa. Twenty-one soil profiles were dug, and the soil samples analysed. Seven dominant soil types are found on Lewa, namely: nitisols, vertisols, cambisols, luvisols, solonetz, fluvisols and gleysols (Figure 4). The soils of the study area are mainly derived from the erosion of geological formations, although in some areas the soils are the result of transportation due to river action and run-off. Much of Lewa is underlain with a black cotton type of vertisol soil which is characteristic of impeded drainage, and which support a characteristic flora. Solonetz soils are deep, red soils and are characterised by their extreme erodibility, low resilience and poor recovery potential which leads to the vegetation on these soils having a low grazing capacity.

CLIMATE

Linsen & Giesen (1983) describe the climate of Lewa as transitional between that of the eastern Kenyan Highlands and the northern Kenyan Lowlands. This climate is described by Ojany & Ogendo (1973) as intermediate between the modified tropical climate of the Kenyan Highlands and the tropical continental/semi-desert climate of eastern Kenya.

The weather on Lewa is affected by it being in the rainshadow of Mount Kenya. Because the study area is at a high altitude, it also has an unusual combination of cold and dry weather (Berger 1989). The Highland areas are characterised by warm to hot days and cool nights.

Temperature

The daily maximum temperatures on Lewa range from 24 to 32 °C, and the daily minimum temperatures from 8 to 16 °C (Linsen & Giesen 1983). According to Botha (1999), the daily maximum temperatures during the wet season are lower than during the dry season. Conversely, the daily minimum temperatures during the wet season are higher than during the dry season. A marked temperature difference occurs along the altitudinal gradient, being warmer in the north than in the south.

Rainfall

Rainfall in the Kenyan Highlands is erratic in time and space, because it usually results from convective cloud formation, which produces localised showers (Thouless 1995). The rainfall follows a typical bimodal distribution pattern. There are two main rainy seasons. The long rains which fall in March to May, and the short rains from October to December. Rainfall records on Lewa have been kept since 1975, and the mean annual precipitation from 1975 to 1996 is 491 mm (Figure 5). The rainfall received on Lewa during the study period is shown in Figure 6.

Periods of prolonged drought are relatively common, occurring every one or two decades (Van Zwanenberg & King 1975). During the wet season of October 1997 to January 1998, Lewa also received an abnormally high rainfall (Figure 5). This has been attributed to the El Niño phenomenon. El Niño often begins early in a given year, and peaks between November and January of that year, or January of the following year. The return period of the El Niño event ranges from 2 to 7 years (Internet 1997)[2]. El Niño is Spanish for "the little boy", referring to the Christ child because this event usually occurs around December. Weather scientists apply the name El Niño to cycles of particular warming in a large part of the tropical Pacific Ocean. These cycles occur every 3 to 8 years and the

[2] http://enso.unl.edu/ndmc/enigma/elnino.htm 1997.

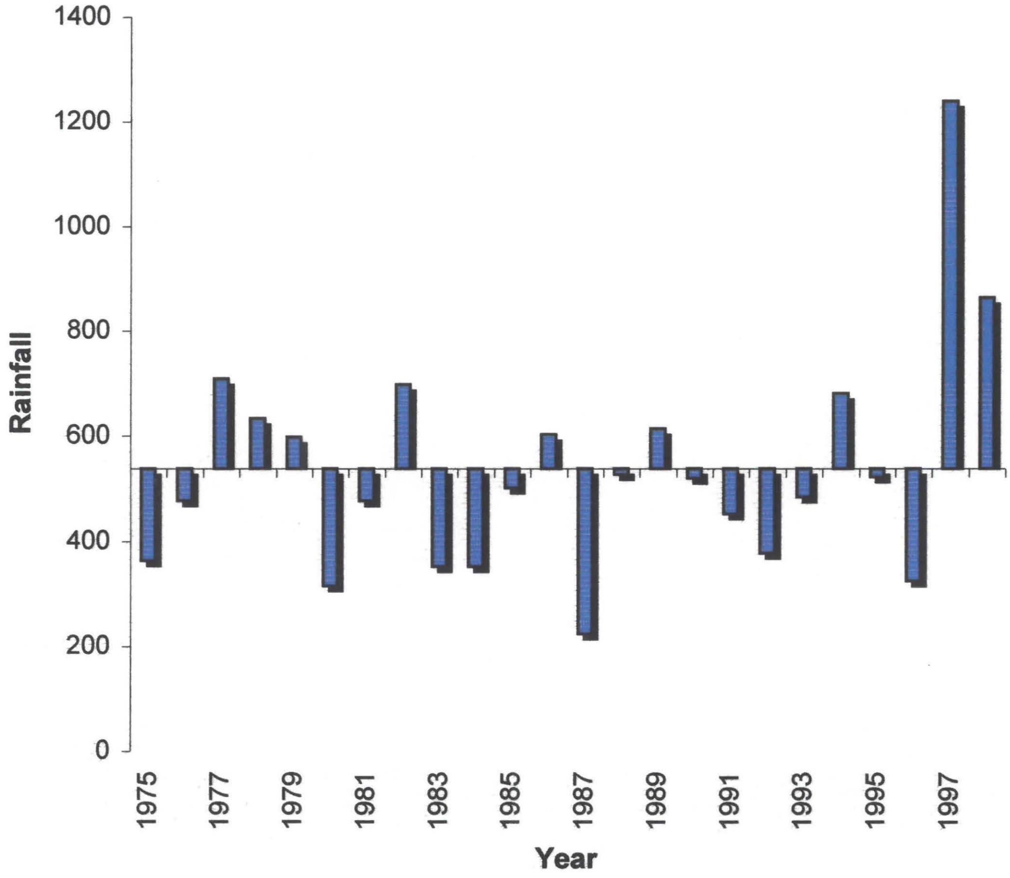

Figure 5 The annual rainfall (mm) on the Lewa Wildlife Conservancy, Kenya, from 1975 to 1998, and the fluctuation with the mean of 537.9 mm.

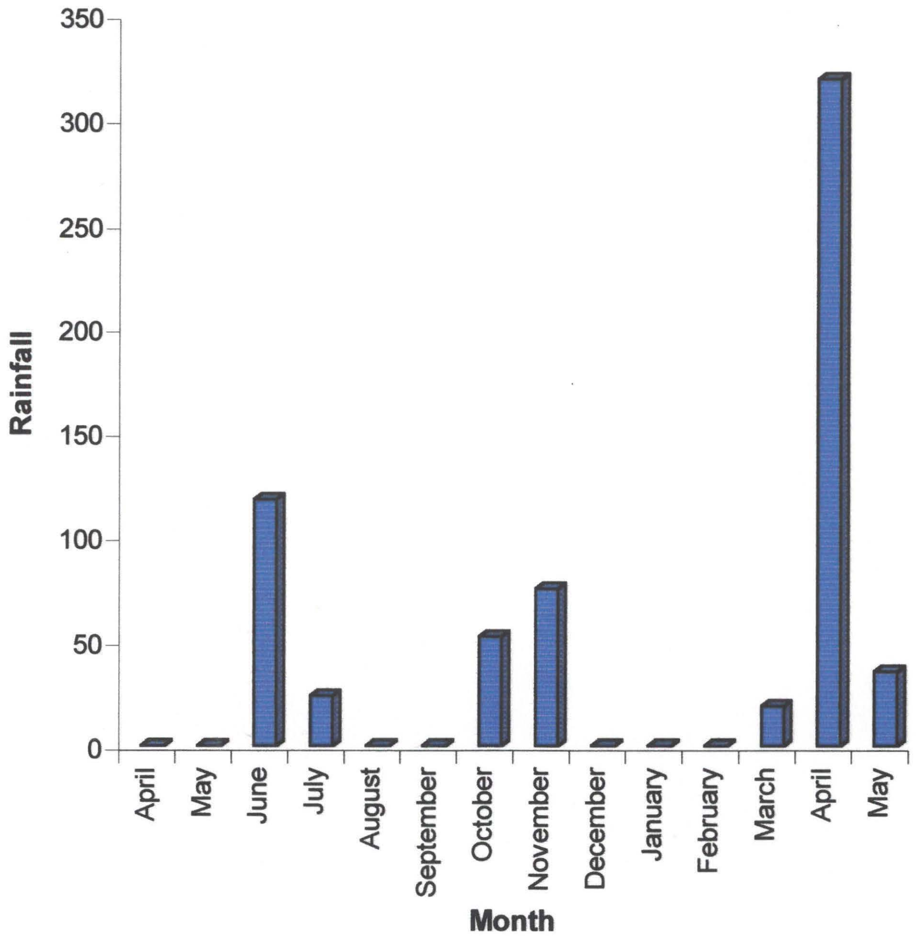

Figure 6 The monthly rainfall (mm) on the Lewa Wildlife Conservancy, Kenya during the study period which lasted from April 1996 to May 1997.

temperature of the ocean usually increases by between 2 and 8 °C. Since 1900, about 17 known incidences of El Niño have influenced the climate of the world. Until 1997 the worst by far was the period 1982 to1983 (Anon 1998).

VEGETATION

The vegetation of Lewa forms a transition from a semi-arid highland to an arid lowland. Most of the area can be physiognomically described as savanna, or more precise, a grassland with a tree and shrub cover of more than 2 % but less than 20 % (Pratt & Gwynne 1977). According to Edwards & Bogdan (1951), the area can also be called a "scattered tree grassland", which is the most extensive vegetation type which occurs at intermediate elevations in Kenya.

The vegetation of Lewa has been divided into 11 plant communities and 26 sub-communities, as identified by Botha (1999)(Figure 7). These plant communities have been placed into four management units which form the basis of the management plan devised by Botha (1999). These four management units are the Forest Management Unit, the Plains Management Unit, the Rivers Management Unit and the Hills and Rocky Outcrops Management Unit (Figure 27).

A plant species checklist for Lewa appears in Appendix A. The dominant plant family on Lewa is the Asteraceae (Compositae), with 21 representative genera. This is also known as the daisy family and forms one of the largest plant families throughout the world (Blundell 1987). Lewa has 10 *Acacia* species, with *Acacia drepanolobium* and *Acacia seyal* being dominant. *Acacia drepanolobium* dominates the areas above 1 650 m in altitude, while *Acacia mellifera*, often associated with *Acacia tortilis*, *Acacia nilotica* and *Commiphora* species, assumes this dominant role in the areas below 1 650 m in altitude. *Acacia xanthophloea* is dominant in virtually all the riverine and swamp vegetation. The dominant grass species throughout the study area is *Pennisetum stramineum*, often accompanied by *Pennisetum mezianum*. The latter occasionally is a major component of the vegetation.

ANIMALS

The wildlife herds in Kenya today are only the remnants of the far larger herds of previous times. Despite their reduced size, however, they cannot be completely accommodated within the existing national parks. When national parks were established in Kenya, little attention was paid to the needs of migratory herds and the conservation of complete ecological units. Therefore, management of national parks must not only be concentrated within the park boundaries, but must include the surrounding areas (Lusigi 1981). Because of a reduction in the natural habitat for Kenya's wildlife, and also the construction of fences to exclude game from pastures and arable land, the remaining game has concentrated in protective areas such as the national parks. Lewa is one of these wildlife refuges. The conservancy concept, whereby adjoining properties amalgamate to form extensive wildlife complexes within which animals can move freely, has proved to be a promising approach to the management of communal wildlife resources in many parts of Africa.

Wildlife has always had access to Lewa and no measures have been taken yet to exclude any game from entering the Conservancy. Lewa also forms part of an old migration route for elephants into the Ngare Ndare Forest. It also provides refuge and highly effective protection for both the black and white rhinoceros populations. All species have benefited from the enhanced level of security afforded by Lewa, particularly the Grevy's zebra and the sitatunga *Tragelaphus spekei*. Six sitatunga were introduced into the Lewa Swamp in 1990. It is difficult to determine their present numbers, although recent game counts have revealed the presence of no less than 12 animals. Grevy's zebra are endangered in the world, and Lewa has more than 15 % of the world population of these attractive animals. On rare occasions wild dog *Lycaon pictus* enter Lewa. Sightings of lesser kudu *Tragelaphus imberbis* on Lewa have also been documented. A mammal checklist for Lewa, including a complete classification of all identified mammals, in which the families and subfamilies are arranged alphabetically, appears in Table 1.

Table 1 A checklist and classification of the mammals that were identified on the Lewa Wildlife Conservancy, Kenya from April 1996 to May 1997. The families and the subfamilies are arranged alphabetically. The references of Meester & Setzer (1971), Walter, Mungall & Grau (1983), Smither's & Skinner (1990) and Wilson & Rheeder (1993) were consulted.

Animal	Family	Subfamily	Genus	Species	Subspecies	Author
Order Insectivora						
Hedgehog	Erinaceidae	Erinaceinae	*Atelerix*	*frontalis*	-	(A. Smith, 1831)
Order Primates						
Vervet monkey	Cercopithecidae	Cercopithecinae	*Chlorocebus*	*aethiops*	-	(Linnaeus, 1758)
Patas monkey	Cercopithecidae	Cercopithecinae	*Erythrocebus*	*patas*	-	(Schreber, 1775)
Syke's monkey	Cercopithecidae	Cercopithecinae	*Cercopithecus*	*albogularis*	-	
Olive baboon	Cercopithecidae	Cercopithecinae	*Papio*	*cynocephalus*	*anubis*	(Linnaeus, 1758)
Colobus monkey	Cercopithecidae	Colobinae	*Colobus*	*guereza*	-	Rüppel, 1835
Lesser bushbaby	Galagonidae	-	*Galago*	*senegalensis*	-	É. Geoffroy, 1796
Order Carnivora						
Bat-eared fox	Canidae	Otocyoninae	*Otocyon*	*megalotis*	-	(Desmarest, 1822)
Black-backed jackal	Canidae	Simocyoninae	*Canis*	*mesomelas*	-	Schreber, 1775
Side-striped jackal	Canidae	Simocyoninae	*Canis*	*adustus*	-	Sundevall, 1847
Wild dog	Canidae	Simocyoninae	*Lycaon*	*pictus*	-	Temminck, 1820
Caracal	Felidae	Felinae	*Caracal*	*caracal*	-	(Schreber, 1776)
African wild cat	Felidae	Felinae	*Felis*	*Silvestris*	-	Schreber, 1775
Serval	Felidae	Felinae	*Leptailurus*	*serval*	-	(Schreber, 1776)
Cheetah	Felidae	Acinonychinae	*Acinonyx*	*jubatus*	-	(Schreber, 1775)
Leopard	Felidae	Pantherinae	*Panthera*	*pardus*	-	(Linnaeus, 1758)
Lion	Felidae	Pantherinae	*Panthera*	*leo*	-	(Linnaeus, 1758)
Dwarf mongoose	Herpestidae	Herpestinae	*Helogale*	*parvula*	-	(Sundevall, 1847)
Egyptian mongoose	Herpestidae	Herpestinae	*Herpestes*	*ichneumon*	-	(Linnaeus, 1758)
Marsh mongoose	Herpestidae	Herpestinae	*Atilax*	*paludinosus*	-	(G. Cuvier, 1829)
Slender mongoose	Herpestidae	Herpestinae	*Galerella*	*sanguinea*	-	(Rüppel, 1836)
White-tailed mongoose	Herpestidae	Herpestinae	*Ichneumia*	*albicauda*	-	(G. Cuvier, 1829)
Spotted hyaena	Hyaenidae	Hyaeninae	*Crocuta*	*crocuta*	-	(Erxleben, 1777)
Striped hyaena	Hyaenidae	Hyaeninae	*Hyaena*	*hyaena*	-	(Linnaeus, 1758)
Cape clawless otter	Mustelidae	Lutrinae	*Aonyx*	*capensis*	-	(Schinz, 1821)
Honey badger	Mustelidae	Mellivorinae	*Mellivora*	*capensis*	-	(Schreber, 1776)
Zorilla	Mustelidae	Mustelinae	*Ictonyx*	*striatus*	-	(Perry, (1810))
Aardwolf	Protelidae	Protelinae	*Proteles*	*cristatus*	-	(Sparrman, 1783)
African civet	Viverridae	Viverrinae	*Civettictus*	*civetta*	-	(Schreber, 1776)
Large-spotted genet	Viverridae	Viverrinae	*Genetta*	*tigrina*	-	(Schreber, 1776)
Order Proboscidea						
African elephant	Elephantidae	-	*Loxodonta*	*africana*	-	(Blumenbach, 1797)

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Table 1 (continued)

Animal	Family	Subfamily	Genus	Species	Subspecies	Author
Order Perissodactyla						
Burchell's zebra	Equidae	-	*Equus*	*burchellii*	-	(Gray, 1824)
Grevy's zebra	Equidae	-	*Equus*	*grevyi*	-	Oustalet, 1882
Black rhinoceros	Rhinocerotidae	-	*Diceros*	*bicornis*	*michaeli*	(Linnaeus, 1758)
White rhinoceros	Rhinocerotidae	-	*Ceratotherium*	*simum*	-	(Burchell, 1817)
Order Hyracoidea						
Southern tree hyrax	Procaviidae	-	*Dendrohyrax*	*arboreus*	-	(A. Smith, 1827)
Rock hyrax	Procaviidae	-	*Procavia*	*capensis*	-	(Pallas, 1766)
Order Tubulidentata						
Aardvark	Orycteropodidae	-	*Orycteropus*	*afer*	-	(Pallas, 1766)
Order Artiodactyla						
Impala	Bovidae	Aepycerotinae	*Aepyceros*	*melampus*	-	(Lichtenstein, 1812)
Jackson's hartebeest	Bovidae	Alcelaphinae	*Alcelaphus*	*buselaphus*	*jacksoni*	(Thomas, 1892)
Grant's gazelle	Bovidae	Antilopinae	*Gazella*	*granti*	-	Brooke, 1872
Gerenuk	Bovidae	Antilopinae	*Litocranius*	*walleri*	-	(Brooke, 1879)
Kirk's dik-dik	Bovidae	Antilopinae	*Madoqua*	*kirkii*	-	(Günther, 1880)
Guenther's dik-dik	Bovidae	Antilopinae	*Madoqua*	*guentheri*	-	Thomas, 1894
Klipspringer	Bovidae	Antilopinae	*Oreotragus*	*oreotragus*	-	(Zimmermann, 1783)
Steenbok	Bovidae	Antilopinae	*Raphicerus*	*campestris*	-	(Thunberg, 1811)
African buffalo	Bovidae	Bovinae	*Syncerus*	*caffer*	-	(Sparrman, 1779)
Bushbuck	Bovidae	Bovinae	*Tragelaphus*	*scriptus*	-	(Pallas, 1766)
Eland	Bovidae	Bovinae	*Tragelaphus*	*oryx*	-	(Pallas, 1766)
Greater kudu	Bovidae	Bovinae	*Tragelaphus*	*strepsiceros*	-	(Pallas, 1766)
Lesser kudu	Bovidae	Bovinae	*Tragelaphus*	*imberbis*	-	(Blyth, 1869)
Sitatunga	Bovidae	Bovinae	*Tragelaphus*	*spekii*	-	Sclater, 1863
Common duiker	Bovidae	Cephalophinae	*Sylvicapra*	*grimmia*	-	(Linnaeus, 1758)
Common waterbuck	Bovidae	Reduncinae	*Kobus*	*ellipsiprymnus*	-	(Ogilby, 1833)
Defassa waterbuck	Bovidae	Reduncinae	*Kobus*	*defassa*	-	(Rüppel, 1835)
Mountain reedbuck	Bovidae	Reduncinae	*Redunca*	*fulvorufula*	-	(Afzelius, 1815)
Reticulated giraffe	Giraffidae	-	*Giraffa*	*camelopardalis*	*reticulata*	de Winton, 1899
Warthog	Suidae	Phacochoerinae	*Phacochoerus*	*aethiopicus*	-	(Pallas, 1766)
Order Pholidota						
Pangolin	Manidae	-	*Manis*	*temminckii*	-	Smuts, 1832
Order Rodentia						
Crested porcupine	Hystricidae	-	*Hystrix*	*africaeaustralis*	-	Peters, 1852

Note: No classification at that particular level is indicated by a hyphen (-)

CHAPTER 3

BROWSE AVAILABILITY AND WOODY VEGETATION ASSESSMENT

INTRODUCTION

In most of the large tracts of land which constitute Africa's wildlife areas, the vegetation has been broadly classified. However, limited detail of the species composition and structure is known, and few attempts have been made to monitor changes in the vegetation (Walker 1976a). Monitoring vegetation and its productivity, and distinguishing between changes attributable to management use and those attributable to climatic variation, browsing pressure and soil fertility, may aid in the planning or modification of the management strategy. However, statistics relating to browsing capacity and other quantitative criteria are meaningless unless a realistic assessment is made of the amount of accessible and usable leaf material available for browsers (Young 1992).

According to Rutherford (1979) it is important to differentiate between the terms browse and available browse. Although the term browse is viewed differently by many authors, it is defined here as: the sum total of plant material on woody plants that is potentially edible to a specified set of browsing animals, and which is regarded as the current season's growth of leaves and twigs. The lowest limit of edibility is thus a critical determinant of the total amount of available browse material. Seasonal changes in the palatability and moisture content of the plant material, as well as greater browsing pressure at certain times of the year, can result in a different and lower threshold of what is accepted as edible. The term available browse usually refers to a more restricted quantity than the term browse. The former is determined on the basis of the maximum height above the ground to which an animal can potentially utilise browse. It is accepted here that the term available browse refers to all the leaves, young twig material, bark, flowers and pods within an accessible height for a particular animal.

Browse utilisation estimation is insensitive in areas where heavy browsing has occurred (Springfield 1961; Stickney 1966; Charlton 1968; Jenson & Scotter 1977). Nevertheless, any study of woody vegetation should include an investigation of its utilisation, particularly when an estimate of browsing capacity is required. Such a discussion will follow later. The actual percentage of available browse that is utilised is difficult to quantify, as a considerable percentage of browse is lost due to inaccessibility, utilisation by other feeders, chemical and mechanical defences, and varying degrees of deciduousness .

Many methods have been devised for estimating available browse (Barnes 1976). A number of the most often used methods were evaluated here. The main aim, however, was to provide a structural description and quantitative assessment of the woody vegetation of Lewa, as a representative of the situation in the central Kenyan Highlands. A secondary aim was to provide an estimation of the percentage utilisation of woody vegetation on Lewa by the browsers present there. The following approaches were used:

THE VEGETATION SURVEY METHOD

Vegetation structure is used world-wide to classify and describe vegetation (Braun-Blanquet 1932; Fosberg 1967; Mueller-Dombois & Ellenberg 1974). To do this, an estimate of foliage production is needed (Walker, Crapper & Penridge 1988). There are numerous techniques to assess available browse, for example:

- The total collection of available browse.
- Direct estimation techniques.
- Quantifying individual plant units such as leaves or twigs.

Rutherford (1979) suggested that the total collection of available browse is only applicable in certain situations. It is also expensive, destructive and labour intensive. Direct estimation techniques are, on the other hand quick, non-destructive and efficient for extensive surveys of leaf material, but the results cannot be examined statistically.

Pauw (1988) developed a technique to determine the available browse at different height levels. Direct measurements of the crown diameter are made at different height levels. This is supplemented with direct visual estimations of the available browse. The ratio between the dry mass of the leaves per standard volume unit is then used to determine the total dry mass of the leaves per species, per height level and per soil surface unit. The total survey is done by one person only and involves only a slight destruction of leaf material.

Smit (1989a, b) developed another method for quantitatively describing woody plant communities. The total survey is done by one person only, involves no destruction of leaf material and is not as labour intensive as the technique developed by Pauw (1988). With the method of Smit (1989a, b) it is also possible to determine the available browse at different height levels. The method is based upon the relationship between the spatial volume of a tree and it's true leaf mass.

Teague, Trollope & Aucamp (1981) defined a Tree Equivalent and a Browse Unit as an *Acacia karroo* tree with a height of 1.5 m. The difference between the Tree Equivalent and the Browse Unit is that all leaf mass above the maximum browse height of 5 m is excluded in the calculation of the Browse Units (Smit 1989a). According to Smit (1994), the Tree Equivalent value is not suitable for heterogeneous woody plant communities because no compensation is made in its calculation for the structural differences which exist between various tree species. Tree Equivalent values also increase arithmetically with an increase in tree height, while tree volume values increase exponentially (Smit 1989a). The ecological implications of trees in savanna areas should also be taken into account. Smit (1989a) lists the three most important implications from an ecological viewpoint:

- Competition with herbaceous vegetation for moisture.
- Food for browsers.
- Creation of subhabitats suitable for desirable grasses.

Bearing these three aspects in mind, the following three quantitative descriptive units are proposed for browse estimates by Smit (1989a):

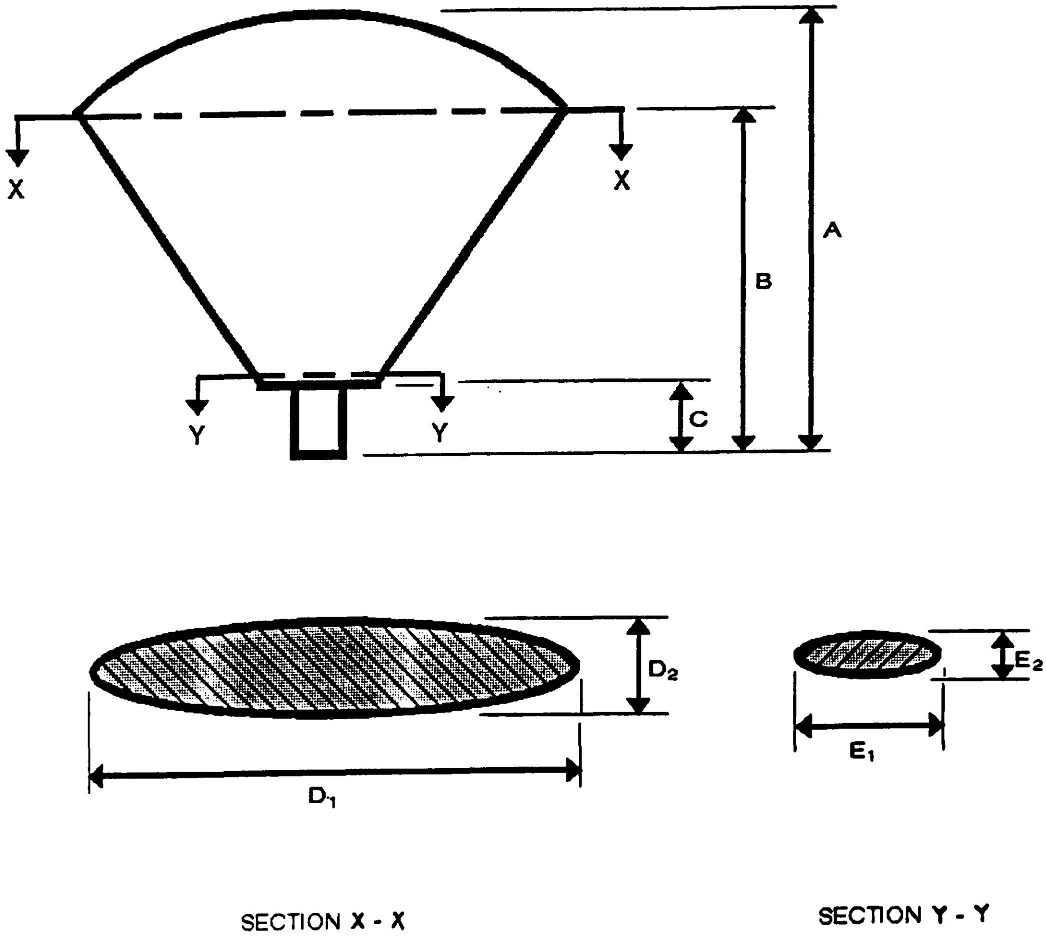
- Evapotranspiration Tree Equivalents (ETTE) : the leaf volume equivalent of a 1.5 m single-stemmed *Acacia karroo* tree.
- Browse Tree Equivalents (BTE) : the leaf mass equivalent of a 1.5 m single-stemmed *Acacia karroo* tree. The browse tree equivalent is a descriptive measure of potential production, and as such, factors contributing to leaf loss must also be considered.
- Canopied Subhabitat Index (CSI) : the canopy spread area of those trees in a transect under which associated grasses like *Panicum maximum* are most likely to occur, and expressed as a percentage of the total transect surface area.

BROWSE AVAILABILITY

METHODS

In this study, the woody vegetation on Lewa was surveyed from April 1996 to June 1996 by using the belt transect method of Smit (1989a). A total of 175 transects were surveyed throughout the study area. Sampling was done along a 100 m line transect with a 2 m range rod held horizontally to delineate the boundaries of the belt transect. All the woody plants present within the transect were identified and counted. The description of an ideal tree was used as a basis for the calculation of the spatial volume of any tree present, regardless of its shape or size. An ideal tree is regarded here as a single tree with a canopy consisting of a dome-shaped crown and a cone-shaped base (Figure 8). The spatial canopy volumes were calculated from the following dimensional measurements in metres, for each tree (Figure 8):

- A : Tree height or the height of the main tree crown, ignoring any small stems protruding from the crown.
- B : Height of the maximum canopy diameter.
- C : Height of the first leaves or potential leaf-bearing stems above the ground.
- D1: Maximum canopy diameter.



Dimensional measurements:

A : Tree height (m), taken as the height of the main tree crown, ignoring any small stems protruding from the crown.
B : Height (m) of the maximum canopy cover.
C : Height (m) of the first leaves or potential leaf-bearing stems above the ground.
D1: Maximum canopy diameter (m).
D2: Maximum canopy diameter (m) perpendicular to D1.
E1: Base diameter (m) of the foliage at height C.
E2: Base diameter (m) of the foliage at height C, and perpendicular to E1.

Figure 8 Schematic illustration of an ideal tree, its measurements and structure, as used to calculate the potential available browse on the Lewa Wildlife Conservancy, for the period April 1996 to June 1996 (Orban 1995).

- D2: Maximum canopy diameter perpendicular to D1.
- E1: Base diameter of the foliage at height C.
- E2: Base diameter of the foliage at height C, and perpendicular to E1.

When a tree canopy is elliptical, the maximum canopy diameter is calculated from the mean between the two measurements (D1 and D2) which are perpendicular to each other, because the theoretical canopy is circular (Smit 1994). For the same reason, two measurements (E1 and E2) are recorded for the diameter of the foliage at height C.

Further analysis of the data was conducted using the Biomass Estimates for Canopy Volume computer programme (BECVOL) as developed by Smit (1989b). This programme calculates the spatial volume of each tree segment. These values are then used to determine the evapotranspiration tree equivalents and the browse tree equivalents to give a measure of the total canopy volume and the total browse volume, respectively. The former values (ETTE) were converted to evapotranspiration tree equivalents per hectare (ETTE/ha) and browse tree equivalents per hectare (BTE/ha) respectively, at any specified Maximum Browse Height (MBH). The browse tree equivalent value and the dry leaf mass of trees below the specified maximum browse height were also determined. The maximum browse height for the giraffe and the elephant was estimated to be 5 m above the ground, and for the black rhinoceros, 2 m above the ground. Only leaf material was taken into consideration for the calculation of browsing capacity, although the other parts of the plants such as the flowers, fruit, twigs and bark are also part of the diet of many browsers. Fallen foliage and the consumption thereof were not taken into consideration. Consequently the browse production values as calculated here will be somewhat conservative.

RESULTS

The vegetation of the study area is classified into 11 plant communities (Figure 7)(Botha 1999). The browse availability of community 11, the *Typha domingensis-Echinochloa colona* swamp, was not considered here as this plant community is not utilised by either the giraffe or the black rhinoceros. The browse availability surveys were therefore conducted in each of the other 10 plant communities identified by Botha (1999). The results of the calculation of browse availability appear in Figures 11 to 13 and Table 2. By plant community, these results were:

1 : *Stipa dregeana - Juniperus procera* tall forest

This plant community is approximately 5 343 ha in size, covers 22 % of the study area and ranges from 1 860 to 2 260 m above sea level. Steep slopes and ravines are characteristic and this community is limited to the Ngare Ndare Forest which largely is a closed canopy forest (Figures 9 and

Figure 9 The *Stipa dregeana - Juniperus procera* tall forest community covers 22 % of the Lewa Wildlife Conservancy and is largely characterised by closed canopy forest.

Figure 10 The *Stipa dregeana - Juniperus procera* tall closed forest on the Lewa Wildlife Conservancy is dominated by woody plant species such as *Juniperus procera*, *Myrsine africana*, *Olea europaea*, *Podocarpus falcatus*, *Psiadia punctulata* and *Scolopia zeyheri*.

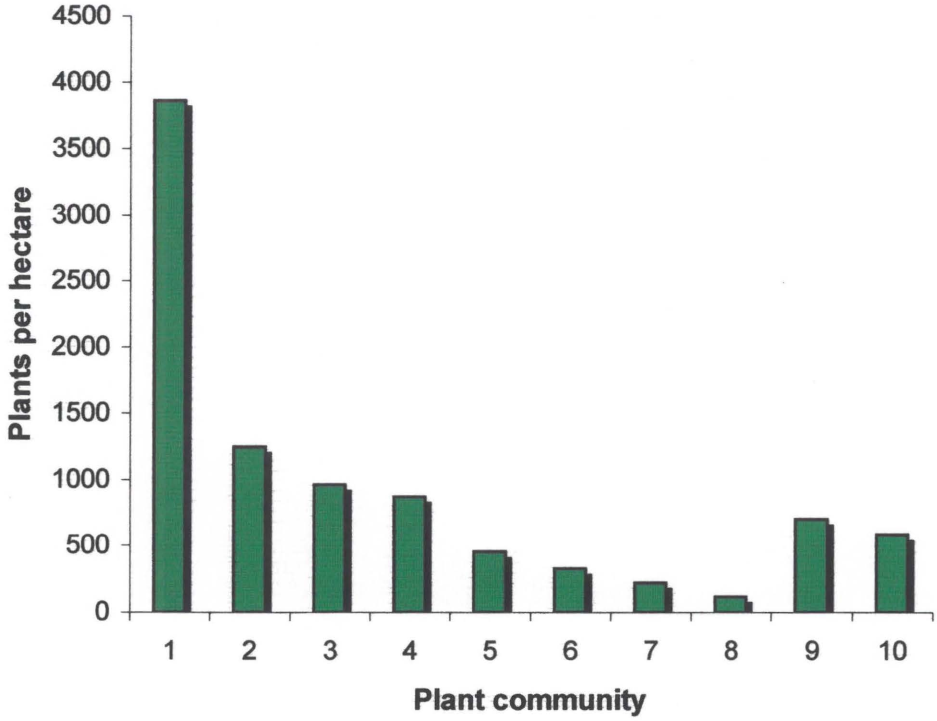


Figure 11 Density (plants per hectare) of the woody plant species in each plant community except the *Typha domingensis* - *Echinochloa colona* swamp on the Lewa Wildlife Conservancy, Kenya, from April 1996 to June 1996. For a description of the plant communities, refer to Table 2.

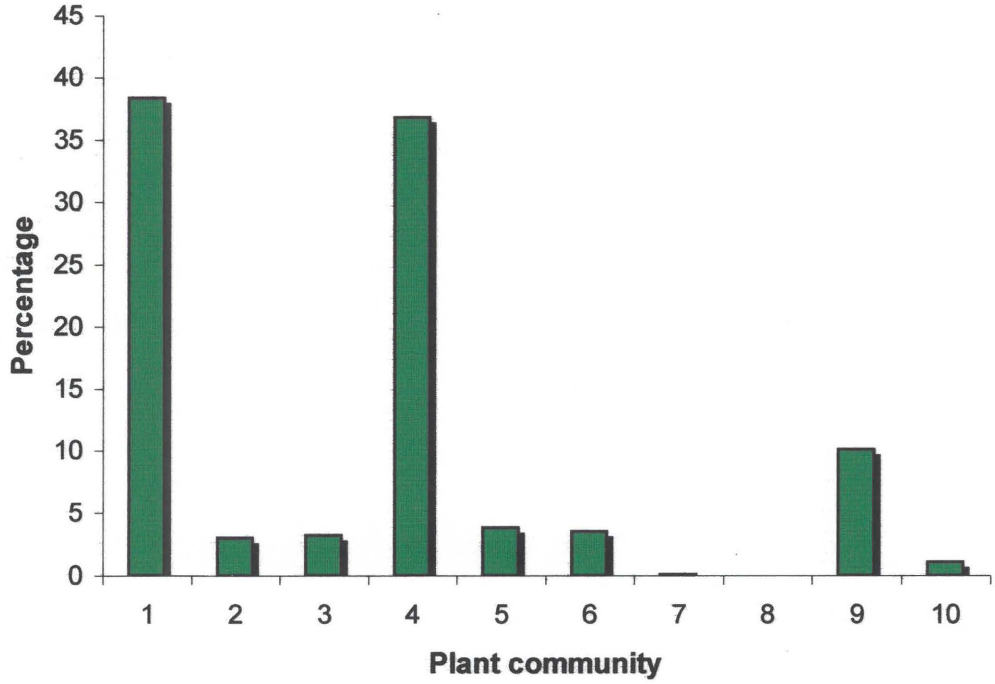


Figure 12 Percentage contribution of the plant communities except the *Typha domingensis - Echinochloa colona* swamp to the total available browse on the Lewa Wildlife Conservancy, Kenya, from April 1996 to June 1996. For a description of the plant communities, refer to Table 2.

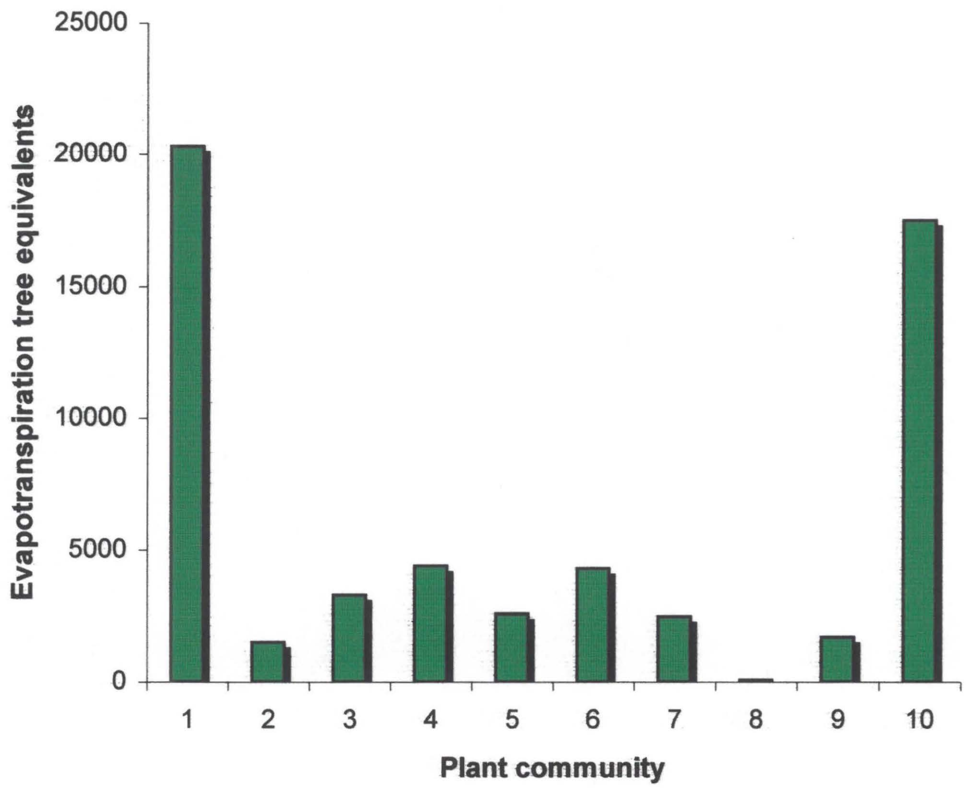


Figure 13 The evapotranspiration tree equivalents per ha for the plant communities except the *Typha domingensis - Echinochloa colona* swamp on the Lewa Wildlife Conservancy, Kenya, from April 1996 to June 1996. For a description of the plant communities, refer to Table 2.

Table 2 A summary of the BECVOL survey data done for the Lewa Wildlife Conservancy, Kenya, from April 1996 to June 1996, after the application of secondary calculations.

ITEM *	PLANT COMMUNITY **									
	1	2	3	4	5	6	7	8	9	10
PLHA	3858	1547	960	1323	327	223	35	82	702	553
LMAS	4541	335	752	602	1015	581	7	16	393	4237
LM20	568	228	311	184	317	470	7	16	224	92
LM50	1164	332	703	594	1015	581	8	16	378	240
BTE	18166	1339	3008	2407	4059	2325	30	65	1573	16949
BTE20	2271	914	1244	735	1269	1879	25	65	896	367
BTE50	4654	1327	2812	2378	4059	2325	30	65	1511	961
20%	12.5	68.3	41.4	30.5	31.3	80.8	76	100	57	2.2
50%	25.6	99.1	93.5	98.8	100	100	100	100	96.1	5.7
SIZE	5343	1633	815	6657	674	1105	1848	543	4817	806

** Plant community index:
1 *Stipa dregeana – Juniperus procera* tall forest
2 *Acacia drepanolobium – Themeda triandra* low thicket
3 *Commiphora africana – Lannea rivae* low thicket
4 *Acacia tortilis – Chrysopogon plumulosis* low thicket
5 *Acacia nilotica – Pennisetum stramineum* low open woodland
6 *Acacia mellifera – Sorghum versicolor* tall sparse shrubland
7 *Pennisetum stramineum – Becium hildebrandtii* short closed grassland
8 *Pennisetum stramineum – Themeda triandra* short closed grassland
9 *Acacia drepanolobium – Acacia seyal* low open woodland
10 *Acacia xanthophloea – Achyranthes aspera* tall closed woodland

* Item abbreviations:
PLHA =Plants per hectare
LMAS =Leaf dry mass (kg) per hectare
LM20 =Leaf dry mass (kg) per hectare below a browsing height of 2 m
LM50 =Leaf dry mass (kg) per hectare below a browsing height of 5 m
BTE =Browse tree equivalents per hectare
BTE20 =Browse tree equivalents per hectare below a browsing height of 2 m
BTE50 =Browse tree equivalents per hectare below a browsing height of 5 m
20% =Percentage of total BTE below a maximum browse height of 2 m
50% =Percentage of total BTE below a maximum browse height of 5 m
SIZE =Size of plant community in hectares

10). Northerly aspects predominate, and the soils are deep, red, humic nitisols, with varying clay contents. This plant community forms the southern boundary of Lewa (Figure 7). Botha (1999) divided the *Stipa dregeana - Juniperus procera* tall forest into four sub-communities, but for the purposes of this study, it is treated as a single entity.

The density of woody species in this community is 3 858 plants per ha (Figure 11 and Table 2). This density is similar to that calculated by Botha (1999). The dominant woody species are *Euclea divinorum, Juniperus procera*, *Myrsine africana, Olea europaea, Podocarpus falcatus, Psiadia punctulata, Rhus natalensis* and *Scolopia zeyheri.* A dominant shrub is an unidentified *Dyschoriste* species which occurs widespread at a density of 700 plants per ha. This shrub is a preferred food plant of the black rhinoceros on Lewa, and as does *Tinnea aethiopica*, it seldom grows to above 2 m in height. The browse of *Tinnea aethiopica* and the *Dyschoriste* species is therefore easily accessible to the black rhinoceros.

The total calculated browse below heights of 2 and 5 m respectively, is 3 034 824 kg (568 kg/ha) and 6 945 900 kg (1 300 kg/ha) respectively. An estimated 10 % of this browse is available for utilisation by the browsers on Lewa. Therefore the total available browse below heights of 2 and 5 m respectively, is 303 482.4 kg (56.8 kg/ha) and 694 590 kg (130 kg/ha) respectively. This plant community contributes 38.4 % (Figure 12) to the total available browse on Lewa and has the highest evapotranspiration tree equivalent per hectare (Figure 13). The evapotranspiration tree equivalent serves as an index for the potential that trees have to compete with one another and is an indication of tree density (Smit 1994). The competition between trees and tree density is therefore highest where leaf mass is highest.

2 : *Acacia drepanolobium - Themeda triandra* low thicket

This plant community is approximately 1 633 ha in size, covers 6.6 % of the study area and ranges from 1 900 to 2 100 m above sea level. Gradual slopes with northerly aspects are predominant. The soils are deep, red nitisols, with a clay content of up to 55 % (Botha 1999). The edge of the Ngare Ndare Forest supports this type of low thicket vegetation (Figure 14).

The density of woody species in this community is 1 547 plants per ha (Figure 11 and Table 2). *Lippia javanica* is dominant in this low thicket, at a density of 655 plants per ha. The black rhinoceros feeds on this shrub, but it is not a preferred food plant. Emslie & Adcock (1994) found that *Lippia javanica* is rejected by the black rhinoceros in the Hluhluwe-Umfolozi Park in South Africa. However, a study by Oloo, Brett & Young (1993) in the Laikipia District of Kenya suggests that the black rhinoceros there consumes a large proportion of *Lippia javanica*, both during the wet and the dry season. *Dodonaea angustifolia* is also a dominant shrub in this community, and it is considered a pioneer species where forest is invading grassland. Botha (1999) also mentions that where logging of *Juniperus procera* has occurred in the forests of Lewa, invasion by *Dodonaea angustifolia* is evident. Other dominant woody

Figure 14 The *Acacia drepanolobium - Themeda triandra* low thicket community is dominated by *Lippia javanica* and occurs on the edge of the Ngare Ndare Forest on the Lewa Wildlife Conservancy.

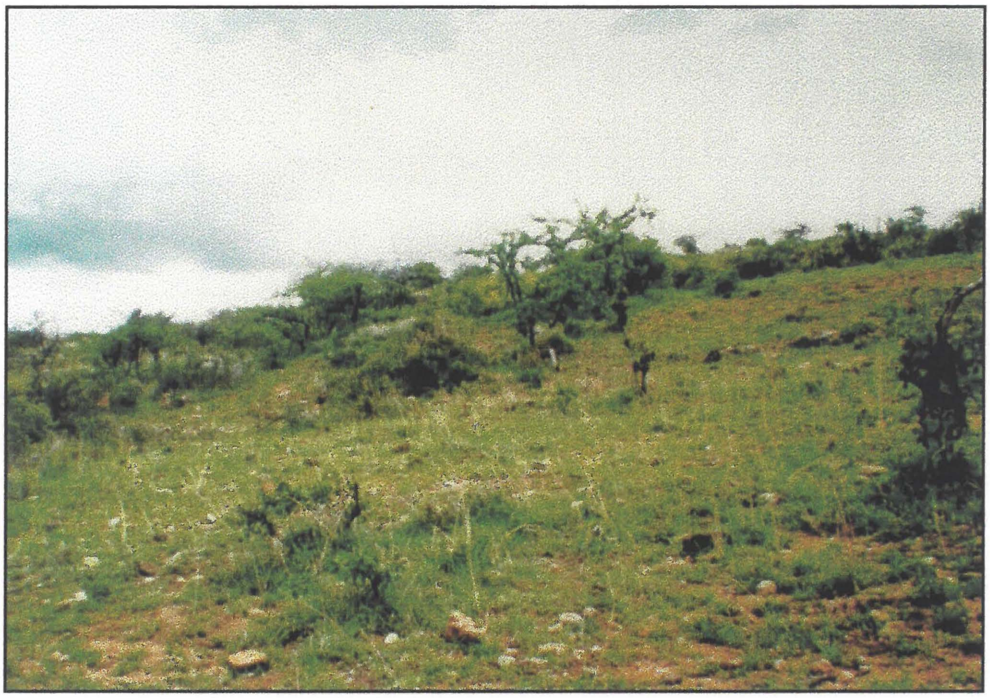


Figure 15 The *Commiphora africana - Lannea rivae* low thicket occurs on the rocky ridges of the Lewa Wildlife Conservancy. This community is prone to erosion which is caused by trampling by the high concentration of game on the hills during the dry season.

species include *Carissa edulis, Dyschoriste sp.*, *Psiadia punctulata*, *Rhus natalensis* and *Tinnea aethiopica*. *Carissa edulis* is a highly preferred food plant of the black rhinoceros on Lewa. Oloo *et al.* (1993) also found that *Carissa edulis* is one of the staple plant species eaten by the black rhinoceros during the wet and the dry season in the Laikipia District of Kenya. Emslie & Adcock (1994), however, found that *Carissa bispinosa* is rejected by the black rhinoceros in the Hluhluwe-Umfolozi Park in South Africa. Both *Carissa* species resemble each other, although their distribution to a large extent does not overlap. It is often found that plant species rejected by the black rhinoceros in South Africa, are highly preferred food items in East Africa. This also applies to the *Rhus* and *Euclea* species, where the black rhinoceros on Lewa often feeds on these plants. However, this does not necessarily mean that these are preferred food plants. Rather, it is likely that at certain times of the year a possible nutritional stress may force the black rhinoceros on Lewa to eat whatever is available. At a current density of 70 plants per ha, *Acacia drepanolobium* seems to have decreased on Lewa when compared to the study done by Botha (1999). The decrease in total available browse may possibly be attributed to the invasion by *Lippia javanica* and *Dodonaea angustifolia* since Botha's field work in 1994.

The total calculated browse below 2 and 5 m is 372 324 kg (228 kg/ha) and 542 156 kg (332 kg/ha) respectively. An estimated 10 % of this is available to browsers, therefore the total available browse is 37 232.4 kg (22.8 kg/ha) and 54 215.6 kg (33.2 kg/ha) respectively. This plant community contributes 3 % to the total available browse on Lewa (Figure 12). It would appear that this percentage is rather low in comparison with the browse available in the *Juniperus procera - Stipa dregeana* tall forest, but this is a shrub forest and most of the available browse is below the height of 2 m.

3 : *Commiphora africana - Lannea rivae* low thicket

This plant community ranges from 1 520 to 1 760 m above sea level and is approximately 815 ha in size, covering 3.3 % of the study area. It occurs mainly in the northeast of Lewa where it is limited to the rocky ridges which have well-drained, shallow, sandy soils (Figure 15). Sheet and gully erosion is evident on the hills, being caused by trampling by the high concentration of livestock and wildlife in these hills during the dry season.

The density of the woody species in this plant community is 960 plants per ha (Figure 11 and Table 2). *Commiphora africana* has a density of 260 plants per ha and is one of the preferred food plants of both the elephant and the black rhinoceros on Lewa. *Acacia brevispica*, *Acacia hockii*, *Acacia nilotica*, *Grewia tembensis, Grewia bicolor, Grewia similis, Lannea rivae* and *Maytenus senegalensis* are all abundant within this plant community. The black rhinoceros on Lewa favours *Acacia brevispica.* Oloo *et al.* (1993) also found that the black rhinoceros in the Laikipia region in Kenya prefers *Acacia brevispica* during the dry season. *Themeda triandra* occurs widespread on the slopes and is regarded as one of the best grazing grasses for the area.

The total calculated browse below 2 and 5 m respectively, is 253 465 kg (311 kg/ha) and 572 945 kg (703 kg/ha). An estimated 10 % of this is available to browsers. Therefore the total available browse calculated below 2 and 5 m is 25 346.5 kg (31.1 kg/ha) and 57 294.5 kg (70.3 kg/ha) respectively. This plant community contributes 3.2 % to the total available browse on Lewa (Figure 12).

4 : *Acacia tortilis - Chrysopogon plumulosis* low thicket

This low thicket community covers an area of approximately 6 657 ha which is 27.1 % of the study area. It is the largest plant community on Lewa (Figure 16 and 17) and straddles the altitudinal gradient from 1 510 to 1 760 m above sea level. It occurs on the cambisolic northern hills and rocky outcrops on the volcanic plains.

The tree density is 1 323 plants per ha (Figure 11 and Table 2). The dominant woody species include *Acacia mellifera*, *Acacia tortilis*, *Acacia nilotica, Boscia angustifolia*, *Commiphora africana, Grewia tembensis*, *Grewia villosa* and *Maytenus senegalensis*. *Acacia mellifera* has a density of 341 plants per ha, and together with the seedlings of *Commiphora africana*, constitutes a high percentage of the diet of the elephant and the black rhinoceros. *Boscia angustifolia* at a density of 105 plants per ha is heavily utilised by the giraffe on Lewa.

The total calculated browse below 2 and 5 m respectively, is 2 329 950 kg (350 kg/ha) and 6 657 000 kg (1 000 kg/ha). An estimated 10 % of this is available to browsers, therefore the total available browse calculated below 2 and 5 m, is 232 995 kg (35 kg/ha) and 665 700 kg (100 kg/ha) respectively. This plant community contributes 36.8 % to the total available browse on Lewa (Figure 12).

5 : *Acacia nilotica - Pennisetum stramineum* low open woodland

This low open woodland community covers approximately 674 ha or 2.7 % of the study area and ranges from 1 660 to 1 780 m above sea level (Figure 18 and 19). Flat to gradual slopes with varying aspects are characteristic. The occurrence of sheet erosion is due to the solonetz soils that occur in these areas and which are naturally prone to erosion. This plant community also occurs on shallow cambisol soils, with a moderate fertility. The eastern and southeastern section of the study area supports this low open woodland community.

The density of the woody vegetation is 327 plants per ha (Figure 11 and Table 2). *Acacia nilotica* is the dominant tree species at a density of 220 plants per ha. The elephant utilises this woodland community to a greater extent than the giraffe or the black rhinoceros. The foliage of many of the *Acacia nilotica* trees is above 2 m, which is out of reach of the black rhinoceros. Kotze & Zacharias (1993) found that an open *Acacia nilotica* woodland has a greater ratio of small to large woody plants.

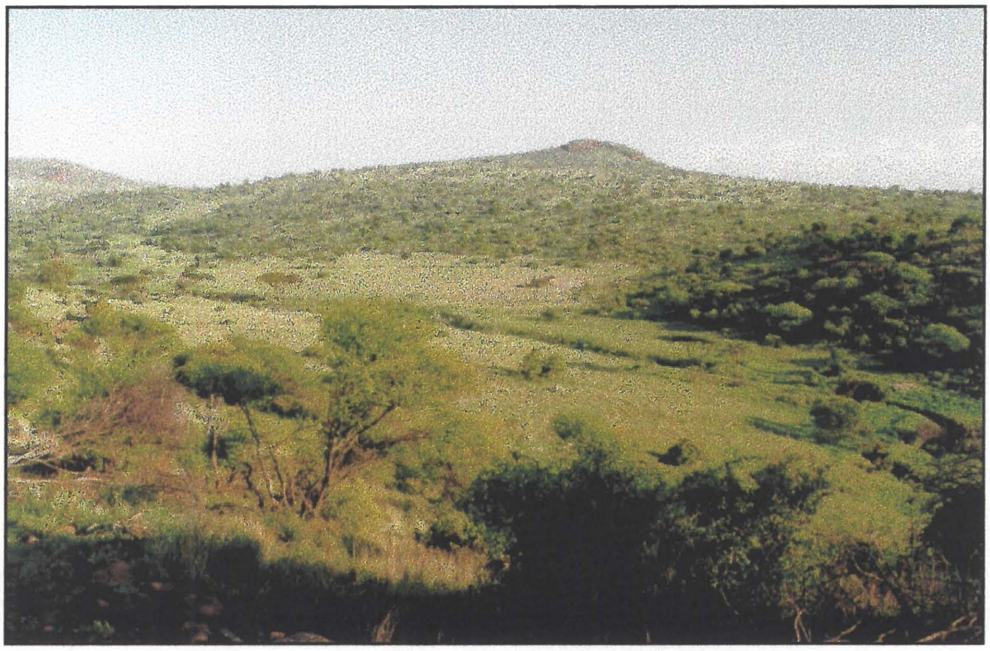


Figure 16 The *Acacia tortilis - Chrysopogon plumulosis* low thicket community covers 27.1 % of the study area and is the largest plant community on the Lewa Wildlife Conservancy.

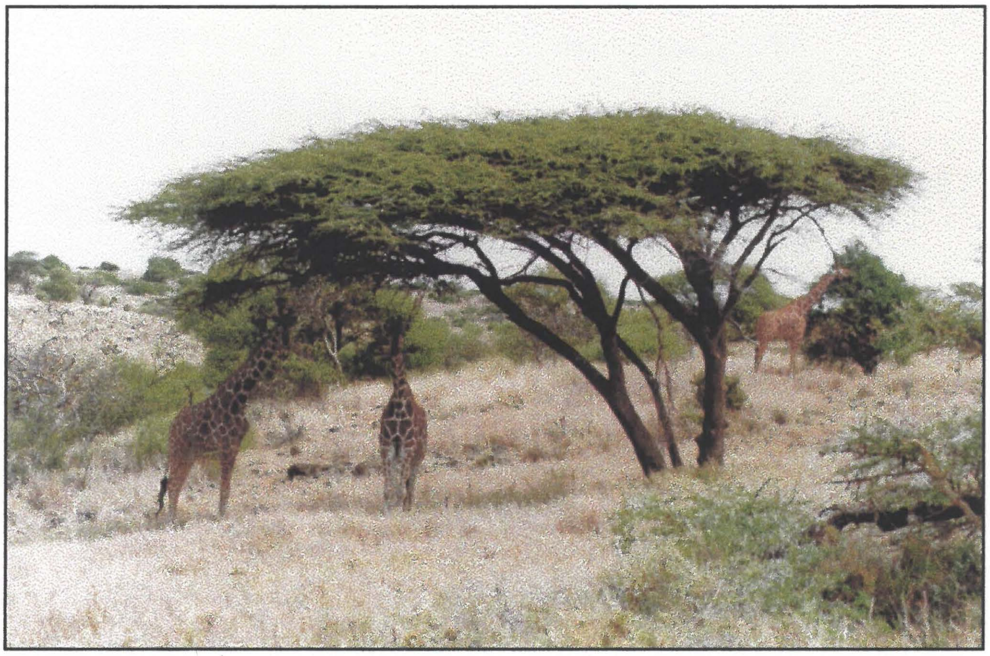


Figure 17 *Acacia tortilis* and *Acacia mellifera* are dominant woody species in the *Acacia tortilis - Chrysopogon plumulosis* low thicket. Note the browse-lines on the *Acacia tortilis* and *Acacia mellifera* trees.

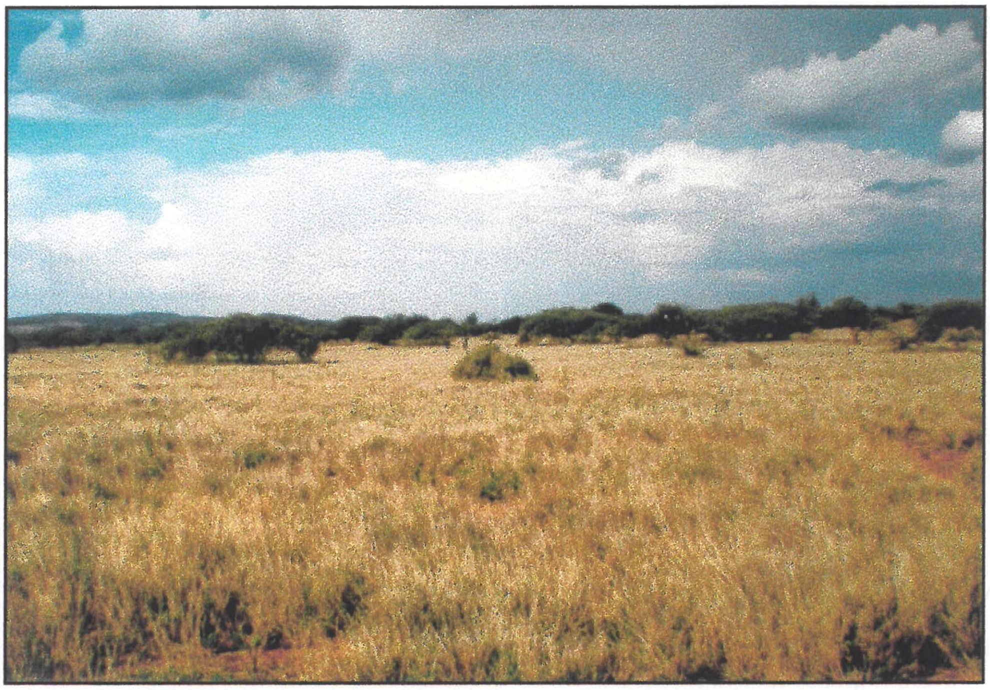


Figure 18 The *Acacia nilotica - Pennisetum stramineum* low open woodland on the Lewa Wildlife Conservancy in Kenya.

Figure 19 Few *Acacia* seedlings occur in the *Acacia nilotica - Pennisetum stramineum* low open woodland, as this community is heavily utilised by the elephant on the Lewa Wildlife Conservancy.

Therefore the browse value for the black rhinoceros is greater in the open *Acacia nilotica* woodland. The limited number of trees below 2 m in height in this plant community on Lewa could possibly be the result of elephant bulls having destroyed these trees in the past. Few *Acacia* seedlings occur in this plant community; also possibly a consequence of elephant destruction. Other dominant tree species include *Acacia drepanolobium*, *Acacia seyal, Commiphora africana* and *Maytenus senegalensis*, all of which are preferred food plants of the elephant and giraffe. The abundance of *Solanum incanum* within this plant community indicates disturbance due to overgrazing.

The total calculated browse below 2 and 5 m, is 213 658 kg (317 kg/ha) and 684 110 kg (1 015 kg/ha) respectively. An estimated 10 % of this is available to browsers. Therefore the total available browse calculated below 2 and 5 m, is 21 365.8 kg (31.7 kg/ha) and 68 411 kg (101.5 kg/ha) respectively. This plant community contributes 3.8 % to the total available browse on Lewa (Figure 12).

6 : *Acacia mellifera - Sorghum versicolor* tall sparse shrubland

This tall sparse shrubland community is 1 105 ha in size and it covers 4.5 % of the study area, ranging from 1 560 to 1 760 m above sea level (Figure 20). Situated in the west and northwestern section of the study area, this tall sparse shrubland is characterised by flat to gradual slopes with varying aspects. A striking characteristic of this plant community is the occurrence of poorly drained, dark, black cotton vertisol soils, with a low surface rock cover.

The sparse distribution of trees within this plant community is reflected by the woody vegetation density of 223 plants per ha (Figure 11 and Table 2). *Acacia mellifera* is a diagnostic species within this plant community where it occurs at a density of 200 plants per ha. This makes this shrubland extremely vulnerable to overutilisation by browsers. A distinct browse-line is visible on many of the *Acacia mellifera* trees, which also indicates overutilisation (Figure 21). Botha (1999) found that most trees in this plant community fall into the 1.5 to 2.5 m height category, making it highly suitable for utilisation by the black rhinoceros. The elephant also favours *Acacia mellifera,* often stripping trees totally of bark and leaves. There is only a limited regeneration of seedlings. Therefore it is of utmost importance that the recommended stocking rate of browsers be adhered to, especially during the dry season. The dominant woody species include *Asparagus falcatus, Boscia coriacea* and *Lycium europaem*. Occasionally the elephants select only for *Asparagus* species. Out of 30 consecutive plants eaten by an elephant cow on Lewa on one occasion, 22 were *Asparagus* species. The black rhinoceros on Lewa also eats an abundance of *Asparagus* species, although a large variety of forbs are selected as well. The conspicuous forb species include *Becium obovatum*, *Helichrysum glumaceum, Indigofera volkensii* and *Pavonia gallaensis*.

The total calculated browse below 2 and 5 m respectively, is 519 350 kg (470 kg/ha) and 642 005 kg (581 kg/ha). An estimated 10 % of this is available to browsers. Therefore the total available browse

Figure 20 The *Acacia mellifera - Sorgum versicolor* tall sparse shrubland on the Lewa Wildlife Conservancy is characterised by poorly drained, black cotton vertisol soils with a low surface rock cover.

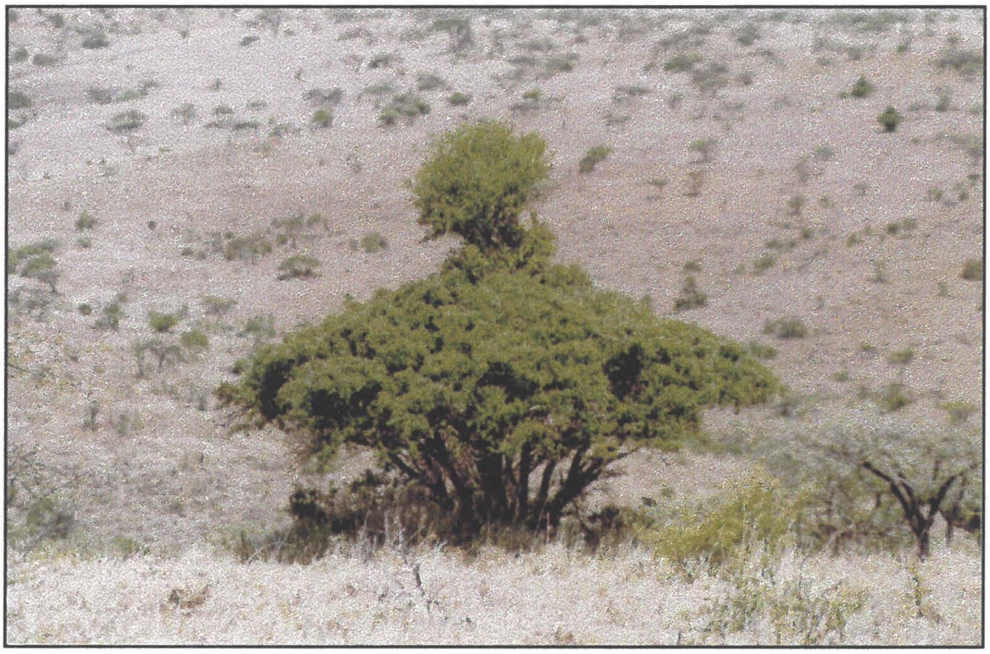


Figure 21 A distinct browse-line is visible on many of the *Acacia mellifera* trees in the *Acacia mellifera - Sorgum versicolor* tall sparse shrubland on the Lewa Wildlife Conservancy.

Figure 22 The *Pennisetum stramineum - Becium hildebrandtii* short closed grassland covers 7.5 % of the study area and occurs on the rolling, gentle slopes and plains of the Lewa Wildlife Conservancy.

Figure 23 The *Pennisetum stramineum - Themeda triandra* short closed grassland occurs in the southwest of the Lewa Wildlife Conservancy and is dominated by *Acacia drepanolobium* and *Acacia mellifera*.

calculated below 2 and 5 m, is 51 935 kg (47 kg/ha) and 64 200.5 kg (58.1 kg/ha) respectively. This plant community contributes 3.5 % to the total available browse on Lewa (Figure 12).

7: *Pennisetum stramineum - Becium hildebrandtii* short closed grassland

This plant community is 1 848 ha in size and covers 7.5 % of the study area. It occurs on rolling, gentle slopes (the "Downs" of Lewa) with varying aspects, at an altitude of 1 700 to 1 740 m above sea level. Deep, black vertisols are the characteristic soils underlying this grassland (Figure 22).

This short closed grassland is very sparsely populated with the seedlings of *Acacia drepanolobium* and *Acacia seyal*. The woody vegetation density is 35 plants per ha (Figure 11 and Table 2), with *Acacia seyal* seedlings contributing 25 plants per ha. Botha (1999) estimated a tree density of 15 plants per ha, which is an indication that the burning programme has not had a detrimental effect, but rather a beneficial one, on the *Acacia* seedlings. *Acacia mellifera* also occurs scattered throughout this grassland. The perennial shrub or climber, *Asparagus falcatus*, occurs scattered throughout this plant community and is favoured by the black rhinoceros and the elephant.

The total calculated browse below 2 m is 22 176 kg (12 kg/ha). An estimated 10 % of this is available to browsers, which yields 2 217.6 kg (1.2 kg/ha) of available browse. This plant community contributes 0.1 % to the total available browse on Lewa (Figure 12).

8 : *Pennisetum stramineum - Themeda triandra* short closed grassland

This plant community is approximately 543 ha in size and covers 2.2 % of the study area. It occurs in the southwest of Lewa, at altitudes of 1 700 to 1 720 m above sea level (Figure 23). The soils characteristic of this plant community are transitional between deep, black vertisols and shallower cambisols.

This short closed grassland community has a woody vegetation density of 82 plants per ha (Figure 11 and Table 2); far higher than 28 plants per ha, which is what Botha (1999) calculated. The only dominant woody species are *Acacia drepanolobium* and *Acacia mellifera*.

The total calculated browse below 2 m is 2 172 kg (4 kg/ha). An estimated 10 % of this is available to browsers. Therefore the total available browse below 2 m is 217.2 kg (0.4 kg/ha). This plant community contributes 0.01 % to the total available browse on Lewa (Figure 12).

9 : *Acacia drepanolobium - Acacia seyal* low open woodland

This plant community is the second largest on Lewa and encompasses an area of 4 817 ha, or 19.6 % of the study area. The core of this low open woodland occurs in the centre of the study area, with pockets on the northern and southern peripheries of this. Flat to gradual-sloped terrain with varying aspects are characteristic. A dominant characteristic of this plant community are the dark, volcanic, black cotton vertisol soils, with a low surface rock cover, at altitudes from 1 500 to 1 960 m above sea level. Vertisols are very fertile soils, but with a high water retention capacity. Nutrients are sometimes held so tightly that they are made unavailable to plants. Maskall (1989) confirmed this phenomenon on Lewa. Sheet and gully erosion is evident, forming mosaics of bare patches throughout this low open woodland.

The density of the woody vegetation is 702 plants per ha (Figure 11 and Table 2), which is dramatically lower than the 1 157 plants per ha as calculated by Botha (1999). This could be explained by the fact that the trees now have a lower resistance to factors such as drought and browsing pressure and therefore, even with decreased browsing pressure, mortalities of the weaker trees are still occurring. *Acacia drepanolobium* is the dominant woody species in this plant community, at a density of 462 plants per ha. Other dominant tree species include *Acacia seyal*, *Balanites aegyptiaca, Boscia coriacea, Boscia mossambicensis* and *Maytenus senegalensis.* Botha (1999) found that the majority of the woody species occur below 2.5 m, making this low open woodland highly suitable for black rhinoceros utilisation. Owen-Smith (1988) states that a black rhinoceroses' preferred browsing level is between 0.5 and 1.2 m.

The *Acacia drepanolobium* and *Acacia seyal* trees have suffered severe destruction and overutilisation by the giraffe and elephant on Lewa (Figure 24 and 25). Herds of up to 40 giraffe were observed feeding in this woodland. A giraffe selects mainly for the shoot tips, thus stunting the growth ability of the tree, which could ultimately lead to the mortality of the tree. The destructive feeding nature of elephants also contributes to the mortalities of these trees. Since 1993, the browsing pressure has been considerably relieved due to the implementation of an intensive culling programme on the giraffe. However, it will take a long time for the trees to recover and regenerate to the original *Acacia drepanolobium - Acacia seyal* forest. A giraffe translocation programme which has been implemented since 1999, should greatly alleviate this problem and thus allow for the regeneration process to initiate itself.

The total calculated browse below 2 and 5 m, is 1 079 008 kg (224 kg/ha) and 1 820 826 kg (378 kg/ha) respectively. An estimated 10 % of this is available to browsers. Therefore the total available browse calculated below 2 and 5 m, is 107 900.8 kg (22.4 kg/ha) and 182 082.6 kg (37.8 kg/ha) respectively. This plant community contributes 10.1 % to the total available browse on Lewa (Figure 12).

Figure 24 The *Acacia* species within the *Acacia drepanolobium - Acacia seyal* low open woodland have suffered severe destruction and overutilisation.

Figure 25 The *Acacia drepanobium - Acacia seyal* low open woodland is heavily utilised by the browsers on the Lewa Wildlife Conservancy, but especially by the elephant and the giraffe.

Figure 26 The *Acacia xanthophloea - Achyranthes aspera* tall closed woodland occurs around the *Typha domingensis - Echinochloa colona* swamp and along most of the streams throughout the Lewa Wildlife Conservancy. A large percentage of the browse in this community is unavailable to the browsers as it occurs above 5 m in height. Elephant bulls are largely the cause of the destruction within this community.

10 : *Acacia xanthophloea - Achyranthes aspera* tall closed woodland

This tall closed woodland encompasses an area of approximately 806 ha (3.3 % of the study area) and occurs around the *Typha domingensis - Echinochloa colona* swamp, and along all the streams throughout Lewa (Figure 26), excluding those in the Ngare Ndare Forest. Deep vertisolic and gleysolic soils are predominant.

The density of the woody vegetation is 533 plants per ha (Figure 11 and Table 2). *Acacia xanthophloea* is the dominant woody species in this plant community, at a density of 140 plants per ha. A large percentage of this browse is not available to browsers as it occurs above 5 m. Other woody species in this plant community include *Achyranthes aspera, Cordia ovalis, Grewia similis, Grewia tembensis* and *Vangueria madagascariensis*. Elephant and giraffe bulls, particularly, utilise this tall closed woodland to a large extent. The elephant bulls cause a large amount of damage, especially to the mature *Acacia xanthophloea* trees. The translocation of 12 elephant bulls from Lewa in 1997 should relieve the pressure on the woody vegetation in these riverine areas. The conspicuous forb species include *Abutilon mauritianum, Achyranthes aspera, Datura stramonium, Senecio schweinfurthii* and *Sida schimperiana.* The impala particularly favour the forb, *Sida schimperiana*, during the dry season. Impala are intermediate feeders, selecting for many seedlings during the dry season. They therefore contribute largely to the lack of regeneration of *Acacia xanthophloea* seedlings in the riverine habitats of Lewa. This aspect will be discussed in detail in Chapter 7.

The total calculated browse below 2 and 5 m, is 74 152 kg (92 kg/ha) and 193 440 kg (240 kg/ha) respectively. An estimated 10 % of this is available to browsers. Therefore the total available browse calculated below 2 and 5 m, is 7 415.2 kg (9.2 kg/ha) and 19 344 kg (24 kg/ha) respectively. This plant community contributes 1.1 % (Figure 12) to the total available browse on Lewa and has the second highest evapotranspiration tree equivalent per hectare (Figure 13).

DISCUSSION

Browse availability is limited by many factors that cannot be ignored when the percentage utilisation of browse by herbivores has to be estimated. A large percentage of browse becomes unavailable as food because of its inaccessibility to browsers. Woody species vary in their degree of deciduousness. Temperature and rainfall fluctuations, incidence of fire and species composition of an area are all factors that affect the period for which leaves remain on trees. Many plants have also developed chemical and physical defences that deter browsers, thereby limiting the available browse. According to Brewer (1994), a large percentage of available browse may also be utilised by other feeders such as insects, nematodes and bacteria. The plants themselves, also utilise some energy to ensure their own regrowth and vigour.

Generally, browsers consume small amounts of the total leaf production of woody plants. Owen & Wiegert (1976) estimated that in most terrestrial ecosystems, less than 10 % of the living material goes to consumers, and that a smaller percentage of this in turn, occurs in the form of browse material. Owen-Smith (1985) postulated that only 2 % of the total leaf production of woody plants was consumed by ungulates. Botha (1999) used a browse tree equivalent availability of 13 % for Lewa. Therefore the estimate that 10 % of the browse on Lewa is available for large herbivore use, is considered here as realistic when calculating stocking rates for Lewa (Chapter 4). Moreover, it is known that the total browse availability below 2 and 5 m respectively on Lewa is 790 107.9 kg and 1 808 273 kg. These figures represent 10 % of the total browse calculated using the BECVOL method. The total browse biomass on Lewa is 18 082 730 kg, which gives 746 kg/ha (Table 3). A comparison with other areas is given in Table 4.

Phenology divides the woody plant species into deciduous and evergreen species. Deciduous species are potentially dominant in subtropical areas because they have a better competitive ability. They have high potential growth rates, rely on deep rooting and often have small and compound leaves. Evergreen species are more specialised to cope with dry conditions. They rely on deep rooting and secondary thickening of their leaves to tolerate desiccation. They have moderate growth rates and long-lived sclerophyllous leaves, making them lower in digestibility than deciduous species (Danckwerts 1989).

The deciduous woody plant species on Lewa are represented by the genera *Acacia, Commiphora, Cordia* and *Grewia*. The evergreen woody plant species are represented by the genera *Balanites, Boscia, Carissa, Euclea, Maytenus, Olea* and *Rhus*. Lewa is dominated by a high incidence of evergreen species. This would tend to indicate that the number of browsers that the area can sustain should remain constant throughout the year, bearing in mind that browse utilisation increases during the dry season.

Botha (1999) divided the plant communities of Lewa into four management units based upon the similarities between the soil, topography and vegetation (Figure 27). These management units are: the Forest Management Unit, the Plains Management Unit, the Hills and Rocky Outcrops Management Unit, and the Rivers Management Unit.

The Forest Management Unit consists of the *Stipa dregeana - Juniperus procera* tall forest and the *Acacia drepanolobium - Themeda triandra* low thicket. This unit is a unique habitat for the black rhinoceros. According to Kotze & Zacharias (1993), forest verges provide important black rhinoceros feeding areas. Although the Forest Management Unit has the highest available browse on Lewa, only a small percentage of the browsers on the ranch actually utilise the forest. This places the other management units at a high risk of overutilisation. Evergreen species are prevalent, and during the dry season the elephants migrate into the forest from the plains. The forest verge vegetation which includes evergreen species such as *Carissa edulis*, *Tinnea aethiopica* and *Dyschoriste* species, is

Table 3 The total browse biomass and 10 % of the browse biomass in each of the ten plant communities, below 2 m and 5 m in height, on the Lewa Wildlife Conservancy. The calculation indicates how the total browse production (kg/ha) is derived from using the total browse biomass and the total available area of the ranch.

PLANT COMMUNITY	TOTAL BROWSE BIOMASS (kg)		10 % BROWSE BIOMASS (kg)	
	< 2 m	< 5 m	< 2 m	< 5 m
1	3 034 824	6 945 900	303 482.2	694 590.0
2	372 324	542 156	37 232.4	54 215.6
3	253 465	572 945	25 346.5	57 294.5
4	2 329 950	6 657 000	232 995.0	665 700.0
5	213 658	684 110	21 365.8	68 411.0
6	519 350	642 005	51 935.0	64 200.5
7	22 176	22 176	2 217.6	2 217.6
8	2 172	2 172	217.2	217.2
9	1 079 008	1 820 826	107 900.8	182 082.6
10	74 152	193 440	7 415.2	19 344.0
TOTAL	7 901 079	18 082 730	790 107.9	1 808 273.0

Total area = 24 600 ha
299 ha (cultivated lands)
\- 60 ha (swamp)

24 241 ha

Therefore 18 082 730 kg / 24 241 ha
= 746 kg/ha

Table 4 A comparison of dry leaf material biomass (kg/ha) in different localities in Africa.

VELD TYPE	COUNTRY	BIOMASS	SOURCE
Open savanna - wet season (Serengeti National Park)	Tanzania	47 - 1 440	Pellew (1983)
Open savanna - dry season (Serengeti National Park)	Tanzania	23 - 1 111	Pellew (1983)
Sahel savanna (Sahelo - Sudanese area)	Sudan	150 - 1 000	Le Houerou (1986)
Savannas in general	—	1 000 - 2 000	Otsyina & McKell (1985)
Semi-arid wooded grassland (Lewa Wildlife Conservancy)	Kenya	746	present study
Arid bushveld (Imberbe Game Ranch)	South Africa	839 - 1 260	Schulze (1992)
Arid bushveld (Villa Nora)	South Africa	517 - 1 065	Schmidt (1992)
Arid and Sour bushveld (Atherstone Nature Reserve)	South Africa	1 200 - 1 930	Pauw (1988)
Sour bushveld (Nylsvley)	South Africa	1 100	Rutherford (1982)
Mopani-veld	—	590 - 2 120	Kelly (1973)
Kalahari duneveld (Kalahari Gemsbok National Park)	South Africa	1 408 - 1 469	Kruger (1994)
Kalahari sandveld (Hwange National Park)	Zimbabwe	3 211	Rushworth (1978)
Combretum-veld (Kruger National Park)	South Africa	1 527	Dayton (1978)

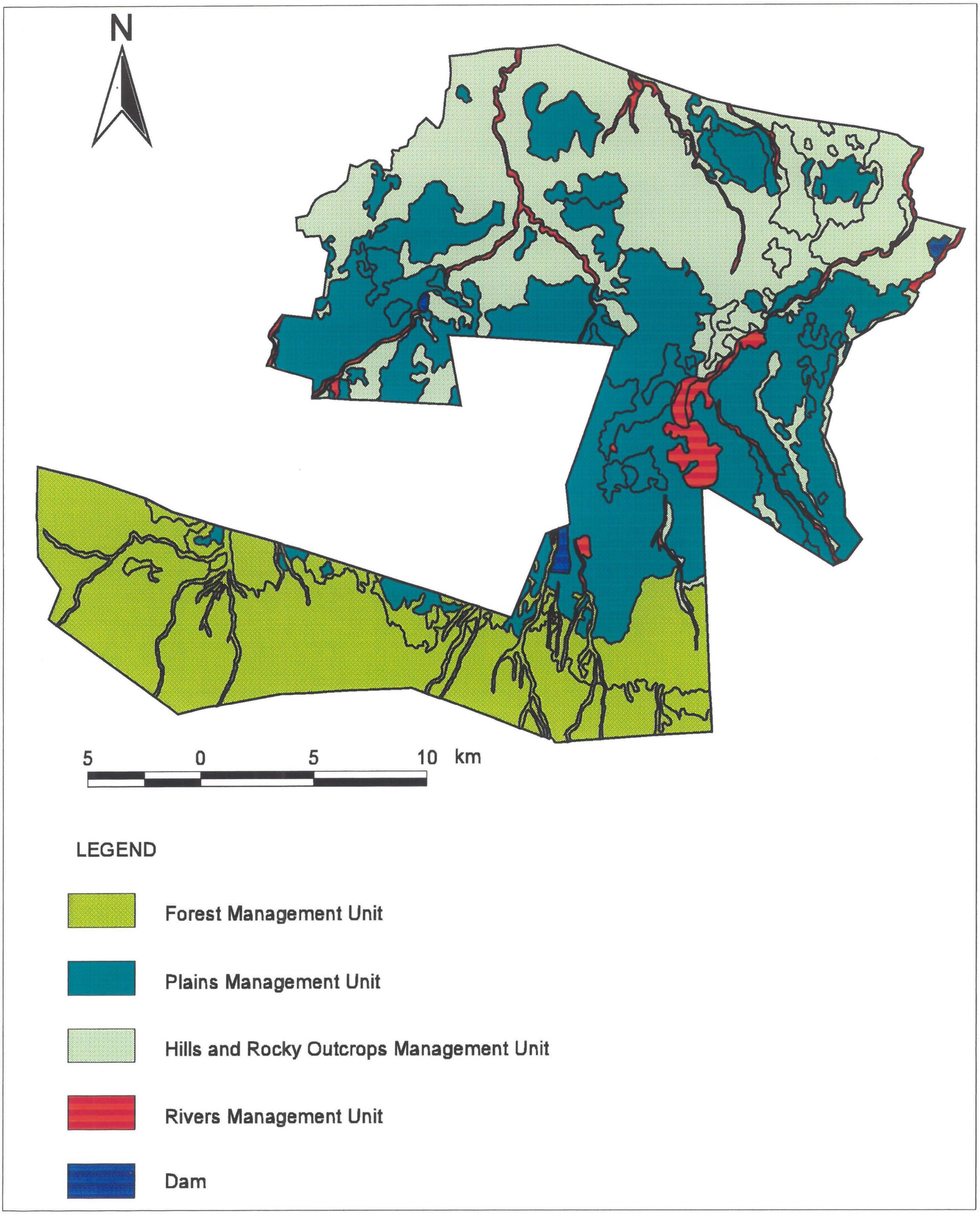


Figure 27 The management units of the Lewa Wildlife Conservancy, Kenya. Source: Botha (1999).

important in sustaining the black rhinoceros. Giraffes occasionally also utilise the bottom slopes of the Forest Management Unit, but they never enter the forest because of its topographical inaccessibility.

The Plains Management Unit consists of the *Acacia nilotica - Pennisetum stramineum* low open woodland, the *Acacia drepanolobium - Acacia seyal* low open woodland, the *Acacia mellifera - Sorghum versicolor* tall sparse shrubland, the *Pennisetum stramineum - Becium hildebrandtii* short closed grassland and the *Pennisetum stramineum - Themeda triandra* short closed grassland. This management unit covers the largest surface area of Lewa, namely 8 987 ha. The vertisol and solonetz soils have characteristic swelling and shrinking properties. Solonetz soils are also prone to erosion and should be rested for rehabilitation. During the wet season, the bulk of the grazers and browsers on Lewa utilise this management unit, thereby contributing to species- and area-selective use. The browsers consume many of the forbs and also the seedlings, with a resultant lack of seedling regeneration and recruitment. Overutilisation by browsers is evident and a distinct browse-line occurs on most of the *Acacia mellifera*, *Boscia angustifolia* and *Balanites aegyptiaca* tree species. The decline and death of many *Acacia* plants are due to the continual browsing pressure exerted by the giraffes. Teague (1989) confirms this by stating that browsers can reduce tree growth by depleting the plant's reserves, tapping its current photosynthesis or by reducing its photosynthetic leaf area. However, Crawley (1983) suggests that infrequent or intermittent defoliation can lead to compensatory growth in trees. It has also been suggested that sustained leaf production can be maintained as long as defoliation intensity does not exceed 50 %. However, on Lewa, the defoliation of woody plants by the giraffes in particular is estimated to exceed 50 %. The ongoing giraffe translocation programme to areas outside Lewa can thus only be beneficial. The Plains Management Unit contributes to the relatively low browsing capacity of Lewa, because of the inclusion of two grassland communities and the occurrence of excessive browsing in some areas.

The Hills and Rocky Outcrops Management Unit consists of the *Commiphora africana - Lannea rivae* low thicket and the *Acacia tortilis - Chrysopogon plumulosis* low thicket. Deciduous species are prevalent. The luvisolic and cambisolic soils are red and shallow, with a relatively low fertility due to a considerable amount of leaching of minerals. Small *Acacia*, *Grewia* and *Commiphora* plants are favoured by the black rhinoceros, making this management unit an important feeding ground, especially during the dry season. The black rhinoceros consumed large quantities of bark and branches of these plants during the dry season. The streams and ravines also provide favourable feeding grounds for the black rhinoceros because there is a high plant diversity in these areas. Large breeding herds of elephant concentrate in this management unit, uprooting many of the smaller trees and pushing over the larger trees to gain access to the roots and bark. This, in turn, makes the browse more accessible to the other browsers, especially the black rhinoceros. Elephants have a clear preference for the *Commiphora* species. During the wet season giraffe bulls also utilise this management unit to a large extent, despite the steep slopes of the unit.

The Rivers Management Unit consists of an *Acacia xanthophloea - Achyranthes aspera* tall closed woodland. The *Typha domingensis - Echinochloa colona* swamp is also included in this management unit, although it is not addressed in this study. The Rivers Management Unit is dominated by a high incidence of trees taller than 5 m. Therefore the foliage is inaccessible to most browsers. Elephant bulls are, however, highly destructive in this area because they push over many of the mature *Acacia xanthophloea* trees to gain access to the foliage, branches and bark. Moreover, some of the large trees are also pushed over by elephant bulls in an act of dominance. These trees are seldom eaten and only contribute to the mass destruction of large trees within this management unit. To date, many of the *Acacia xanthophloea* forests within the Rivers Management Unit have been fenced off to prevent access by the elephant and giraffe. During the dry season, the giraffe bulls utilise this management unit to a large extent, but the cows and calves tend to remain on the plains and hills. Besides elephant and giraffe use of the large trees, seedling regeneration and recruitment is not occurring. It has been speculated that browsing of the seedlings by the elephant, giraffe and impala contributes to this lack of regeneration and recruitment. The fences that surround these *Acacia xanthophloea* forests should therefore exclude all browsing game, at least until regeneration has exceeded the 1.5 m height.

CONCLUSIONS

The browse production of the Forest Management Unit is the highest of the four management units on Lewa, although it is not utilised to its full potential due to its topographical inaccessibility. It is an important feeding ground for both the elephant and black rhinoceros, especially during the dry season.

The Plains Management Unit is under severe browsing pressure, especially from the giraffe. Overutilisation is evident by the distinct browse-lines on many trees, uprooted trees and lack of seedlings. Browse utilisation increases during the dry season due to a higher crude protein level relative to other plant species. The ongoing giraffe translocation programme is therefore of vital importance to the regeneration of the Plains Management Unit.

The Rocky Hills and Outcrops Management Unit is heavily utilised by the elephant breeding herds during the dry season. The proposed burning programme for the Plains Management Unit should assist in detracting game from the hills, thereby allowing regeneration to occur and the effects of trampling to subside. The large plant species diversity makes this management unit an important feeding ground for the black rhinoceros, especially during the dry season.

The Rivers Management Unit is under severe pressure from the browsers. The differential utilisation of *Acacia xanthophloea* seedlings by the elephant, giraffe and impala populations on Lewa, accounts for a significant proportion of lost recruitment in this management unit. The total exclusion of a large proportion of *Acacia xanthophloea* forests from use by the browsers may be the only answer to facilitate the regeneration process.

The woody vegetation of Lewa is under severe pressure from several sources, especially outside the borders of the ranch. Factors such as livestock grazing, fuelwood utilisation, poaching and general impact from human movement prevent the access of browsers like the elephant and giraffe to their former wet season feeding grounds. This causes an influx of animals onto Lewa, without an equal level of emigration by the same species. Dublin (1986) states that the relative contribution of elephants to the loss of adult trees or the inhibition of woodland regeneration may be highly dependent on local weather conditions. The importance of monitoring the number of browsers on Lewa is evident by the mass destruction of the woody vegetation. Browser stocking rates should not be exceeded, especially during the dry season, because this season is when the browsing pressure is greatest. Translocation and culling programmes are a vital management practice where sport hunting is not allowed.

CHAPTER 4

BROWSING CAPACITY AND STOCKING RATE

INTRODUCTION

Vegetation and ecological surveys of the natural resources of conserved areas are essential for the establishment of efficient wildlife management programmes and conservation policies (Bredenkamp & Theron 1978). Determining the ecological capacity and the productivity of an area should be a vital part in the management programme of any conservation area. Ecological capacity as used here, is the potential of an area to support herbivores through grazing and/or browsing and/or fodder production over an extended number of years, without the deterioration of the ecosystem (Botha 1999). Bothma (1996) refers to ecological capacity as a characteristic of the entire habitat in which the vegetation, herbivores and predators are all a part. It is also referred to as carrying capacity in some literature, but this term is not used here because of the confusion surrounding it (Dhont 1988).

The browsing capacity of a given area gives an indication of that area's potential to carry a certain number of animals in a good productive and reproductive condition over a prolonged time, without the deterioration of the resources (Kruger 1994). The stocking rate is the wildlife manager's estimate of an allowable land to animal relationship that will provide the most beneficial returns in terms of a given management objective. In other words, stocking rate is an expression of the number of animals per unit area that the wildlife manager actually runs on his range. Whereas the ecological capacity of a given area is a product of the quantity and quality of the natural resources present, the stocking rate is a personal preference of a given wildlife manager. It can vary with the stated aims of the area involved, but it should never exceed the ecological capacity. The stocking rate of different game species on a wildlife area is determined by the type and condition of the different available habitats and the management objectives for the area (Thompson 1986; Bothma 1996). Stocking rate is one of the most important range management decisions influencing animal performance and range condition. Therefore great care should be taken in formulating a realistic stocking rate. Whatever the final stocking rate, it should be conservative to cope with variable rainfall conditions and the range quality and quantity at the worst part of the dry season. For those management options requiring higher stocking rates, a possible alternative is to base the number of game on the mean annual rainfall for all the rainfall years which fall below the long-term annual mean. This approach will provide a viable strategy for coping with periodic droughts (Trollope 1990).

To ensure the continued survival of the black rhinoceros and to promote its population growth on Lewa, it was necessary to determine the browse available to the seven browsers on Lewa. These included the black rhinoceros *Diceros bicornis michaeli*, eland *Tragelaphus oryx*, elephant *Loxodonta africana*, gerenuk *Litocranius walleri*, reticulated giraffe *Giraffa camelopardalis reticulata*, Greater kudu *Tragelaphus strepsiceros* and impala *Aepyceros melampus*. To maximise the breeding rates of the black rhinoceros, they should be stocked at maximum productivity densities, which are around 75 % of the maximum number of animals that a habitat can sustain (McCullough 1992).

The aims of this study were to determine the potential standing browse biomass and the available browse on Lewa, to calculate a browsing capacity for the Conservancy and hence, to determine the optimum stocking rate for these browsers. Four different browse tree equivalent availabilities were compared here. The results obtained were compared with the number of browsers present on Lewa, and their performance observed during the study period to evaluate which browse tree equivalent availability provides the most reliable estimate of the browsing capacity of Lewa.

METHODS

The woody vegetation of Lewa was surveyed by using the BECVOL method of Smit (1989a) to determine the standing browse biomass. This method has been used successfully in other areas (Orban 1995; Vermaak 1996; Botha 1999). Comparative data for Lewa are thus provided because Botha (1999) used this method to calculate the standing browse biomass for Lewa in an earlier study.

The BECVOL method quantitatively describes woody plant communities, based upon the relationship between the spatial volume of a tree and it's true leaf mass. Estimates of canopy volume and dry leaf mass were used as a basis to estimate the standing browse biomass of the woody vegetation of Lewa. The BECVOL method is not an approximation but it calculates the actual potential of vegetation biomass production and indirectly, therefore the browsing capacity. Browsing capacity is defined in terms of the number of browser units per hectare (BU/ha). A browser unit is defined as a kudu cow of 140 kg that browses exclusively (Snyman 1991). The BECVOL method is not labour - intensive and it involves no destruction of leaf material. It is also possible to determine the standing browse biomass on different height levels. During the current assessment, the maximum browse height for giraffe and elephant was estimated at 5 m, and for black rhinoceros, eland, gerenuk, kudu and impala at 2 m.

According to Owen-Smith (1985), the daily food requirement for an adult kudu is approximately 3 % of the animals' body mass. An adult kudu cow of 140 kg would therefore require 4.2 kg of dry leaf material per day, or 1 533 kg per year to do well. Small animals are equated to larger animals on the basis of relative energy requirements, using the metabolic mass equivalent of $M^{0.75}$, where M = metabolic mass (Meissner 1982). Browser unit replacement values were then calculated by substituting the mean metabolic mass of a non-lactating female (Ledger 1963; Pratt & Gwynne 1977) into the following equation:

$$BU = M^{0.75} / 140^{0.75}$$

M = Metabolic mass of specified animal in kg
BU = Browser unit equivalent = a 140 kg kudu cow that represents 1 BU

The mean metabolic mass and the browser unit equivalents of the browsers on Lewa appear in Table 5 (Meissner 1982; Kruger 1994; Bothma 1996).

The net primary production is the total amount of plant material produced by woody plants, and all of it is potentially available for consumption by herbivores. The available primary production is the amount of plant material accessible to a given species, provided that it is part of that herbivore's diet (Delany 1982). Thus the plant material eaten by a herbivore depends on its dietary habits and mobility. Depending on the rainfall received, the annual fluctuations in browse production can be considerable. At certain times, but particularly so when their demands are approaching or exceeding the available resources, browsers can have a considerable impact on the vegetation of their range. Conversely, Brewer (1994) indicates that at times, the harvesting of plant material may be excessively high in any ecosystem. Kormondy (1996) found that most of the available energy produced in the vegetation is unused, and that a fair amount of energy is expended in plant respiration. Consequently, it becomes evident that a large percentage of the net primary production becomes unavailable to browsers because of a number of factors. A certain percentage of all the browse in any area is inaccessible to browsers because some woody plants vary in their degree of deciduousness and their secondary plant compound (tannins and toxins) content which may deter some browsers. According to Brewer (1994), a high percentage of the available primary production may also be utilised by other feeders such as insects, collembolans, nematodes and bacteria. The plants themselves also utilise some energy to ensure their own regrowth and vigour.

For most South African game ranches, only 10 % of the total browse tree equivalents is available (Smith 1992). Kruger (1994) used a browse tree equivalent availability of 10 % in a calculation of the browsing capacity of the vegetation of the Kalahari Gemsbok National Park. Botha (1999) used a browse tree equivalent availability of 13 % because of the bimodal rainfall received on Lewa and the subsequent differences in the vegetation growing period and phenology. The estimated consumption by mammals (grazers and browsers) in the *Acacia* savannas of Kenya ranged between 9.5 and 18.2 % (Phillipson 1975). Shugart (1998) found that the primary production consumed by herbivores in woodland and shrubland was only 5 %. Past research indicates that the estimated percentage consumption of available browse by herbivores seldom exceeds 10 % for any area (Brewer 1994; Visser 1995; Shugart 1998). Owen & Wiegert (1976) estimated that in most terrestrial ecosystems, less than 10 % of the living material goes to consumers, and that a smaller percentage of this, in turn, occurs in the form of browse material. Bearing these factors in mind, a realistic browse tree equivalent availability had to be formulated for Lewa. A comparison was therefore made between four of the above percentages. These are: 5 % (Shugart 1998), 10 % (Kruger 1994), 13 % (Botha 1999) and 18.2 % (Phillipson 1975). The results obtained were compared with the number of browsers present on Lewa.

Table 5 A comparison of the present situation on Lewa with the four browse availabilities used in the present study. The estimated number of browsers (**NO**) and the resultant stocking rate (**SR**) (ha/browser) and browsing capacity (**BC**)(BU/ha) are given for the seven large browsers on the Lewa Wildife Conservancy, Kenya, from April 1996 to June 1996.

BROWSER	MASS (KG)	BROWSE UNIT (BU) EQUIVALENT	PRESENT			5%			10%			13%			18.2 %		
			NO	SR	BC	NO	SR	BC	NO	SR	BC	NO	SR	BC	NO	SR	BC
Eland	460	2.44	146	166	0.01	26	932	0	66	367	0.01	121	200	0.01	187	130	0.01
Elephant	3 750	11.77	178	136	0.06	27	898	0.01	60	404	0.02	71	341	0.02	105	231	0.04
Gerenuk	25	0.27	50	485	0	25	970	0	50	485	0	50	485	0	70	346	0
Reticulated giraffe	818	3.76	196	124	0.03	57	425	0.01	100	242	0.02	120	202	0.02	163	149	0.03
Kudu	140	1.00	30	808	0	15	1 616	0	30	808	0	50	485	0	50	485	0
Impala	40	0.39	600	40	0.01	75	323	0	200	121	0	280	87	0	400	61	0
Black rhinoceros	880	3.97	21	1 154	0	17	1 426	0	25	970	0	36	673	0.01	40	606	0.01
Total	N/A	N/A	1 221	20	0.11	242	100	0.02	531	46	0.05	728	33	0.06	1 015	24	0.09

Table 6 Present and recommended number of browsers and browsing capacities (LSU/ha) for the seven large browsers on the Lewa Wildlife Conservancy, Kenya, in 1996. The browsing capacity, expressed in LSU, is given in brackets.

BROWSER	LSU EQUIVALENT	PRESENT NO. OF BROWSER	TOTAL BROWSING CAPACITY	RECOMMENDED NO. OF BROWSERS	RECOMMENDED BROWSING CAPACITY
Eland	1.02	146	0.01 (119.14 LSU)	66	0 (53.86 LSU)
Elephant	4.90	178	0.03 (610.54 LSU)	60	0.01 (205.80 LSU)
Gerenuk	0.11	50	0 (5.5 LSU)	50	0 (5.5 LSU)
Reticulated giraffe	1.57	196	0.01 (307.72 LSU)	100	0.01 (157 LSU)
Kudu	0.42	30	0 (12.6 LSU)	30	0 (12.6 LSU)
Impala	0.16	600	0 (48 LSU)	200	0 (16 LSU)
Black rhinoceros	1.65	21	0 (34.65 LSU)	25	0 (41.25 LSU)
Total	N/A	1 221	0.05 LSU / ha (1 138.15 LSU)	531	0.02 LSU / ha (492.01 LSU)

Table 7 Present and recommended number of browsers and browsing capacities (LSU/ha) for the seven large browsers on the Lewa Wildlife Conservancy, Kenya, in 1994. The browsing capacity, expressed in LSU, is given in brackets.

BROWSER	LSU EQUIVALENT	PRESENT NO. OF BROWSER	TOTAL BROWSING CAPACITY	RECOMMENDED NO. OF BROWSERS	RECOMMENDED BROWSING CAPACITY
Eland	1.02	181	0.01 (147.70 LSU)	150	0.005 (122.40 LSU)
Elephant	-	-	-	-	-
Gerenuk	0.11	28	0 (3.08 LSU)	28	0 (3.08 LSU)
Reticulated giraffe	1.57	231	0.02 (362.67 LSU)	102	0.01 (160.14 LSU)
Kudu	0.42	45	0 (18.90 LSU)	45	0 (18.90 LSU)
Impala	0.16	508	0 (40.64 LSU)	255	0 (20.40 LSU)
Black rhinoceros	1.65	22	0 (36.30 LSU)	22	0 (36.30 LSU)
Total	N/A	1 015	(609.29 LSU)	602	0.015 (361.22 LSU)

RESULTS AND DISCUSSION

In this study, the browsing capacity was defined in terms of the number of browser units that can be carried per hectare (BU/ha). However, browsing capacity can also be expressed as the number of large stock units per hectare (LSU/ha), or simply as the number of large stock units (LSU). A large stock unit is defined as an animal with a mass of 450 kg, with a growth rate of 500 g per day, on forage with a mean digestible energy concentration of 55 percent (Meissner 1982). Botha (1999) expressed the browsing capacity of Lewa in large stock units per hectare. Therefore, for comparative reasons, the browsing capacity in this study was also expressed in large stock units per hectare (Tables 6 and 7). Botha (1999) omitted the use of elephants in an estimation of browsing capacity. For this reason, his total recommended browsing capacity (0.015 LSU/ha)(361.22 LSU)(Table 7) is considerably lower than that recommended in the present study (0.02 LSU/ha)(492.01 LSU)(Table 6). If the present recommended browsing capacity were recalculated by omitting the elephants, then the recommended browsing capacity would be 0.01 LSU/ha (286.21 LSU). This is considerably lower than that recommended by Botha (1999) because he used a browse tree equivalent availability of 13 %, and in the present study a browse tree equivalent of 10 % is recommended. It is however, not realistic to omit the elephants in this estimation of browsing capacity because elephants are always present on Lewa.

The total browse available on Lewa at or below maximum browse heights of 2 and 5 m respectively is 7 901 079 kg and 18 082 730 kg. If a browse tree equivalent availability of 5 % (Shugart 1998) is used, then the total available browse biomass would be 395 053.95 kg and 904 136.50 kg respectively. The number of browse units are derived from the assumed consumption rate for a browse unit (3 % of body mass = 4.2 kg/day = 1 533 kg/year) (Owen-Smith 1985). The available browse on Lewa below 2 m should therefore be able to sustain 257.41 BU, and the available browse between 2 and 5 m should be able to sustain 333.98 BU. Therefore the browsing capacity of the woody vegetation on Lewa would be 0.02 BU/ha (591.39 BU).

If a browse tree equivalent availability of 10 % (Kruger 1994) is used, then the total available browse biomass below 2 and 5 m respectively is 790 107.9 kg and 1 808 273 kg. Therefore the available browse on Lewa below 2 m should be able to sustain 515.46 BU, and the available browse between 2 and 5 m should be able to sustain 665.47 BU. The browsing capacity of the woody vegetation on Lewa would be 0.05 BU/ha (1 180.93 BU).

If a browse tree equivalent availability of 13 % (Botha 1999) is used, then the total available browse biomass below 2 and 5 m respectively is 1 027 140.27 kg and 2 350 754.90 kg. Therefore the available browse on Lewa below 2 m should be able to sustain 670.39 BU, and the available browse between 2 and 5 m should be able to sustain 862.99 BU. The browsing capacity of the woody vegetation on Lewa would be 0.06 BU/ha (1 533.38 BU).

If a browse tree equivalent availability of 18.2 % (Phillipson 1975) is used, then the total available browse biomass below 2 and 5 m respectively is 1 437 996.38 kg and 3 291 056.86 kg. Therefore the available browse on Lewa below 2 m should be able to sustain 940 BU, and the available browse between 2 and 5 m should be able to sustain 1 208.7 BU. The browsing capacity of the woody vegetation on Lewa would be 0.09 BU/ha (2 148.7 BU).

The browsing capacity estimates range from 0.02 BU/ha to 0.09 BU/ha. During the study period, Lewa was stocked at 0.11 BU/ha (2 732.36 BU). This figure grossly exceeds even the highest browsing capacity estimate of 0.09 BU/ha. A browsing capacity of 0.03 BU/ha is recommended for the dense bushveld areas of South Africa (Van Rooyen, pers. comm.)[3]. The vegetation of Lewa is classified as savanna, which is more open than dense bushveld. This provides evidence that a browsing capacity of 0.05 BU/ha may even be too high for Lewa. The stocking rate for browsers on Lewa determined during the study period was thought to have exceeded the browsing capacity of the vegetation for the following reasons:

- The appearance of distinct browse-lines on many of the trees on Lewa.
- The destruction of the woody vegetation in certain areas on Lewa, especially by elephants.
- The opening up of mature woodland and their transformation into open grassy plains with scattered trees.
- One black rhinoceros bull already lost condition, probably because of nutritional stress.

The relatively low browsing capacity of Lewa can be attributed to various factors:

- The *Stipa dregeana - Juniperus procera* tall forest and the *Acacia drepanolobium - Themeda triandra* low thicket communities constitute 6 976 ha of the study area (28 %) and are not readily utilised by the giraffe population due to the extreme density of the woody vegetation and topographical inaccessibility of the area. The giraffe are therefore forced to utilise the hills and valleys, which are sensitive areas prone to overutilisation.
- The *Pennisetum stramineum - Themeda triandra* short closed grassland and the *Pennisetum stramineum - Becium hildebrandtii* short closed grassland communities form 2 391 ha of the study area (10 %) and cannot sustain any browsers permanently.
- The *Acacia xanthophloea - Achyranthes aspera* tall closed woodland community forms 806 ha of the study area (3 %) and has suffered severe destruction as a result of the elephant bulls pushing over mature *Acacia xanthophloea* trees. Most of the available browse there is now above 5 m in height, and therefore inaccessible to browsers.
- The *Typha domingensis - Echinochloa colona* swamp forms 60 ha of the study area (0.2 %), but is not utilised by the majority of the browsers on Lewa.
- Cultivated lands on Lewa constitute 299 ha (1 % of the study area) which are unavailable to game.

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Therefore, the total area that is relatively inaccessible or unutilised by most of the browsers on Lewa is 10 532 ha, which is 43 % of the total area of Lewa.

The target browsers studied were the black rhinoceros, the elephant and the giraffe. Stocking rates and browsing capacities for these browsers are discussed and recommendations on future stocking rates are given. The results appear in Table 5, with recommendations given in the section below.

Black rhinoceros

During the study period Lewa was stocked with 21 black rhinoceroses, which equates to 83.37 BU (1 154 ha/black rhinoceros). A number of black rhinoceros deaths have already occurred on Lewa. These deaths were the result of fights caused by a single male black rhinoceros, which has subsequently been removed from Lewa. No deaths as a result of fighting between black rhinoceroses have occurred since the removal of this male. Aggressive behaviour between the black rhinoceroses on Lewa can, however, possibly be attributed to limited range size and territorial conflict. This aspect will have to be monitored closely and the removal of particular animals will have to be considered when necessary. Territorial behaviour sets a limit to the numbers of competing black rhinoceroses that can co-exist in any given reserve. According to Adcock (1994), the range size for a black rhinoceros in the Laikipia region of Kenya, varies from 1 500 to 7 000 ha. If the smallest of these range sizes were used for the black rhinoceros on Lewa, it would mean that a stocking rate of only 16 black rhinoceroses would be recommended for Lewa. The available browse below 2 m in height will sustain 25 black rhinoceroses, provided that the recommended stocking rate of the other browsers is complied with. When using a browse availability of 10 %, the browsing capacity for the black rhinoceros on Lewa is 0.004 BU/ha or 99.25 BU. The recommended stocking rate on Lewa is 970 ha/black rhinoceros (25 black rhinoceroses). If any fighting occurs between the black rhinoceros, then the stocking rate of these browsers would have to be decreased. This would therefore mean that the stocking rate of the other browsers on Lewa would be allowed to increase to compensate for the decrease in the black rhinoceros stocking rate.

Elephant

During the study period Lewa was stocked with approximately 178 elephants, which equates to 2 095.06 BU (136 ha/elephant). Thouless (1995) found that large elephant herds in the Laikipia region have ranges of between 10 000 and 220 000 ha. The estimated browsing capacity for elephants in the savannas of South Africa is 286 ha/elephant (Hall-Martin 1992). The available browse below 2 m in height will sustain a total of 13 elephants, and the available browse between 2 and 5 m in height will sustain 47 elephants if a browse availability of 10 % is used. Therefore the recommended browsing capacity of Lewa for elephants is 0.02 BU/ha or 494.35 BU. The recommended stocking rate on Lewa is 404 ha/elephant (60 elephants). Because of the current condition of the vegetation of Lewa, a conservative stocking rate for elephants has been recommended. However, because the elephants are able to migrate in and out of Lewa, larger herds can be accommodated periodically. These herds will have to be monitored closely. Removal of entire herds or destructive individuals will have to be considered as soon as excessive vegetation destruction is detected. Elephants are known to change vegetation structure over a period of time (Guy 1976; Okula & Sise 1986; Kalemera 1989; Ben-Shahar 1993; Prins & Van der Jeugd 1993; Tchamba 1995; Dublin 1996; Leuthold 1996). Vegetation decline and destruction, primarily of the *Acacia* species, are already prevalent on Lewa. This decline and destruction can be attributed mainly to the large elephant herds which now have access to Lewa. The lack of *Acacia* seedling regeneration and recruitment due to browsing by species other than elephants also clearly indicates a vegetation decline. A reduction in the number of elephants on Lewa will decrease vegetation decline and deterioration so as to benefit the habitat preferences of the black rhinoceros. Adcock & Emslie (1994) state that elephants can reduce black rhinoceros food, but only when the elephants are at high densities and after years of cumulative elephant impact. This is exactly the scenario on Lewa.

Giraffe

During the study period Lewa was stocked with 196 giraffe, which equates to 736.96 BU (124 ha/giraffe). Hall-Martin (1974a) found that giraffe range sizes vary from 400 to 500 ha for South Africa, Zaire and Kenya. The available browse on Lewa below 2 m in height can sustain 26 giraffe, and the available browse between 2 and 5 m in height can sustain 74 giraffe if a browse availability of 10 % is used. Therefore the recommended browsing capacity of Lewa for giraffe is 0.016 BU/ha or 376 BU. The recommended stocking rate on Lewa is 242 ha/giraffe (100 giraffe). Kruger (1994) recommended a stocking rate of 150 ha/giraffe in the Kalahari Gemsbok National Park in South Africa, where this area has approximately double the available browse when compared to Lewa (Table 4). Continued overutilisation of the available browse by the giraffe will result in woody vegetation decline, both in productivity and abundance. In numerous plant communities on Lewa, a distinct giraffe browse-line is already visible evidence of overutilisation by the giraffe. Plant communities especially subjected to overutilisation by the giraffe should therefore be given the opportunity to regenerate.

CONCLUSIONS

The results of the study indicate that the browsing capacity of the woody vegetation has already been exceeded. Factors such as browse-lines, habitat destruction and changes in the structure of the vegetation are all indications that the browsers are overutilising their habitat. When comparing the current browsing capacity of 0.11 BU/ha to even the highest estimated browsing capacity of 0.09 BU/ha, a 21.36 % reduction of browsers on Lewa would have to be made. It can clearly be seen that by using a browse availability of 13 % an overestimation of the stocking rate for the black rhinoceros on Lewa is obtained. It therefore appears that a browse availability of less than 13 % for Lewa is realistic. A browse availability of 5 % is considered very conservative for Lewa. A browse availability of 10 % is therefore recommended for Lewa. Because of the bimodal rainfall received on Lewa, the stocking rate of some of the browsers may be allowed to increase during periods of above-average rainfall.

The recommendation based on this study for the management of browsers on Lewa is to reduce their numbers by approximately 57 %. The recommended stocking rate for each of the browsers on Lewa is as follows: 25 black rhinoceros, 66 eland, 60 elephant, 50 gerenuk, 100 reticulated giraffe, 200 impala and 30 greater kudu. This implies a reduction from the current browsing capacity of 0.11 BU/ha to a browsing capacity of 0.05 BU/ha. This reduction may seem gross, but the woody vegetation of Lewa will not recover or regenerate with a higher browser stocking rate.

The stocking rate of the eland, elephant, giraffe and impala already exceeds the browsing capacity of the woody vegetation. This is not so much seen in their performance or condition, but in the poor condition of the woody browse on Lewa, especially during the dry season. It is recommended that the stocking rate of these browsers be reduced. The numbers of kudu and the gerenuk should be allowed to increase, but their condition will have to monitored, especially during periods of drought. The available browse on Lewa will sustain approximately 25 black rhinoceroses. Their growth rate is increasing, despite a series of deaths resulting from fights and other unfortunate incidences. It is not known whether the fights are as a result of overstocking of black rhinoceroses, and hence territorial conflicts. Close monitoring of this situation is paramount to the continued health of the black rhinoceros population on Lewa. If fighting should occur, the culprit bulls should be removed from Lewa immediately.

A discussion of the various factors which influence the browsing capacity of Lewa, leads one to believe that a browsing capacity estimate based solely on canopy volume and dry leaf mass, is in fact an oversimplification of a complex set of calculations. The browsing capacity that was estimated in the present study is based on a single year of observations, and an error of judgement is not impossible. The stocking rate reductions presented here may be excessive; and only through the implementation of an adaptive management approach, where the range condition is monitored and the stocking rate manipulated, will trends in the vegetation condition be noticeable. The stocking rate should then be adjusted according to the management objectives and the changing environmental factors. Vegetation structure and condition will be the key element of monitoring, not animal condition.

CHAPTER 5

HABITAT SELECTION

INTRODUCTION

Ever since the observations of the earliest travellers, it has been acknowledged that a relationship exists between animals and their environment. The maintenance of mixed ungulate populations in an area, without detriment to either habitat or animals, requires insight into the habitat needs, habitat use and potential interspecific competition among the animals of the area (Scogings, *et al.* 1990). The degree of dependency of a ruminant on a certain habitat is determined by the availability of preferred food, the minimum size of the area for daily and seasonal activities, the absence of extreme competition, the availability of cover and free surface water, the freedom to escape unnatural climatic extremes and the opportunity for reproduction (Pienaar 1974). A striking feature of African herbivore communities is the relatively large number of species with almost similar ecological requirements that often coexist in the same area. This has led to a number of studies on ecological separation, which are the mechanisms reducing interspecific competition and preventing possible competitive exclusion (e.g.: Lamprey 1963; Jarman 1974; Hirst 1975; Leuthold 1978; Weaver 1995).

Herbivore habitats within Lewa comprise vegetative and topographical features. The use by a given species of these features is centred in its habitat (Odum 1971). Stoddart, Smith & Box (1975) define habitat by the physical characteristics of the area that an animal inhabits. Various research studies on African ungulates and their habitat preferences have been conducted (Lamprey 1963; Pienaar 1974; Hirst 1975; Engelbrecht 1986; Scogings, *et al.* 1990; Wentzel 1990; Theron 1991; Dekker 1996; Vermaak 1996). From these studies it is clear that the uneven distribution of large herbivores in a specific area is the result of preferences for certain habitats above others (Jarman 1974; Pienaar 1974; McNaughton & Georgiades 1986). Habitats are selected by a species according to the speciality of its niche and the extent of the special physical adaptations which the species has developed to successfully exploit the niche. Species adapt to certain parts of the environment where they can always be found (Thompson 1986). According to Johnson (1980), four hierarchical orders of habitat selection can be distinguished:

- First order selection - the geographical area in which the species occurs.
- Second order selection - the range of the species within the geographical area.
- Third order selection - the utilisation of different habitat components within the range of the species.
- Fourth order selection - the selection of certain food plants from the available habitat components.

The fact that a species is invariably associated with a certain habitat or habitat elements, automatically means that the minimum requirements for existence are present (Riney 1982). The presence or availability of water inevitably plays an important role in determining habitat preferences (Pettifer & Stumpf 1981; Engelbrecht 1986; Bothma & Van Rooyen 1996), but it is the physical structure of the habitat that is the decisive factor if water and food are available in more than one place (Joubert 1996). Species composition and structure are the two components of the vegetation which form an important part of the habitat. The species that constitute the vegetation will determine whether or not the food source is sufficient. The structure of the vegetation plays an equally important role in determining whether or not the habitat is suitable.

A number of other reasons exist for the habitat preferences shown by animals. Research has shown that forage production and degree of utilisation (Wentzel, Bothma & Van Rooyen 1991), environmental temperature (Simpson 1972), height of the grass (Bell 1971; Ferrar & Walker 1974; Bothma & Van Rooyen 1996), defence mechanisms (Cooper & Owen-Smith 1985; Hay & Van Hoven 1988; Furstenburg & Van Hoven 1994), availability of food at certain height classes (Sauer, Theron & Skinner 1977; Pellew 1983a) and plant phenology (Sauer, *et al*. 1977; Novellie 1983; Engelbrecht 1986) are all possible reasons for these preferences. These factors operate in different magnitudes and directions, sometimes opposingly and at other times together (Ben-Shahar 1986).

Ecologically, social aggregations of the same animal species occupying a particular space could be defined as a population. Before understanding the characteristics of such a particular population for effective management, one must be able to measure and interpret a number of its features (Smuts 1974). The major aspects of game populations relevant to game ranch management are: the growth, age and sex composition, the social organisation, and the behaviour of the populations. These aspects can act alone or in combination, but all of them are connected with the population's ability to multiply. Knowledge of the population structure of game is important because it indicates the health and growth of a population. It is therefore important to know the number of game in an area, so as to determine if the area is under- or overutilised (Bothma 1996).

On an area like Lewa where man has an influence on the functioning of the ecosystem through management, factors such as fences, veld burning programmes and roads will definitely influence the habitat preferences of the animals. Concern has already been expressed there over the abundance of elephant and giraffe on Lewa, and whether their numbers posed a threat to an increase in the black rhinoceros population. The aim of this study was therefore to examine the habitat preferences of these browsers. To do so, various environmental characteristics to which the browsers showed preference, were identified. An objective evaluation was then made as to whether these characteristics contributed to the ecological separation of these species or not. The relationships or not between the browsers and these environmental characteristics were also established.

METHODS

Field collection of the data

Numerous methods exist to determine the habitat preferences and interactions of herbivores with each other and their respective habitats. The specific method chosen is usually dictated by local circumstances (Smuts 1974). The terrain and size of Lewa suggested that the use of road transects with repeated observations over time, was the most applicable method.

At the commencement of the habitat selection surveys, an updated vegetation map of Lewa was unavailable, and the area was therefore subdivided into 10 broad habitat types. The data collection lasted from May 1996 to May 1997. Eight road transects were delineated throughout the study area (Figure 28). The road transect lengths varied from 7 to 21 km and totalled 100.6 km. The study area was surveyed three times a month on a fixed route which was traversed by vehicle. The road transects traversed all the habitat types in the study area and took 6 days to complete. Speed of travel was adjusted to the individual habitat type and respective season. Observation speeds during the wet season tended to be slower due to the poor condition of the roads. Road transects were often impossible to complete during the wet season because of impassability. The road transects were done in the early morning and the late afternoon. To minimise observer bias, the route direction was reversed on alternate surveys. Care was taken to prevent double-counting of any visually identifiable animals along a transect.

Qualitative vegetation data were collected on the basis of herbivore occurrence and are thus reflective of herbivore-habitat preferences. When a black rhinoceros, an elephant or a giraffe was sighted, the vehicle was stopped and pertinent environmental characteristics, which might determine herbivore-habitat preferences, were recorded by category on a field data sheet (Appendix B). Individual animals or herds were recorded as one observation.

To reflect the realities of the phenological cycle of plants, all the data were divided according to the season; dry or wet, depending on the rainfall patterns on Lewa. Dry season data were defined as that collected from 1 May to 30 September and from 1 February to 31 March. Wet season data were collected from 1 October to 31 January and from 1 April to 30 April. Rainfall in the study area is, however, often erratic and does not necessarily occur in the seasons depicted in Chapter 2.

A total of 1 076 observations were made on Lewa: 95 for the black rhinoceros, 300 for the elephant and 681 for the giraffe. The low number of observations for the black rhinoceros can be attributed to the fact that there were only 21 animals on Lewa at the time of the study and that they were not always sighted while undertaking habitat selection surveys.

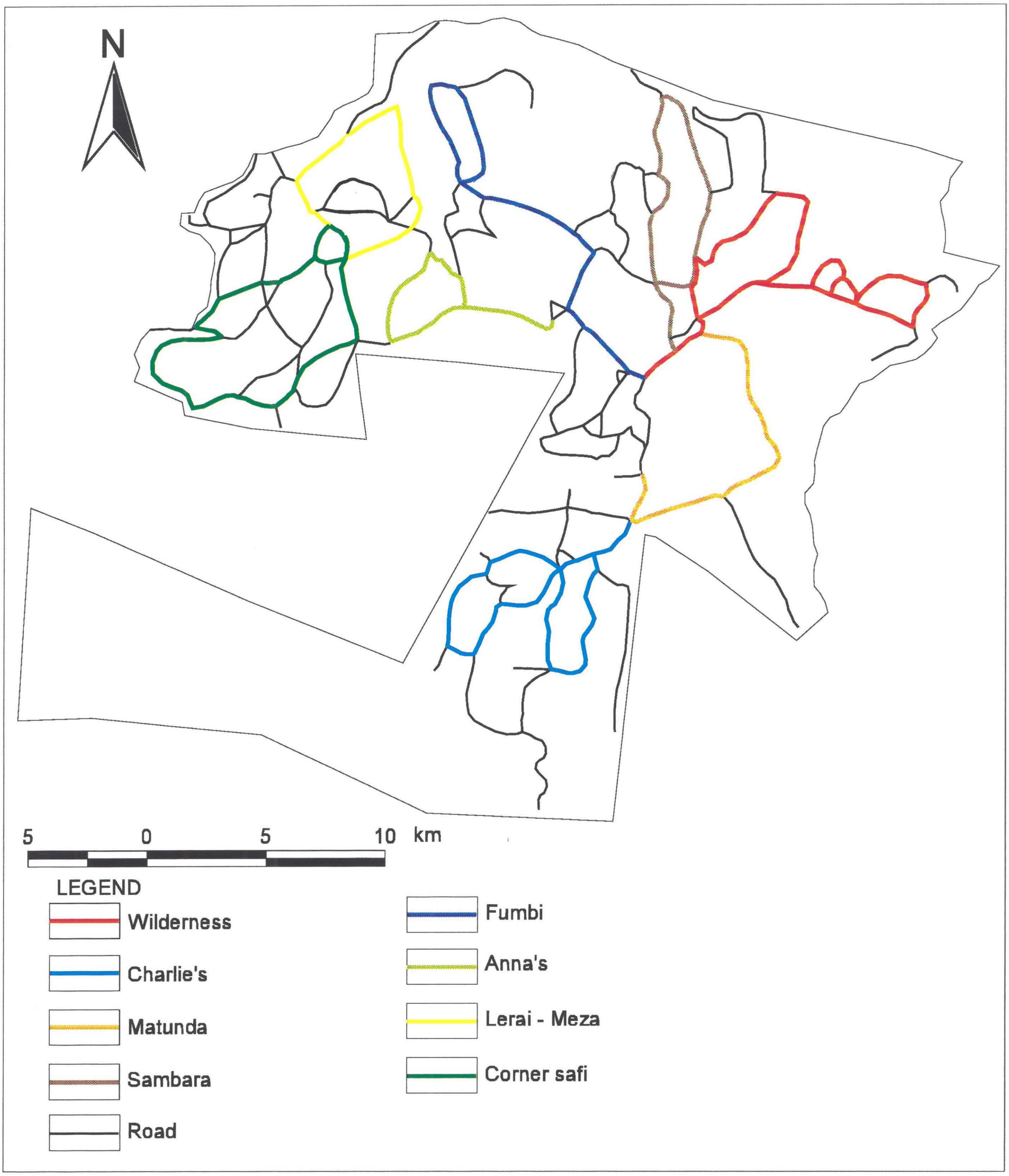

Figure 28 Eight road transects were delineated throughout the Lewa Wildlife Conservancy and were used in the determinationn of the habitat selection of the black rhinoceros, elephant and giraffe populations.

The following aspects were recorded at each sighting:

Animal:

- Black rhinoceros
- Elephant
- Reticulated giraffe

Date and time of observation:

The date of each observation was noted to determine the seasonal habitat preference of the browsers. The time of each observation was recorded to determine whether the time of day had any bearing on the selection of a particular habitat.

Grid reference:

Co-ordinates were read using a Magellan Geographical Positioning System (GPS). These co-ordinates were used to plot a map of animal distribution to assist in determining the habitat preference of the browsers.

Group composition: Adapted from Bothma (1996)

- Males - identified by distinct male characteristics.
- Females - identified by distinct female characteristics.
- Juveniles - identified by small size, immature features and characteristics.
- Total herd size - number of animals in the herd.

Activity: Adapted from Engelbrecht (1986) & Wentzel (1990)

- Browsing - when more than half the group was engaged in browsing.
- Grazing - when more than half the group was engaged in grazing.
- Drinking - at least one of the herd was drinking water.
- Walking - moving without delay.
- Resting - animals lying down or standing.

Distance from water:

The available water sources were noted throughout the year. The distance of each sighting from the nearest water source was recorded to determine whether this characteristic had any influence on habitat selection. Class intervals included the following distances from water:

- 0 - 50 m
- 51 - 250 m
- 251 - 500 m
- 501 - 1 000 m
- 1 001 - 2 000 m
- > 2 000 m

Habitat type:

The following habitat types were identified before the commencement of the habitat selection surveys:

- Shrub forest
- Open grassland plains
- Mixed woodland hills
- Mixed woodland plains
- Mixed *Acacia* hills
- Mixed *Acacia* plains
- *Acacia nilotica* woodland
- *Acacia drepanolobium* woodland
- *Acacia drepanolobium* - *Acacia seyal* woodland
- *Acacia xanthophloea* riverine woodland

Aspect of the slopes:

Aspect is the compass direction towards which a slope faces. It is expressed as degrees relative to true North (Gabriel & Talbot 1984). The aspects N, NE, E, SE, S, SW, W or NW were determined using a compass.

Landscape position:

The landscape unit where the group was sighted, was recorded. The options used were:

- Plains
- Gentle slopes
- Steep slopes
- Valleys
- Plateaus
- Riverbed

Tree canopy cover: Adapted from Edwards (1983)

- 0 - 10 % - crown gap ≥ 10 m
- 11 - 20 % - crown gap < 10 - 5 m
- 21 - 30 % - crown gap < 5 - 2 m
- > 30 % - crown gap < 2 m

Bush canopy cover: Adapted from Edwards (1983)

- 0 - 10 % - crown gap ≥ 10 m
- 11 - 20 % - crown gap < 10 - 5 m
- > 20 % - crown gap < 5 m

Woody vegetation density:

- Sparse - visibility > 100 m
- Open - visibility > 50 - 100 m
- Medium - visibility 20 - 50 m
- Dense - visibility < 20 m

Grass cover: Adapted from Ben-Shahar (1986)

- Sparse - grass sparsely spread in areas, with annual grasses and forbs.
- Medium - a good canopy cover with occasional open areas.
- Dense - maximal canopy cover with few or no open areas.

Statistical analysis of the data

Simple quantitative studies express habitat selection in terms of the proportion of animals seen in each habitat type. An extension of this concept is the comparison of observed habitat use with expected habitat use according to habitat availability (Hirst 1975). Such studies usually involve classical statistical techniques of hypothesis testing (Williams 1973). The null hypothesis tested is that the distribution of animals in an area is random over all habitat types, meaning that the expected occurrence of animals would be in proportion to the relative occurrence of the different habitats in the area. Several methods of multivariate analyses have been used to analyse the complex interrelationships between herbivores and the many facets of their environments (Ferrar & Walker 1974; Hirst 1975; Beardall, Joubert & Retief 1984). Studies using multivariate analysis techniques do not require information on the amount of habitat available; a record of habitat variables at each animal location is usually sufficient. Multivariate analyses are more accessible now because of the development of rapid, flexible computer programmes such as Detrended Correspondence Analysis and Correspondence Analysis (Scogings, *et. al.* 1990).

Three statistical analysis programmes were considered, but only one of these gave meaningful results for the categorical nature of the data that were collected on Lewa.

Detrended Correspondence Analysis (DECORANA) is a computer programme designed primarily for ecologists with data on the occurrence of a set of species in a set of samples (Evans 1994). One of the limitations of DECORANA is that the determination of the dominant gradient affecting community composition has to be done as a separate step (Ter Braak 1986). This can be tedious and time consuming, especially if the data set is large. DECORANA was applied to the habitat selection data, but no meaningful results were obtained. The results that emanated were, in fact, already known. The data set was also excessively large. Therefore the interpretation of the ordination diagram would have proved tedious for the type of results obtained.

Canonical Community Ordination (CANOCO) is a computer programme designed for data analysis in community ecology. Canonical ordination is a class of techniques for relating the composition of plant communities to their environment. The use of canonical ordination greatly improves the power to detect the specific effects of environmental variables (Ter Braak 1988). CANOCO has none of the disadvantages of DECORANA, although limitations are present. One major limitation is that the independent (environmental) variables are assumed to be measured without error and to be constant within a site (Palmer 1993). A second limitation is that CANOCO cannot cope with missing values. Therefore sightings with missing values in the environmental data have to be deleted (Ter Braak 1987). The habitat selection data were subjected to CANOCO, but another limitation of the programme was discovered when all of the data could not be accommodated in the programme. CANOCO can cope with up to 500 observations, but the number of observations in the habitat selection data used here exceeded 1 000.

Categorical modeling (CATMOD) is a procedure for categorical data modeling. The categorical modeling procedure (PROC CATMOD) provides a wide variety of categorical data analyses and analyses data that can be represented by a multiway contingency table. PROC CATMOD fits linear models to functions of response frequencies and can be used for linear modeling, log-linear modeling, logistic regression and repeated measurement analysis. CATMOD uses maximum-likelihood estimation of parameters for log-linear models and the analysis of generalised logits. CATMOD uses weighted-least-squares estimation of parameters for a wide range of general linear models (SAS® 1990).

The habitat selection data collected on Lewa were subjected to the CATMOD procedure. This is a unique but time-consuming procedure. Detailed analysis of the data was performed, and reliable, meaningful results were obtained. Categorical data of this type are ideally suited for submission to the CATMOD procedure according to Van der Linde (pers. comm.)[4].

In the current study, each observation entailed 13 variables. The data associated with each of these variables were investigated in groups of categories (Appendix C). The variables were submitted to CATMOD by the designated browser species (V4A), the activity (V7A) and by the season of observation (V14A). The herd size (V5) was used as a weighting factor. Data specific to each browser species were considered individually by its variables. Models were then created using CATMOD (Table 8). Different groupings of variables (e.g. A, B, C, D, E) (Appendix C) were created if a model could not be built for the first grouping used. Groups of categories of variables were then played off against each other until a model was obtained. For example, group B of V2 (habitat type) was played off against every other group of categories of all the other variables, until a viable model was built. Such a model was one with the highest maximum likelihood ratio, with as many categories per variable and as many variables as possible in the model (Figure 29). In other words, categories had to be regrouped and a CATMOD analysis performed on each regrouping, until immediately prior to the mathematical collapse of the model. This aspect was extremely time-consuming, although a thorough analysis of the data was performed in this way and every combination of category groups per variable was explored. Important information for further research on this topic is provided here, as it signifies firstly, that the categories of group A (Appendix C), for example, were initially too finely defined, and secondly, not enough data were collected to ensure that each category of group A (Appendix C) had at least one observation.

CATMOD then generated output displayed as "maximum-likelihood analysis-of variance" tables and "analysis of maximum-likelihood estimates" for each browser species data set. Contrast statements were drawn up, per odds ratio, to determine the chi-square value and the probability for testing the significance of the odds ratio in question. The probability (P) of each variable was examined for statistical significance. Where $P < 0.05$, this was considered as statistically significant, although probabilities of up to 0.078 were also accepted in the data interpretation. Probability can be defined as the likelihood or chance that a particular event will occur (Berenson & Levine 1996). The probability of the occurrence of any event ranges from .00 (no possibility of the event occurring) to 1.00 (the event is certain to happen) (Spatz & Johnston 1984).

When looking at the odds ratio of a particular variable in a multivariate model it is certain that those odds ratios have been corrected for all other variables in the model. Therefore there will be no confounding of the odds ratio of the specific variable with other variables in the model (Groeneveld, pers. comm.)[5]. The odds ratio represents the probability of a success (here the sighting of a specific browser species) compared with the probability of failure (here the sighting of a browser species other than that used in the success sighting). For example, if an event is twice as likely to occur than not to

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Table 8 Models used in the determination of the odds ratio's and probabilities in the habitat preference analysis for the black rhinoceros, elephant and giraffe populations on the Lewa Wildlife Conservancy, Kenya, from May 1996 to May 1997 by using the CATMOD procedure.

BROWSER	ACTIVITY	SEASON	MODEL NUMBER	MODEL
Black rhinoceros	not specified	wet	1	V2E V3A V6B V8C V9C V10B V11B V12B
Black rhinoceros	not specified	dry	2	V2E V3A V6B V8C V9C V10B V11B V12B
Black rhinoceros	browsing	wet	3	V2E V3B V6C V8C V9D V10B * V12B *
Black rhinoceros	browsing	dry	4	V2E V3B V6C V8C V9D V10B * V12B
Black rhinoceros	browsing	dry	5	V2E V3B V6C V8C V9C V10B V11A V12B
Black rhinoceros	walking	wet	6	V2E V3B * V8C V9C * V11A V12B
Black rhinoceros	walking	dry	7	V2E V3B V6B V8C V9C V10B V11A V12B
Black rhinoceros	walking	dry	8	V2E V3B * V8C V9C * V11A V12B
Black rhinoceros	resting	wet	9	* V3B * V8C V9C V10B V11A V12A
Black rhinoceros	resting	wet	10	* * * * V9D V10B * V12C
Black rhinoceros	resting	dry	11	V2B V3B V6B V8C V9C V10B V11A V12A
Black rhinoceros	resting	dry	12	* V3B * V8C V9C V10B V11A V12A
Elephant	not specified	wet	13	V2B V3A V6A V8B V9A V10B V11B V12B
Elephant	not specified	dry	14	V2B V3A V6A V8B V9A V10B V11B V12B
Elephant	browsing	wet	15	V2A V3A V6A V8B V9C V10A V11B V12B
Elephant	browsing	wet	16	V2E V3B V6C V8C V9D V10B * V12B
Elephant	browsing	dry	17	V2A V3A V6A V8B V9C V10A V11B V12B
Elephant	browsing	dry	18	V2E V3B V6C V8C V9D V10B * V12B
Elephant	walking	wet	19	V2E V3B * V8C V9D * * V12B
Elephant	walking	wet	20	V2E V3B V6B V8C V9D V10B * V12B
Elephant	walking	wet	21	V2E V3B V6B V8B V9C V10B V11A V12B
Elephant	walking	dry	22	V2E V3B V6B V8B V9C V10B V11A V12B
Elephant	walking	dry	23	V2E V3B V6B V8C V9D V10B * V12B
Elephant	resting	wet	24	V2E * * * V9C V10B * V12C
Elephant	resting	wet	25	* * * * V9D V10B * V12C
Elephant	resting	dry	26	V2E V3B V6B V8C V9C V10B V11B V12C
Elephant	resting	dry	27	V2E * * * V9C V10B * V12C
Giraffe	not specified	wet	28	V2B V3A V6A V8A V9A V10B V11B V12A
Giraffe	not specified	wet	29	V2E V3B V6C V8C V9D V10B V11B V12B
Giraffe	not specified	dry	30	V2B V3A V6A V8A V9A V10B V11B V12A
Giraffe	browsing	wet	31	V2B V3A V6A V8A V9C V10A V11B V12B
Giraffe	browsing	wet	32	V2E V3B V6C V8C V9D V10B * V12B
Giraffe	browsing	dry	33	V2B V3A V6A V8A V9C V10A V11B V12B
Giraffe	walking	wet	34	V2E V3B V6B V8B V9C V10B V11A V12A
Giraffe	walking	dry	35	V2E V3B V6B V8B V9D V10B * V12B
Giraffe	walking	dry	36	V2E V3B V6B V8C V9D V10B * V12B
Giraffe	resting	wet	37	V2E * V6B V8C V9D V10B V11B V12B
Giraffe	resting	dry	38	V2E * V6B V8C V9D V10B V11B V12B

Note: missing variables indicated by an asterisk (*)

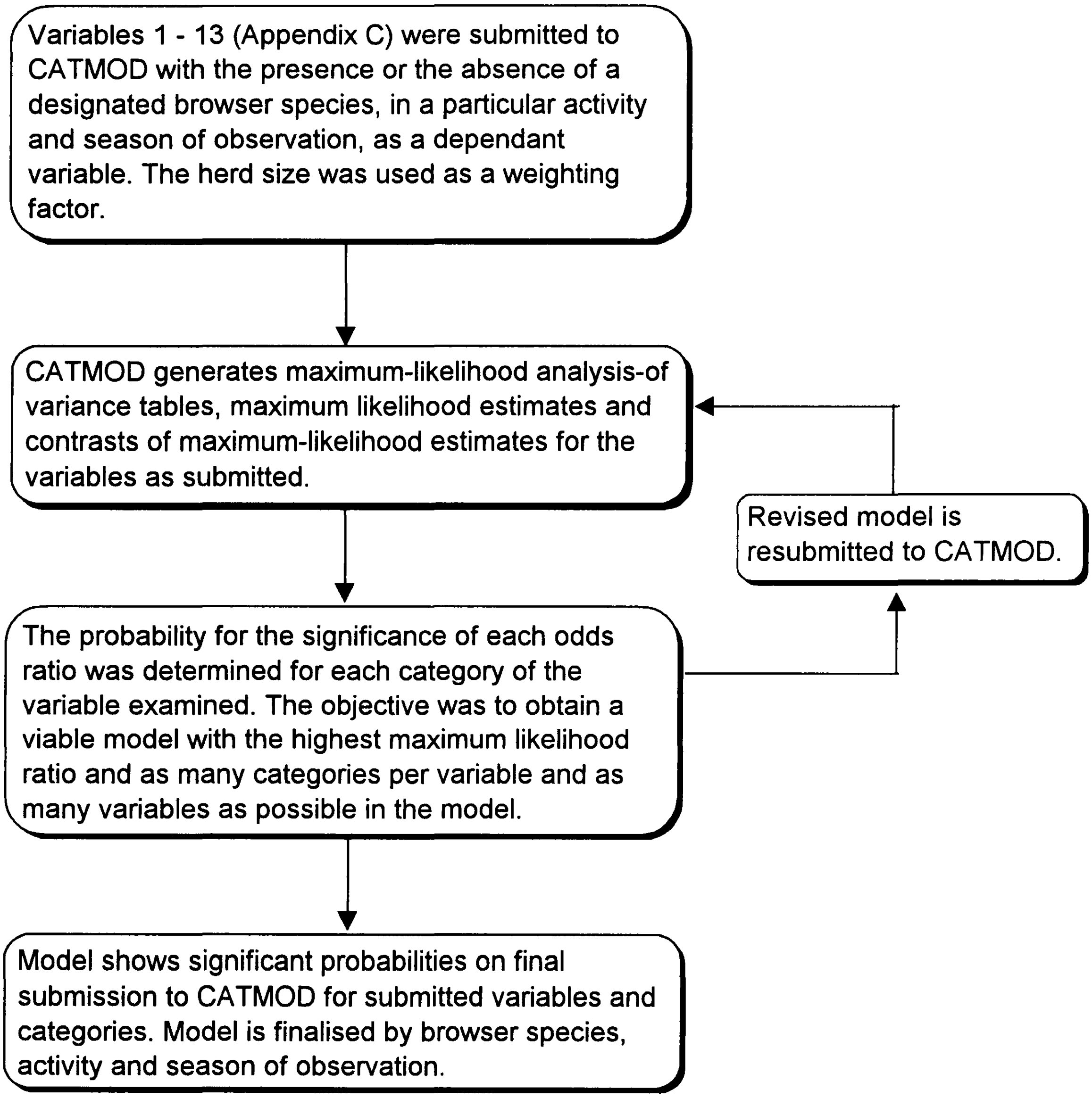

Figure 29 Flow chart illustrating the process involved in submitting habitat preference data to CATMOD analysis.

occur, the odds are 2:1 that it will occur (Freund & Simon 1991). The odds ratios were not determined within the PROC CATMOD. The probability tests the null hypothesis that the true odds ratio is actually 1. When the probability is small enough, the null hypothesis can be rejected as can the probability. For example, a probability of 0.0002 signifies that one is rejecting the null hypothesis by two chances in 10 000.

RESULTS AND DISCUSSION

The results of the CATMOD analysis by the type of browser (black rhinoceros, elephant and giraffe) are presented in Tables 9 to 11. Appendix C is the interpretation of the variables presented in Tables 9 to 11. Each data set was considered separately, and models were built with the maximum number of variables possible, until immediately prior to the collapse of the model. The interpretation of these models provided data specific to each individual browser.

Black rhinoceros

On Lewa the black rhinoceros is mostly indifferent in its selection of habitats, although the open grassland plains, the mixed woodland plains and the *Acacia nilotica* woodland are utilised to a lesser degree (Table 9). It is 19 times more likely to observe a black rhinoceros browsing in the *Acacia drepanolobium - Acacia seyal* woodland, than on the mixed woodland plains (P = 0.0000). The black rhinoceroses all have distinct ranges that incorporate most of the habitats on Lewa. During both the wet and dry seasons, a clear preference is shown for the *Acacia drepanolobium - Acacia seyal* woodland, although the mixed woodland hills are also utilised to a large extent. It is more likely to observe a black rhinoceros in the mixed woodland hills (Odds ratio = 5:1 ; P = 0.0338) or the *Acacia drepanolobium - Acacia seyal* woodland (Odds ratio = 15:1 ; P = 0.0000), than on the mixed woodland plains. The *Acacia drepanolobium - Acacia seyal* low open woodland is the second largest plant community on Lewa and it is therefore included in the range of many of the black rhinoceroses. In the southwest of Lewa, this plant community constitutes the range of six of the black rhinoceroses. Most of the sightings of the black rhinoceros were also made in this plant community. Therefore the data could possibly be biased in that direction. The forest, forest margins and the shrub forest are also utilised to a large extent and constitute the range of six of the black rhinoceroses. Road transects did not traverse the forest because observations would have been limited in the dense vegetation.

The black rhinoceros population on Lewa was observed in habitats where the woody vegetation is sparse. During the wet season, it was more likely to observe a black rhinoceros browsing in habitats where the woody vegetation is sparse, rather than medium (Odds ratio = 31:1 ; P = 0.0005). Similarly, during the dry season, it was six times more likely to observe a black rhinoceros browsing in habitats where the woody vegetation was sparse rather than medium (P = 0.0152). The vegetation on Lewa is predominantly open woodland, facilitating black rhinoceros sightings, especially during the dry

Table 9 Odds ratio's and probabilities, categorised by season and activity, for the black rhinoceros on the Lewa Wildlife Conservancy, Kenya, from May 1996 to May 1997, indicating their presence in category A, as opposed to category B, for the specific variable measured.

WET SEASON								DRY SEASON							
variable	group number	number of categories	category A	category B	A:B	probability	model number	variable	group number	number of categories	category A	category B	A:B	probability	model number
Activity - not specified															
Habitat type	E	3	Drep sey (1)	MWH (2)	3:1	0.0481	1	Habitat type	E	3	Drep sey (1)	MWH (2)	3:1	0.0552	2
Habitat type	E	3	Drep sey (1)	MWP (3)	15:1	0.0000	1	Habitat type	E	3	Drep sey (1)	MWP (3)	4:1	0.0030	2
Habitat type	E	3	MWH (2)	MWP (3)	5:1	0.0338	1	*	*	*	*	*	*	*	*
Time observed	A	9	07:00 - 08:00 (2)	16:00 - 17:00 (8)	7:1	0.0124	1	Time observed	A	9	16:00 - 17:00 (8)	07:00 - 08:00 (2)	5:1	0.0008	2
Time observed	A	9	11:00 - 12:00 (6)	06:00 - 07:00 (1)	26:1	0.0002	1	Time observed	A	9	16:00 - 17:00 (8)	08:00 - 09:00 (3)	3:1	0.0148	2
Time observed	A	9	11:00 - 12:00 (6)	07:00 - 08:00 (2)	11:1	0.0011	1	Time observed	A	9	16:00 - 17:00 (8)	09:00 - 10:00 (4)	3:1	0.0498	2
Time observed	A	9	11:00 - 12:00 (6)	08:00 - 09:00 (3)	29:1	0.0001	1	Time observed	A	9	16:00 - 17:00 (8)	11:00 - 12:00 (6)	4:1	0.0647	2
Time observed	A	9	11:00 - 12:00 (6)	09:00 - 10:00 (4)	16:1	0.0039	1	Time observed	A	9	16:00 - 17:00 (8)	15:00 - 16:00 (7)	7:1	0.0252	2
Time observed	A	9	11:00 - 12:00 (6)	15:00 - 16:00 (7)	9:1	0.0254	1	Time observed	A	9	17:00 - 18:00 (9)	07:00 - 08:00 (2)	2:1	0.0558	2
Time observed	A	9	11:00 - 12:00 (6)	16:00 - 17:00 (8)	77:1	0.0000	1	*	*	*	*	*	*	*	*
Time observed	A	9	11:00 - 12:00 (6)	17:00 - 18:00 (9)	21:1	0.0002	1	*	*	*	*	*	*	*	*
Time observed	A	9	15:00 - 16:00 (7)	16:00 - 17:00 (8)	9:1	0.0343	1	*	*	*	*	*	*	*	*
Aspect	B	4	N (2)	E (1)	6:1	0.0018	1	Aspect	B	4	E (1)	S (3)	3:1	0.0423	2
Aspect	B	4	W (4)	E (1)	3:1	0.0509	1	Aspect	B	4	N (2)	S (3)	5:1	0.0008	2
Aspect	B	4	W (4)	S (3)	5:1	0.0080	1	Aspect	B	4	N (2)	W (4)	2:1	0.0201	2
Aspect	B	4	N (2)	S (3)	10:1	0.0003	1	*	*	*	*	*	*	*	*
Distance from water	C	3	501 - 1 000 m (2)	0 - 500 m (1)	4:1	0.0023	1	Distance from water	C	3	501 - 1 000 m (2)	0 - 500 m (1)	3:1	0.0027	2
Distance from water	C	3	> 1 000 m (3)	0 - 500 m (1)	3:1	0.0784	1	Distance from water	C	3	> 1 000 m (3)	0 - 500 m (1)	10:1	0.0000	2
*	*	*	*	*	*	*	*	Distance from water	C	3	> 1 000 m (3)	501 - 1 000 m (2)	4:1	0.0000	2
Landscape position	C	3	Plain (2)	Slope (1)	4:1	0.0218	1	Landscape position	C	3	Valley (3)	Slope (1)	3:1	0.0232	2
Woody veg. density	B	3	Sparse (3)	Medium (1)	10:1	0.0004	1	Woody veg. density	B	3	Sparse (3)	Medium (1)	4:1	0.0085	2
Woody veg. density	B	3	Sparse (3)	Open (2)	5:1	0.0009	1	Woody veg. density	B	3	Sparse (3)	Open (2)	3:1	0.0167	2
*	*	*	*	*	*	*	*	Grass cover	A	3	Medium (2)	Dense (1)	2:1	0.0131	2
*	*	*	*	*	*	*	*	Grass cover	A	3	Medium (2)	Sparse (3)	8:1	0.0035	2
Activity - browsing															
Habitat type	E	3	Drep sey (1)	MWH (2)	5:1	0.0394	3	Habitat type	E	3	Drep sey (1)	MWP (3)	4:1	0.0146	4
Habitat type	E	3	Drep sey (1)	MWP (3)	19:1	0.0000	3	*	*	*	*	*	*	*	*
*	*	*	*	*	*	*	*	Time observed	B	3	15:00 - 18:00 (3)	06:00 - 09:00 (1)	2:1	0.0336	4
Aspect	C	5	N (2)	S (5)	6:1	0.0227	3	Aspect	C	5	E (1)	S (5)	13:1	0.0245	5
Aspect	C	5	W (4)	S (5)	5:1	0.0293	3	Aspect	C	5	N (2)	S (5)	25:1	0.0031	5
*	*	*	*	*	*	*	*	Aspect	C	5	NE (3)	S (5)	22:1	0.0066	5
*	*	*	*	*	*	*	*	Aspect	C	5	W (4)	S (5)	10:1	0.0439	5
*	*	*	*	*	*	*	*	Aspect	C	5	N (2)	W (4)	3:1	0.0516	5
Distance from water	C	3	501 - 1 000 m (2)	0 - 500 m (1)	3:1	0.0678	3	Distance from water	C	3	> 1 000 m (3)	0 - 500 m (1)	6:1	0.0005	4
*	*	*	*	*	*	*	*	Distance from water	C	3	> 1 000 m (3)	500 - 1 000 m (2)	4:1	0.0039	4
Landscape position	C	3	Plain (2)	Slope (1)	5:1	0.0293	3	Landscape position	C	3	Plain (2)	Slope (1)	7:1	0.0321	5
Woody veg. density	B	3	Open (2)	Medium (1)	9:1	0.0039	3	Woody veg. density	B	3	Sparse (3)	Medium (1)	6:1	0.0152	5
Woody veg. density	B	3	Sparse (3)	Medium (1)	31:1	0.0005	3	Woody veg. density	B	3	Sparse (3)	Open (2)	6:1	0.0095	5
*	*	*	*	*	*	*	*	Grass cover	A	3	Medium (2)	Dense (1)	3:1	0.0183	5
Activity - walking															
*	*	*	*	*	*	*	*	Habitat type	E	3	Drep sey (1)	MWP (3)	13:1	0.0590	7
Time observed	B	3	9:00 - 12:00 (2)	06:00 - 09:00 (1)	49:1	0.0239	6	*	*	*	*	*	*	*	*
Time observed	B	3	9:00 - 12:00 (2)	15:00 - 18:00 (3)	31:1	0.0563	6	*	*	*	*	*	*	*	*
*	*	*	*	*	*	*	*	Distance from water	C	3	501 - 1 000 m (2)	0 - 500 m (1)	20:1	0.0019	7
*	*	*	*	*	*	*	*	Distance from water	C	3	> 1 000 m (3)	0 - 500 m (1)	47:1	0.0005	7
*	*	*	*	*	*	*	*	Bush canopy cover	A	3	11 - 20 % (2)	0 - 10 % (1)	13:1	0.0514	8
Woody veg. density	B	3	Sparse (3)	Medium (1)	58:1	0.0417	6	*	*	*	*	*	*	*	*
Woody veg. density	B	3	Sparse (3)	Open (2)	49:1	0.0220	6	*	*	*	*	*	*	*	*

WET SEASON								DRY SEASON							
variable	group number	number of categories	category A	category B	A:B	probability	model number	variable	group number	number of categories	category A	category B	A:B	probability	model number
Activity - resting															
*	*	*	*	*	*	*	*	Habitat type	B	7	Acac nil (1)	MAH (3)	86:1	0.0241	11
Time observed	B	3	09:00 - 12:00 (2)	06:00 - 09:00 (1)	14:1	0.0736	9	*	*	*	*	*	*	*	*
*	*	*	*	*	*	*	*	Aspect	B	4	N (2)	E (1)	74:1	0.0197	11
*	*	*	*	*	*	*	*	Aspect	B	4	N (2)	S (3)	37:1	0.0566	11
*	*	*	*	*	*	*	*	Distance from water	C	3	> 1 000 m (3)	0 - 500 m (1)	42:1	0.0316	11
*	*	*	*	*	*	*	*	Distance from water	C	3	> 1 000 m (3)	501 - 1 000 m (2)	16:1	0.0637	11
*	*	*	*	*	*	*	*	Landscape position	C	3	Plain (2)	Slope (1)	34:1	0.0550	11
*	*	*	*	*	*	*	*	Landscape position	C	3	Plain (2)	Valley (3)	6:1	0.0466	12
Woody veg. density	C	2	Medium (1)	Open (2)	5:1	0.0734	10	Woody veg. density	A	4	Dense (1)	Open (3)	278:1	0.0475	11
*	*	*	*	*	*	*	*	Woody veg. density	A	4	Medium (2)	Open (3)	637:1	0.0239	11
*	*	*	*	*	*	*	*	Grass cover	B	2	Dense (1)	Medium (2)	33:1	0.0279	11

season. Emslie & Adcock (1994) state that thick bush is not necessarily good black rhinoceros habitat. Plant species composition and plant size may suggest that such areas are unsuitable for the black rhinoceros. On the contrary, dense habitat provides shade and also shelter, which are important requirements for the black rhinoceros. During the dry season, the black rhinoceroses on Lewa indicated a clear preference for resting in habitats where the woody vegetation was of medium density (Odds ratio = 637:1 ; P = 0.0239) or dense (Odds ratio = 278:1 ; P = 0.0475), rather than open or sparse.

The black rhinoceros was also observed in habitats where the grass cover was medium to dense. On Lewa, the grass cover is quite dense and tall on the plains. Generally, where the grass cover is dense, the growth of woody vegetation is inhibited to a large extent. Tall grass areas decrease the browse value of the range (Kotze & Zacharias 1993; Emslie & Adcock 1994). A current change from woody vegetation to grassland is evident on Lewa, with limited seedling regeneration occurring. This change may well have a detrimental effect on the available black rhinoceros habitat. Therefore any management action taken which aims to encourage the development of patches of shorter grass is likely to favour the black rhinoceros. Managing black rhinoceros habitat therefore also entails managing grazer numbers to permit a desired burning regime, whilst limiting grass interference with the production of black rhinoceros food.

Lewa is situated on the northern foothills of Mount Kenya, therefore this is the dominant aspect. The black rhinoceros is mostly observed on the north-facing slopes. During the wet season, when browse is more available and accessible, the black rhinoceros is limited to the north- and west-facing slopes. It is more likely to observe a black rhinoceros on the north- (Odds ratio = 10:1 ; P = 0.0003) or the west-facing (Odds ratio = 5:1 ; P = 0.0080) slopes, than on the south-facing slopes. During the dry season, on the other hand, when browse is limited and competition for food resources is present, their range tends to increase and they also utilise the north- (Odds ratio = 25:1 ; P = 0.0031), east- (Odds ratio = 13:1 ; P = 0.0245), northeast- (Odds ratio = 22:1 ; P = 0.0066) and west-facing (Odds ratio = 10:1 ; P = 0.0439) slopes, rather than the south-facing slopes.

A clear habitat preference is also found for the plains, especially during the wet season (Odds ratio = 4:1 ; P = 0.0218). The reason for this is that a wide variety of forbs occur on the plains after the rains. Emslie & Adcock (1994) found that forbs are important in the diet of the black rhinoceros, especially during the wet season flush. During the dry season, the valleys and riverine habitats are also utilised (Odds ratio = 3:1 ; P = 0.0232), especially by the black rhinoceros bulls. The plains, however, are still favoured as an overall habitat. Each black rhinoceros on Lewa has a specific range and is reluctant to move far out of this range, even when food becomes less available during the dry season. Therefore the difference in landscape position selection between the various black rhinoceroses on Lewa was negligible across the seasons. However, the bulls do tend to move around more than the cows. Competition with other browsers, such as elephants, could have limited the dry season use of the valleys and hills by the black rhinoceros. If so, then this is an indication of ecological separation between these two browsers. Utilisation of the woody vegetation by the black rhinoceros is lower on the steep slopes than on the plains and in the hills. The accessibility of an area may have an important influence on the degree to which certain parts of Lewa are utilised by the black rhinoceros.

No significance could be found between the presence of a black rhinoceros and its distance from water, although during the dry season, these animals were observed further away from water than in the wet season. This is probably because some of the pools and other water sources dry up during the dry season, decreasing the chances of locating a black rhinoceros close to water. Black rhinoceroses are water-dependent, but they do not have to drink daily (Schenkel & Schenkel-Hulliger 1969). The black rhinoceros on Lewa usually drinks at night. Therefore during the day, when all the observations were made, they may not have needed to be close to water. Water sources are nevertheless plentiful on Lewa. Therefore habitat selection by the black rhinoceros does not appear to be based upon the availability of water. No actual sighting was made of a black rhinoceros drinking throughout the study period.

The black rhinoceros observations were mostly made from 11:00 to 12:00 during the wet season. The vegetation of Lewa is denser during the wet than the dry season. Therefore a black rhinoceros was often not located until 11:00 or even later. Once located, it was found that they were already resting, resuming feeding from approximately 15:00 onwards. No black rhinoceros was ever observed resting from 06:00 to 09:00 in the mornings, or from 15:00 to 18:00 in the afternoons.

Elephant

The elephant indicates a clear preference for different habitats during both the wet and the dry seasons on Lewa (Table 10). The mixed *Acacia* plains (Odds ratio = 2:1 ; P = 0.0286), mixed woodland plains (Odds ratio = 5:1 ; P = 0.0001), *Acacia nilotica* woodland (Odds ratio = 10:1 ; P = 0.0000) and riverine habitats (Odds ratio = 33:1 ; P = 0.0091) are utilised to a greater extent during the wet than the dry season, whereas the mixed *Acacia* hills (Odds ratio = 4:1 ; P = 0.0008) and the mixed woodland hills (Odds ratio = 4:1 ; P = 0.0001) are preferred during the dry season. The bull elephants, particularly, also utilise the *Acacia xanthophloea* riverine habitat during the dry season. Large *Acacia xanthophloea* trees are then pushed over; with habitat destruction clearly evident. With the recent translocation of 12 of these bulls, a noticeable regeneration of the riverine woodland vegetation should ensue. Elephant bulls were often observed resting in the *Acacia xanthophloea* riverine habitat. The *Acacia drepanolobium - Acacia seyal* woodland is the least preferred habitat of the elephants. This is an indication of the ecological separation between the elephant, the giraffe and the black rhinoceros on Lewa. It was more likely to observe an elephant in the *Acacia nilotica* woodland (Odds ratio = 85:1 ; P = 0.0000), the *Acacia xanthophloea* riverine habitat (Odds ratio = 33:1 ; P = 0.0091) or on the mixed woodland plains (Odds ratio = 31:1 ; P = 0.0000), than in the *Acacia drepanolobium - Acacia seyal* woodland. The *Acacia nilotica* woodland is heavily utilised by the elephant bulls, especially during the wet season. It was more likely to observe an elephant in the *Acacia nilotica* woodland during the wet season, than in the *Acacia drepanolobium - Acacia seyal*

Table 10 Odds ratio's and probabilities, categorised by season and activity, for the elephant on the Lewa Wildlife Conservancy, Kenya, from May 1996 to May 1997, indicating their presence in category A, as opposed to category B, for the specific variable measured.

WET SEASON								DRY SEASON							
variable	group number	number of categories	category A	category B	A:B	probability	model number	variable	group number	number of categories	category A	category B	A:B	probability	model number
Activity - not specified															
Habitat type	B	7	Acac nil (1)	Drep sey (2)	10:1	0.0000	13	Habitat type	B	7	MAH (3)	Drep sey (2)	2:1	0.0467	14
Habitat type	B	7	Acac nil (1)	MAP (4)	5:1	0.0016	13	Habitat type	B	7	MAH (3)	MWP (6)	4:1	0.0008	14
Habitat type	B	7	Acac nil (1)	MWH (5)	6:1	0.0011	13	Habitat type	B	7	MWH (5)	Drep sey (2)	2:1	0.0229	14
Habitat type	B	7	MAH (3)	Drep sey (2)	4:1	0.0002	13	Habitat type	B	7	MWH (5)	MAP (4)	2:1	0.0418	14
Habitat type	B	7	MAH (3)	MWH (5)	2:1	0.0026	13	Habitat type	B	7	MWH (5)	MWP (6)	4:1	0.0001	14
Habitat type	B	7	MAP (4)	Drep sey (2)	2:1	0.0286	13	Habitat type	B	7	MAP (4)	MWP (6)	2:1	0.0262	14
Habitat type	B	7	MWP (6)	Drep sey (2)	5:1	0.0001	13	•	•	•	•	•	•	•	•
Habitat type	B	7	MWP (6)	MAP (4)	2:1	0.0169	13	•	•	•	•	•	•	•	•
Habitat type	B	7	MWP (6)	MWH (5)	3:1	0.0076	13	•	•	•	•	•	•	•	•
Habitat type	B	7	Riverine (7)	Drep sey (2)	33:1	0.0091	13	•	•	•	•	•	•	•	•
Habitat type	B	7	Riverine (7)	MAP (4)	16:1	0.0368	13	•	•	•	•	•	•	•	•
Habitat type	B	7	Riverine (7)	MWH (5)	19:1	0.0277	13	•	•	•	•	•	•	•	•
Time observed	A	9	06:00 - 07:00 (1)	09:00 - 10:00 (4)	3:1	0.0339	13	Time observed	A	9	06:00 - 07:00 (1)	08:00 - 09:00 (3)	2:1	0.0385	14
Time observed	A	9	07:00 - 08:00 (2)	09:00 - 10:00 (4)	3:1	0.0082	13	Time observed	A	9	06:00 - 07:00 (1)	16:00 - 17:00 (8)	3:1	0.0005	14
Time observed	A	9	08:00 - 09:00 (3)	06:00 - 07:00 (1)	3:1	0.0008	13	Time observed	A	9	07:00 - 08:00 (20	16:00 - 17:00 (8)	2:1	0.0037	14
Time observed	A	9	08:00 - 09:00 (3)	07:00 - 08:00 (2)	2:1	0.0010	13	Time observed	A	9	08:00 - 09:00 (3)	17:00 - 18:00 (9)	2:1	0.0069	14
Time observed	A	9	08:00 - 09:00 (3)	09:00 - 10:00 (4)	8:1	0.0000	13	Time observed	A	9	09:00 - 10:00 (4)	17:00 - 18:00 (9)	2:1	0.0044	14
Time observed	A	9	08:00 - 09:00 (3)	15:00 - 16:00 (7)	3:1	0.0151	13	Time observed	A	9	10:00 - 11:00 (5)	08:00 - 09:00 (3)	3:1	0.0177	14
Time observed	A	9	08:00 - 09:00 (3)	15:00 - 16:00 (7)	2:1	0.0046	13	Time observed	A	9	10:00 - 11:00 (5)	16:00 - 17:00 (8)	4:1	0.0007	14
Time observed	A	9	11:00 - 12:00 (6)	06:00 - 07:00 (1)	3:1	0.0264	13	Time observed	A	9	11:00 - 12:00 (6)	06:00 - 07:00 (1)	5:1	0.0002	14
Time observed	A	9	11:00 - 12:00 (6)	07:00 - 08:00 (2)	3:1	0.0496	13	Time observed	A	9	11:00 - 12:00 (6)	07:00 - 08:00 (2)	7:1	0.0000	14
Time observed	A	9	11:00 - 12:00 (6)	15:00 - 16:00 (7)	3:1	0.0477	13	Time observed	A	9	15:00 - 16:00 (7)	06:00 - 07:00 (1)	12:1	0.0000	14
Time observed	A	9	16:00 - 17:00 (8)	09:00 - 10:00 (4)	4:1	0.0046	13	Time observed	A	9	15:00 - 16:00 (7)	07:00 - 08:00 (2)	17:1	0.0000	14
Time observed	A	9	17:00 - 18:00 (9)	09:00 - 10:00 (4)	5:1	0.0008	13	Time observed	A	9	15:00 - 16:00 (7)	16:00 - 17:00 (8)	37:1	0.0000	14
Aspect	A	8	SW (7)	N (2)	3:1	0.0001	13	Aspect	A	8	SW (7)	E (1)	2:1	0.0147	14
Aspect	A	8	SW (7)	NW (4)	3:1	0.0048	13	Aspect	A	8	SW (7)	N (2)	2:1	0.0127	14
Aspect	A	8	SW (7)	W (8)	4:1	0.0000	13	Aspect	A	8	SW (7)	NE (3)	2:1	0.0205	14
Aspect	A	8	S (5)	W (8)	3:1	0.0015	13	Aspect	A	8	NW (4)	E (1)	3:1	0.0001	14
Aspect	A	8	NE (3)	W (8)	3:1	0.0068	13	Aspect	A	8	NW (4)	N (2)	3:1	0.0001	14
Aspect	A	8	NE (3)	E (1)	2:1	0.0211	13	Aspect	A	8	NW (4)	NE (3)	3:1	0.0005	14
Aspect	A	8	S (5)	E (1)	2:1	0.0087	13	Aspect	A	8	NW (4)	S (5)	4:1	0.0001	14
Aspect	A	8	SW (7)	E (1)	4:1	0.0001	13	Aspect	A	8	W (8)	N (2)	2:1	0.0369	14
Aspect	A	8	S (5)	N (2)	2:1	0.0138	13	Aspect	A	8	W (8)	S (5)	2:1	0.0221	14
Aspect	A	8	SW (7)	SE (6)	3:1	0.0135	13	Aspect	A	8	W (8)	E (1)	2:1	0.0575	14
Distance from water	B	5	51 - 250 m (2)	251 - 500 m (3)	3:1	0.0008	13	Distance from water	B	5	0 - 50 m (1)	51 - 250 m (2)	4:1	0.0046	14
Distance from water	B	5	501 - 1 000 m (4)	0 - 50 m (1)	2:1	0.0269	13	Distance from water	B	5	0 - 50 m (1)	251 - 500 m (3)	5:1	0.0002	14
Distance from water	B	5	501 - 1 000 m (4)	251 - 500 m (3)	3:1	0.0000	13	Distance from water	B	5	0 - 50 m (1)	501 - 1 000 m (4)	8:1	0.0000	14
Distance from water	B	5	> 1 000 m (5)	251 - 500 m (3)	2:1	0.0013	13	Distance from water	B	5	0 - 50 m (1)	> 1 000 m (5)	3:1	0.0182	14
•	•	•	•	•	•	•	•	Distance from water	B	5	51 - 250 m (2)	501 - 1 000 m (4)	2:1	0.0232	14
Landscape position	A	6	Plato (3)	Gentle slope (1)	6:1	0.0005	13	Landscape position	A	6	Valley (6)	Gentle slope (1)	5:1	0.0000	14
Landscape position	A	6	Plato (3)	Plain (2)	10:1	0.0000	13	Landscape position	A	6	Valley (6)	Plain (2)	7:1	0.0000	14
Landscape position	A	6	Plato (3)	Steep slope (5)	10:1	0.0000	13	Landscape position	A	6	Valley (6)	Steep slope (5)	3:1	0.0174	14
Landscape position	A	6	Valley (6)	Gentle slope (1)	6:1	0.0000	13	Landscape position	A	6	Steep slope (5)	Gentle slope (1)	2:1	0.0252	14
Landscape position	A	6	Valley (6)	Plain (2)	9:1	0.0000	13	Landscape position	A	6	Steep slope (5)	Plain (2)	2:1	0.0231	14
Landscape position	A	6	Valley (6)	Steep slope (5)	9:1	0.0000	13	•	•	•	•	•	•	•	•
Bush canopy cover	B	2	0 - 10 % (1)	> 10 % (2)	3:1	0.0185	13	•	•	•	•	•	•	•	•
Woody veg. density	B	3	Medium (1)	Sparse (3)	3:1	0.0096	13	Woody veg. density	B	3	Open (2)	Medium (1)	2:1	0.0006	14
Woody veg. density	B	3	Open (2)	Sparse (3)	3:1	0.0038	13	Woody veg. density	B	3	Sparse (3)	Medium (1)	7:1	0.0000	14
•	•	•	•	•	•	•	•	Woody veg. density	B	3	Sparse (3)	Open (2)	4:1	0.0000	14
Grass cover	A	3	Dense (1)	Medium (2)	2:1	0.0422	13	Grass cover	A	3	Medium (2)	Dense (1)	2:1	0.0277	14

WET SEASON variable	group number	number of categories	category A	category B	A:B	probability	model number	DRY SEASON variable	group number	number of categories	category A	category B	A:B	probability	model number
Activity - browsing															
Habitat type	A	10	Acac nil (2)	Drep sey (3)	85:1	0.0000	15	Habitat type	A	10	MAH (4)	MWP (7)	3:1	0.0423	17
Habitat type	A	10	Acac nil (2)	MAH (4)	15:1	0.0001	15	Habitat type	A	10	MWH (6)	MWP (7)	3:1	0.0194	17
Habitat type	A	10	Acac nil (2)	MWH (6)	26:1	0.0000	15	*	*	*	*	*	*	*	*
Habitat type	A	10	MWP (7)	Drep sey (3)	31:1	0.0000	15	*	*	*	*	*	*	*	*
Habitat type	A	10	MWP (7)	MAH (4)	5:1	0.0009	15	*	*	*	*	*	*	*	*
Habitat type	A	10	MWP (7)	MWH (6)	10:1	0.0000	15	*	*	*	*	*	*	*	*
Habitat type	A	10	MWP (7)	MAP (5)	3:1	0.0116	15	*	*	*	*	*	*	*	*
Habitat type	A	10	OGP (8)	Drep sey (3)	17:1	0.0054	15	*	*	*	*	*	*	*	*
Habitat type	A	10	OGP (8)	MWH (6)	5:1	0.0510	15	*	*	*	*	*	*	*	*
Time observed	A	9	06:00 - 07:00 (1)	15:00 - 16:00 (7)	6:1	0.0155	15	Time observed	A	9	06:00 - 07:00 (1)	09:00 - 10:00 (4)	4:1	0.0005	17
Time observed	A	9	07:00 - 08:00 (2)	15:00 - 16:00 (7)	5:1	0.0162	15	Time observed	A	9	06:00 - 07:00 (1)	16:00 - 17:00 (8)	3:1	0.0019	17
Time observed	A	9	08:00 - 09:00 (3)	06:00 - 07:00 (1)	2:1	0.0260	15	Time observed	A	9	07:00 - 08:00 (2)	09:00 - 10:00 (4)	2:1	0.0202	17
Time observed	A	9	08:00 - 09:00 (3)	07:00 - 08:00 (2)	3:1	0.0040	15	Time observed	A	9	07:00 - 08:00 (2)	17:00 - 18:00 (9)	5:1	0.0000	17
Time observed	A	9	08:00 - 09:00 (3)	09:00 - 10:00 (4)	6:1	0.0010	15	Time observed	A	9	08:00 - 09:00 (3)	17:00 - 18:00 (9)	4:1	0.0003	17
Time observed	A	9	08:00 - 09:00 (3)	15:00 - 16:00 (7)	14:1	0.0002	15	Time observed	A	9	10:00 - 11:00 (5)	07:00 - 08:00 (2)	3:1	0.0447	17
Time observed	A	9	08:00 - 09:00 (3)	16:00 - 17:00 (8)	2:1	0.0096	15	Time observed	A	9	10:00 - 11:00 (5)	16:00 - 17:00 (8)	5:1	0.0019	17
Time observed	A	9	11:00 - 12:00 (6)	07:00 - 08:00 (2)	4:1	0.0458	15	Time observed	A	9	11:00 - 12:00 (6)	09:00 - 10:00 (4)	9:1	0.0000	17
Time observed	A	9	11:00 - 12:00 (6)	09:00 - 10:00 (4)	9:1	0.0053	15	Time observed	A	9	11:00 - 12:00 (6)	16:00 - 17:00 (8)	7:1	0.0001	17
Time observed	A	9	11:00 - 12:00 (6)	15:00 - 16:00 (7)	20:1	0.0007	15	Time observed	A	9	15:00 - 16:00 (7)	07:00 - 08:00 (2)	85:1	0.0001	17
Time observed	A	9	16:00 - 17:00 (8)	15:00 - 16:00 (7)	6:1	0.0083	15	Time observed	A	9	15:00 - 16:00 (7)	11:00 - 12:00 (6)	21:1	0.0098	17
Time observed	A	9	17:00 - 18:00 (9)	07:00 - 08:00 (2)	2:1	0.0285	15	Time observed	A	9	15:00 - 16:00 (7)	16:00 - 17:00 (8)	155:1	0.0000	17
Time observed	A	9	17:00 - 18:00 (9)	09:00 - 10:00 (4)	5:1	0.0050	15	Time observed	A	9	15:00 - 16:00 (7)	17:00 - 18:00 (9)	389:1	0.0000	17
Time observed	A	9	17:00 - 18:00 (9)	15:00 - 16:00 (7)	11:1	0.0007	15	Time observed	A	9	16:00 - 17:00 (8)	17:00 - 18:00 (9)	3:1	0.0128	17
Aspect	A	8	SW (7)	E (1)	3:1	0.0014	15	Aspect	A	8	SW (7)	E (1)	2:1	0.0287	17
Aspect	A	8	SW (7)	N (2)	5:1	0.0000	15	Aspect	A	8	SW (7)	NE (3)	6:1	0.0002	17
Aspect	A	8	SW (7)	NE (3)	3:1	0.0573	15	Aspect	A	8	SW (7)	SE (6)	7:1	0.0008	17
Aspect	A	8	SW (7)	NW (4)	3:1	0.0542	15	Aspect	A	8	NW (4)	N (2)	5:1	0.0000	17
Aspect	A	8	SW (7)	W (8)	4:1	0.0009	15	Aspect	A	8	NW (4)	NE (3)	12:1	0.0000	17
Aspect	A	8	S (5)	E (1)	3:1	0.0020	15	Aspect	A	8	NW (4)	SE (6)	14:1	0.0000	17
Aspect	A	8	S (5)	N (2)	4:1	0.0001	15	Aspect	A	8	N (2)	NE (3)	2:1	0.0375	17
Aspect	A	8	S (5)	W (8)	3:1	0.0007	15	Aspect	A	8	N (2)	S (5)	4:1	0.0001	17
*	*	*	*	*	*	*	*	Aspect	A	8	N (2)	SE (6)	3:1	0.0455	17
*	*	*	*	*	*	*	*	Aspect	A	8	W (8)	S (5)	6:1	0.0000	17
*	*	*	*	*	*	*	*	Aspect	A	8	W (8)	SE (6)	4:1	0.0066	17
Distance from water	B	5	51 - 250 m (2)	251 - 500 m (3)	2:1	0.0129	15	Distance from water	B	5	51 - 250 m (2)	501 - 1 000 m (4)	3:1	0.0072	17
Distance from water	B	5	501 - 1 000 m (4)	51 - 250 m (2)	2:1	0.0469	15	Distance from water	B	5	251 - 500 m (3)	501 - 1 000 m (4)	2:1	0.0498	17
Distance from water	B	5	501 - 1 000 m (4)	251 - 500 m (3)	5:1	0.0000	15	Distance from water	B	5	> 1 000 m (5)	251 - 500 m (3)	2:1	0.0148	17
Distance from water	B	5	> 1 000 m (5)	251 - 500 m (3)	5:1	0.0000	15	Distance from water	B	5	> 1 000 m (5)	501 - 1 000 m (4)	3:1	0.0000	17
Landscape position	C	3	Slope (1)	Plain (2)	5:1	0.0002	15	Landscape position	C	3	Slope (1)	Plain (2)	3:1	0.0045	17
Landscape position	C	3	Valley (3)	Slope (1)	8:1	0.0000	15	Landscape position	C	3	Valley (3)	Slope (1)	5:1	0.0003	17
Landscape position	C	3	Valley (3)	Plain (2)	43:1	0.0000	15	Landscape position	C	3	Valley (3)	Plain (2)	14:1	0.0000	17
Tree canopy cover	B	2	> 10 % (2)	0 - 10 % (1)	2:1	0.0014	16	Tree canopy cover	A	4	11 - 20 % (2)	0 - 10 % (1)	3:1	0.0038	17
*	*	*	*	*	*	*	*	Tree canopy cover	A	4	11 - 20 % (2)	21 - 30 % (3)	7:1	0.0191	17
Woody veg. density	B	3	Medium (1)	Sparse (3)	17:1	0.0005	15	Woody veg. density	B	3	Open (2)	Medium (1)	2:1	0.0365	17
Woody veg. density	B	3	Open (2)	Sparse (3)	12:1	0.0016	15	Woody veg. density	B	3	Sparse (3)	Medium (1)	13:1	0.0000	17
*	*	*	*	*	*	*	*	Woody veg. density	B	3	Sparse (3)	Open (2)	8:1	0.0000	17
Grass cover	A	3	Dense (1)	Medium (2)	2:1	0.0002	15	Grass cover	A	3	Medium (2)	Dense (1)	2:1	0.0671	17
Grass cover	A	3	Sparse (3)	Medium (2)	2:1	0.0268	15	Grass cover	A	3	Sparse (3)	Dense (1)	2:1	0.0335	18
Activity - walking															
Habitat type	E	3	MWH (2)	Drep sey (1)	17:1	0.0161	19	Habitat type	E	3	Drep sey (1)	MWP (3)	32:1	0.0418	22
Habitat type	E	3	MWH (2)	MWP (3)	11:1	0.0215	20	Habitat type	E	3	MWH (2)	MWP (3)	35:1	0.0056	22
Time observed	B	3	06:00 - 9:00 (1)	09:00 - 12:00 (2)	7:1	0.0690	21	Time observed	B	3	06:00 - 09:00 (1)	15:00 - 18:00 (3)	6:1	0.0773	22
Time observed	B	3	06:00 - 9:00 (1)	15:00 - 18:00 (3)	23:1	0.0019	21	Time observed	B	3	09:00 - 12:00 (2)	15:00 - 18:00 (3)	9:1	0.0256	23
Aspect	B	4	N (2)	E (1)	5:1	0.0261	20	Aspect	B	4	S (3)	E (1)	133:1	0.0010	22
Aspect	B	4	S (3)	E (1)	5:1	0.0493	20	Aspect	B	4	S (3)	N (2)	31:1	0.0006	22
*	*	*	*	*	*	*	*	Aspect	B	4	W (4)	E (1)	60:1	0.0021	22
*	*	*	*	*	*	*	*	Aspect	B	4	W (4)	N (2)	14:1	0.0010	22

WET SEASON								DRY SEASON							
variable	group number	number of categories	category A	category B	A:B	probability	model number	variable	group number	number of categories	category A	category B	A:B	probability	model number
Distance from water	B	5	51 - 250 m (2)	0 - 50 m (1)	168:1	0.0085	21	Distance from water	B	5	0 - 50 m (1)	251 - 500 m (3)	18:1	0.0713	22
Distance from water	B	5	51 - 250 m (2)	251 - 500 m (3)	113:1	0.0013	21	Distance from water	B	5	0 - 50 m (1)	501 - 1 000 m (4)	197:1	0.0025	22
Distance from water	B	5	51 - 250 m (2)	501 - 1 000 m (4)	68:1	0.0042	21	Distance from water	B	5	0 - 50 m (1)	> 1 000 m (5)	111:1	0.0087	22
Distance from water	B	5	51 - 250 m (2)	> 1 000 m (5)	440:1	0.0005	21	Distance from water	B	5	51 - 250 m (2)	501 - 1 000 m (4)	13:1	0.0776	22
*	*	*	*	*	*	*	*	Distance from water	B	5	251 - 500 m (3)	501 - 1 000 m (4)	11:1	0.0112	22
Landscape position	D	2	Plain (2)	Slope (1)	15:1	0.0052	20	Landscape position	C	3	Plain (2)	Slope (1)	46:1	0.0021	22
*	*	*	*	*	*	*	*	Landscape position	C	3	Valley (3)	Slope (1)	33:1	0.0235	22
Tree canopy cover	B	2	> 10 % (2)	0 - 10 % (1)	71:1	0.0107	21	*	*	*	*	*	*	*	*
*	*	*	*	*	*	*	*	Bush canopy cover	A	3	0 - 10 % (1)	11 - 20 % (2)	172:1	0.0744	22
Woody veg. density	B	3	Open (2)	Medium (1)	28:1	0.0074	21	Woody veg. density	B	3	Open (2)	Medium (1)	171:1	0.0050	22
Woody veg. density	B	3	Open (2)	Sparse (3)	5:1	0.0452	20	Woody veg. density	B	3	Sparse (3)	Medium (1)	227:1	0.0083	22
Grass cover	A	3	Medium (2)	Dense (1)	15:1	0.0450	21	*	*	*	*	*	*	*	*
Activity - resting															
Habitat type	E	3	Drep sey (1)	MWP (3)	73:1	0.0176	24	Habitat type	E	3	MWH (2)	Drep sey (1)	1 992:1	0.0079	26
*	*	*	*	*	*	*	*	Habitat type	E	3	MWH (2)	MWP (3)	2341:1	0.0037	26
*	*	*	*	*	*	*	*	Time observed	B	3	09:00 - 12:00 (2)	06:00 - 09:00 (1)	36 586:1	0.0052	26
*	*	*	*	*	*	*	*	Time observed	B	3	09:00 - 12:00 (2)	15:00 - 18:00 (3)	7:1	0.0675	26
*	*	*	*	*	*	*	*	Time observed	B	3	15:00 - 18:00 (3)	06:00 - 09:00 (1)	5 128:1	0.0086	26
*	*	*	*	*	*	*	*	Aspect	B	4	S (3)	E (1)	41:1	0.0064	26
*	*	*	*	*	*	*	*	Aspect	B	4	S (3)	N (2)	177:1	0.0151	26
*	*	*	*	*	*	*	*	Aspect	B	4	S (3)	W (4)	525:1	0.0196	26
*	*	*	*	*	*	*	*	Landscape position	C	3	Plain (2)	Slope (1)	396:1	0.0160	26
*	*	*	*	*	*	*	*	Landscape position	C	3	Valley (3)	Slope (1)	58:1	0.0210	26
Tree canopy cover	B	2	> 10 % (2)	0 - 10 % (1)	8:1	0.0176	25	Tree canopy cover	B	2	0 - 10 % (1)	> 10 % (2)	48:1	0.0326	26
*	*	*	*	*	*	*	*	Bush canopy cover	B	2	> 10 % (2)	0 - 10 % (1)	70:1	0.0782	26
Grass cover	B	2	Medium (2)	Dense (1)	21:1	0.0178	24	Grass cover	B	2	Dense (1)	Medium (2)	4:1	0.0057	27

woodland (Odds ratio = 85:1 ; P = 0.0000), the mixed Acacia hills (Odds ratio = 15:1 ; P = 0.0001) or the mixed woodland hills (Odds ratio = 26:1 ; P = 0.0000). Ecological separation from the black rhinoceros and giraffe is therefore present, because the black rhinoceros and giraffe seldom utilise the *Acacia nilotica* woodland. Woodland decline is not as evident in this *Acacia nilotica* woodland because grasses and forbs constitute a large proportion of the elephants' diet during the wet season. However, few seedlings occur in this *Acacia nilotica* woodland, as a result of the elephants' selectivity for seedlings. It is expected that because of the browsing pressure by elephants, that the *Acacia nilotica* woodland will be converted to an open, scattered grassland over time, when it will become incapable of sustaining any browsers, especially during the dry season. The browsing capacity of Lewa will, therefore, effectively be reduced as well. The correct stocking rate of elephants is consequently essential. Du Toit (1991) states that a wildlife manager must decide on a maximum number of elephants for his area, based on the recommended browsing capacity and also interactions with other browsers. Thereafter, he should try to maintain a balance between grassland and woodland habitats. Viljoen (1991) describes the optimum elephant habitat as mixed woodland and grassland with an adequate supply of fresh food and water. This rather aptly describes Lewa.

The study further revealed that during the rains when forage of all types is abundant, the elephants are primarily grazers, concentrating on the plains habitats. They switch to a predominantly browse diet during the dry season, moving into the valleys and hills, where browse is more abundant. Dougall & Sheldrick (1964), Field (1971) and Barnes (1982) found that woody vegetation maintained higher crude protein levels relative to grasses during the dry season. The nutritional quality of grasses declines rapidly as they begin to age in the dry season. Therefore a balanced woodland / grassland habitat is essential for elephants.

During the wet season, the majority of the elephant population on Lewa migrates northwards out of the area. Observations were, however, possible when the elephants concentrated on the plains north of Lewa. During the dry season, the elephants move into the hills and valleys of Lewa, where the tree canopy cover is between 11 and 20 % (Odds ratio = 7:1 ; P = 0.0191). *Acacia tortilis* and *Acacia xanthophloea* provide most of the shade. This supports the hypothesis that the presence of shade is an important element in elephant habitat. Weaver (1995) also indicates that the elephants in the Klaserie Private Nature Reserve, South Africa, prefer habitats with an increased canopy cover.

A dense grass cover is selected for during the wet season when the elephants predominantly are grazers. During this season it was twice as likely to observe an elephant in habitats where the grass cover is dense, rather than medium (P = 0.0002). During the dry season, when the elephants on Lewa inhabit the hills and change to a predominantly browse diet, the grass cover there ranges from medium (Odds ratio = 2:1 ; P = 0.0671) to sparse (Odds ratio = 2:1 ; P = 0.0335).

The elephant on Lewa utilises all of the topographical positions, although there is a preference for the plateaus (Odds ratio = 10:1 ; P = 0.0000) and plains (Odds ratio = 15:1 ; P = 0.0052) during the wet season, and for the slopes (Odds ratio = 2:1 ; P = 0.0231) and valleys (Odds ratio = 7:1 ; P = 0.0000) during the dry season. The steep slopes are utilised by elephants to a large extent, indicating an ecological separation with the black rhinoceros and giraffe on Lewa which were both seldom observed on such steep slopes. The south- and the southwest-facing slopes are mostly utilised during the wet season. It was more likely to observe an elephant browsing on the south- (Odds ratio = 4:1 ; P = 0.0001) or the southwest-facing (Odds ratio = 5:1 ; P = 0.0000) slopes, than on the north-facing slopes. Few observations were made of elephants inhabiting the north- or the east-facing slopes. During the dry season, when the elephants migrate onto Lewa, they spread over the entire area, utilising mainly the north-, northwest-, west-, southwest- and south-facing slopes. Ecological separation is then partially achieved between the elephant and the black rhinoceros because the latter mainly utilises the north-facing slopes. The plains and the bottom of the valleys are easy terrain for walking by the elephants. Elephants also make use of the roads on Lewa to move between the various habitat types.

As is found with the black rhinoceros, one would assume that because water on Lewa is readily available, the need to remain close to water is not essential for an elephant. During the dry season, the elephants did indeed remain closer to the water and were usually observed within 500 m of water. It was eight times more likely to observe an elephant within 50 m of water during the dry season, than at distances of between 500 and 1 000 m away from it (P = 0.0000). During the wet season, on the other hand, the elephants were mostly observed at distances greater than 500 m away from water. This evidence concurs with the body of literature on the topic (Laws 1970a; De Villiers 1981). Viljoen (1989), however, found that the availability and quality of the vegetation and not the location of water seem to be the major factors influencing the habitat choice of elephants.

Elephants were observed feeding at most times of the day, although they do tend to rest from 11:00 to 15:00, resuming feeding at approximately 15:00. It was more likely to find an elephant resting from 09:00 to 12:00, than from 06:00 to 09:00 (Odds ratio = 36 386:1 ; P = 0.0052) or from 15:00 to 18:00 (Odds ratio = 7:1 ; P = 0.0675).

Giraffe

During both the wet and the dry seasons, the giraffe has a preference for the mixed *Acacia* plains, the mixed woodland plains and the *Acacia drepanolobium - Acacia seyal* woodland (Table 11). It was more likely to observe a giraffe browsing on the mixed *Acacia* plains (Odds = 21:1 ; P = 0.0043), the mixed woodland plains (Odds ratio = 7:1 ; P = 0.0660) or in the *Acacia drepanolobium - Acacia seyal* woodland (Odds ratio = 27:1 ; 0.0027), than in the riverine habitat. Although the giraffe on Lewa was occasionally observed in the *Acacia nilotica* woodland, most of the other habitats are preferred. An ecological separation is therefore found between the giraffe and the elephant, where the latter utilises the *Acacia nilotica* woodland to a great extent (Table 10). Hirst (1975), Beardall *et al.* (1984) and Scogings *et al.* (1990) all found that the giraffe utilises a wide variety of habitats in African savannas and that no particular preferences can be determined. On the whole, this was also proved to be true

Table 11 Odds ratio's and probabilities, categorised by season and activity, for the giraffe on the [illegible]ervancy, Kenya, from May 1996 to May 1997, indicating their presence in category A, as opposed to category B, for the specific variable measured.

WET SEASON								DRY SEASON							
variable	group number	number of categories	category A	category B	A:B	probability	model number	variable	group number	number of categories	category A	category B	A:B	probability	model number
Activity - not specified															
Habitat type	B	7	MAP (4)	Acac nil (1)	4:1	0.0155	28	Habitat type	B	7	Drep sey (2)	MWH (5)	3:1	0.0076	30
Habitat type	B	7	Drep sey (2)	Riverine (7)	28:1	0.0289	28	Habitat type	B	7	MAP (4)	MWH (5)	3:1	0.0091	30
Habitat type	B	7	MAH (3)	Riverine (7)	31:1	0.0234	28	Habitat type	B	7	MAH (3)	MWH (5)	2:1	0.0736	30
Habitat type	B	7	MAP (4)	Riverine (7)	49:1	0.0109	28	Habitat type	B	7	MAP (4)	Acac nil (1)	3:1	0.0745	30
Habitat type	B	7	MWH (5)	Riverine (7)	23:1	0.0379	28	Habitat type	B	7	Drep sey (2)	Riverine (7)	33:1	0.0739	30
Habitat type	B	7	MWP (6)	Riverine (7)	21:1	0.0472	28	Habitat type	B	7	MAP (4)	Riverine (7)	34:1	0.0718	30
Time observed	A	9	06:00 - 07:00 (1)	11:00 - 12:00 (6)	23:1	0.0000	28	Time observed	A	9	06:00 - 07:00 (1)	15:00 - 16:00 (7)	39:1	0.0000	30
Time observed	A	9	07:00 - 08:00 (2)	11:00 - 12:00 (6)	26:1	0.0000	28	Time observed	A	9	07:00 - 08:00 (2)	06:00 - 07:00 (1)	2:1	0.0570	30
Time observed	A	9	08:00 - 09:00 (3)	11:00 - 12:00 (6)	13:1	0.0000	28	Time observed	A	9	07:00 - 08:00 (2)	10:00 - 11:00 (5)	2:1	0.0403	30
Time observed	A	9	09:00 - 10:00 (4)	11:00 - 12:00 (6)	24:1	0.0000	28	Time observed	A	9	07:00 - 08:00 (2)	11:00 - 12:00 (6)	4:1	0.0007	30
Time observed	A	9	10:00 - 11:00 (5)	11:00 - 12:00 (6)	37:1	0.0004	28	Time observed	A	9	07:00 - 08:00 (2)	15:00 - 16:00 (7)	81:1	0.0000	30
Time observed	A	9	15:00 - 16:00 (7)	11:00 - 12:00 (6)	24:1	0.0000	28	Time observed	A	9	08:00 - 09:00 (3)	11:00 - 12:00 (6)	3:1	0.0105	30
Time observed	A	9	16:00 - 17:00 (8)	11:00 - 12:00 (6)	40:1	0.0000	28	Time observed	A	9	08:00 - 09:00 (3)	15:00 - 16:00 (7)	62:1	0.0000	30
Time observed	A	9	17:00 - 18:00 (9)	11:00 - 12:00 (6)	30:1	0.0000	28	Time observed	A	9	09:00 - 10:00 (4)	06:00 - 07:00 (1)	3:1	0.0180	30
Time observed	A	9	07:00 - 08:00 (2)	08:00 - 09:00 (3)	2:1	0.0342	28	Time observed	A	9	09:00 - 10:00 (4)	11:00 - 12:00 (6)	4:1	0.0003	30
Time observed	A	9	16:00 - 17:00 (8)	08:00 - 09:00 (3)	3:1	0.0017	28	Time observed	A	9	09:00 - 10:00 (4)	15:00 - 16:00 (7)	101:1	0.0000	30
Time observed	A	9	17:00 - 18:00 (9)	08:00 - 09:00 (3)	2:1	0.0170	28	Time observed	A	9	10:00 - 11:00 (5)	15:00 - 16:00 (7)	36:1	0.0000	30
•	•	•	•	•	•	•	•	Time observed	A	9	11:00 - 12:00 (6)	15:00 - 16:00 (7)	22:1	0.0002	30
•	•	•	•	•	•	•	•	Time observed	A	9	16:00 - 17:00 (8)	11:00 - 12:00 (6)	3:1	0.0036	30
•	•	•	•	•	•	•	•	Time observed	A	9	17:00 - 18:00 (9)	06:00 - 07:00 (1)	2:1	0.0570	30
•	•	•	•	•	•	•	•	Time observed	A	9	17:00 - 18:00 (9)	11:00 - 12:00 (6)	3:1	0.0015	30
•	•	•	•	•	•	•	•	Time observed	A	9	17:00 - 18:00 (9)	15:00 - 16:00 (7)	77:1	0.0000	30
Aspect	A	8	SE (6)	E (1)	4:1	0.0458	28	Aspect	A	8	E (1)	NW (4)	4:1	0.0001	30
Aspect	A	8	SE (6)	N (2)	4:1	0.0322	28	Aspect	A	8	E (1)	W (8)	2:1	0.0286	30
Aspect	A	8	SE (6)	NE (3)	4:1	0.0530	28	Aspect	A	8	N (2)	NW (4)	3:1	0.0011	30
Aspect	A	8	SE (6)	NW (4)	7:1	0.0032	28	Aspect	A	8	NE (3)	NW (4)	4:1	0.0005	30
Aspect	A	8	SE (6)	S (5)	5:1	0.0148	28	Aspect	A	8	S (5)	NW (4)	5:1	0.0000	30
Aspect	A	8	SE (6)	SW (7)	7:1	0.0046	28	Aspect	A	8	SE (6)	NW (4)	3:1	0.0150	30
Aspect	A	8	SE (6)	W (8)	4:1	0.0376	28	Aspect	A	8	W (8)	NW (4)	2:1	0.0309	30
Aspect	A	8	E (1)	NW (4)	2:1	0.0681	28	Aspect	A	8	S (5)	W (8)	2:1	0.0147	30
•	•	•	•	•	•	•	•	Aspect	A	8	SW (7)	W (8)	3:1	0.0110	30
Distance from water	A	6	0 - 50 m (1)	501 - 1 000 m (4)	4:1	0.0070	28	Distance from water	A	6	51 - 250 m (2)	0 - 50 m (1)	3:1	0.0309	30
Distance from water	A	6	0 - 50 m (1)	1 001 - 2 000 m (5)	3:1	0.0324	28	Distance from water	A	6	51 - 250 m (2)	1 001 - 2 000 m (5)	3:1	0.0020	30
Distance from water	A	6	51 - 250 m (2)	501 - 1 000 m (4)	2:1	0.0645	28	Distance from water	A	6	251 - 500 m (3)	0 - 50 m (1)	3:1	0.0261	30
Distance from water	A	6	251 - 500 m (3)	501 - 1 000 m (4)	2:1	0.0382	28	Distance from water	A	6	251 - 500 m (3)	1 001 - 2 000 m (5)	2:1	0.0001	30
•	•	•	•	•	•	•	•	Distance from water	A	6	501 - 1 000 m (4)	1 001 - 2 000 m (5)	2:1	0.0004	30
Landscape position	A	6	Gentle slope (1)	Valley (6)	3:1	0.0200	28	Landscape position	A	6	Gentle slope (1)	Valley (6)	2:1	0.0201	30
Landscape position	A	6	Steep slope (5)	Valley (6)	4:1	0.0078	28	Landscape position	A	6	Steep slope (5)	Valley (6)	4:1	0.0045	30
•	•	•	•	•	•	•	•	Landscape position	A	6	Steep slope (5)	Plain (2)	3:1	0.0562	30
Tree canopy cover	B	2	0 - 10 % (1)	> 10 % (2)	2:1	0.0515	29	Tree canopy cover	B	2	0 - 10 % (1)	> 10 % (2)	2:1	0.0042	30
Bush canopy cover	B	2	> 10 % (2)	0 - 10 % (1)	3:1	0.0245	29	Bush canopy cover	B	2	> 10 % (2)	0 - 10 % (1)	4:1	0.0007	30
Woody veg. density	A	4	Medium (2)	Sparse (4)	6:1	0.0000	28	Woody veg. density	A	4	Medium (2)	Sparse (4)	3:1	0.0038	30
Woody veg. density	A	4	Open (3)	Sparse (4)	3:1	0.0012	28	Woody veg. density	A	4	Open (3)	Sparse (4)	2:1	0.0320	30
Grass cover	A	3	Sparse (3)	Medium (2)	2:1	0.0170	29	Grass cover	A	3	Sparse (3)	Medium (2)	2:1	0.0160	30
Grass cover	A	3	Sparse (3)	Dense (1)	2:1	0.0093	29	Grass cover	A	3	Sparse (3)	Dense (1)	2:1	0.0735	30
Activity - browsing															
Habitat type	B	7	Drep sey (2)	Acac nil (1)	5:1	0.0343	31	Habitat type	B	7	Drep sey (2)	Acac nil (1)	9:1	0.0050	33
Habitat type	B	7	MAP (4)	Acac nil (1)	4:1	0.0523	31	Habitat type	B	7	MAH (3)	Acac nil (1)	6:1	0.0344	33
Habitat type	B	7	Drep sey (2)	MWP (6)	4:1	0.0416	31	Habitat type	B	7	MAP (4)	Acac nil (1)	11:1	0.0027	33
Habitat type	B	7	Drep sey (2)	Riverine (7)	27:1	0.0027	31	Habitat type	B	7	MWP (6)	Acac nil (1)	8:1	0.0187	33
Habitat type	B	7	MAH (3)	Riverine (7)	17:1	0.0020	31	Habitat type	B	7	MAP (4)	MWH (5)	3:1	0.0660	33
Habitat type	B	7	MAP (4)	MWP (6)	3:1	0.0558	31	•	•	•	•	•	•	•	•
Habitat type	B	7	MAP (4)	Riverine (7)	21:1	0.0043	31	•	•	•	•	•	•	•	•
Habitat type	B	7	MWH (5)	Riverine (7)	12:1	0.0042	31	•	•	•	•	•	•	•	•
Habitat type	B	7	MWP (6)	Riverine (7)	7:1	0.0660	31	•	•	•	•	•	•	•	•

WET SEASON								DRY SEASON							
variable	group number	number of categories	category A	category B	A:B	probability	model number	variable	group number	number of categories	category A	category B	A:B	probability	model number
Time observed	A	9	06:00 - 07:00 (1)	11:00 - 12:00 (6)	11:1	0.0024	31	Time observed	A	9	06:00 - 07:00 (1)	15:00 - 16:00 (7)	65:1	0.0003	33
Time observed	A	9	07:00 - 08:00 (2)	08:00 - 09:00 (3)	3:1	0.0143	31	Time observed	A	9	07:00 - 08:00 (2)	06:00 - 07:00 (1)	3:1	0.0051	33
Time observed	A	9	07:00 - 08:00 (2)	11:00 - 12:00 (6)	18:1	0.0002	31	Time observed	A	9	07:00 - 08:00 (2)	08:00 - 09:00 (3)	2:1	0.0196	33
Time observed	A	9	08:00 - 09:00 (3)	11:00 - 12:00 (6)	6:1	0.0146	31	Time observed	A	9	07:00 - 08:00 (2)	10:00 - 11:00 (5)	5:1	0.0015	33
Time observed	A	9	09:00 - 10:00 (4)	11:00 - 12:00 (6)	11:1	0.0064	31	Time observed	A	9	07:00 - 08:00 (2)	11:00 - 12:00 (6)	3:1	0.0249	33
Time observed	A	9	15:00 - 16:00 (7)	08:00 - 09:00 (3)	3:1	0.0447	31	Time observed	A	9	07:00 - 08:00 (2)	15:00 - 16:00 (7)	198:1	0.0000	33
Time observed	A	9	15:00 - 16:00 (7)	11:00 - 12:00 (6)	21:1	0.0007	31	Time observed	A	9	08:00 - 09:00 (3)	15:00 - 16:00 (7)	81:1	0.0002	33
Time observed	A	9	16:00 - 17:00 (8)	08:00 - 09:00 (3)	3:1	0.0036	31	Time observed	A	9	09:00 - 10:00 (4)	06:00 - 07:00 (1)	4:1	0.0031	33
Time observed	A	9	16:00 - 17:00 (8)	11:00 - 12:00 (6)	22:1	0.0001	31	Time observed	A	9	09:00 - 10:00 (4)	08:00 - 09:00 (3)	3:1	0.0091	33
Time observed	A	9	17:00 - 18:00 (9)	11:00 - 12:00 (6)	12:1	0.0014	31	Time observed	A	9	09:00 - 10:00 (4)	15:00 - 16:00 (7)	253:1	0.0000	33
•	•	•	•	•	•	•	•	Time observed	A	9	10:00 - 11:00 (5)	15:00 - 16:00 (7)	36:1	0.0030	33
•	•	•	•	•	•	•	•	Time observed	A	9	11:00 - 12:00 (6)	15:00 - 16:00 (7)	61:1	0.0006	33
•	•	•	•	•	•	•	•	Time observed	A	9	16:00 - 17:00 (8)	10:00 - 11:00 (5)	3:1	0.0253	33
•	•	•	•	•	•	•	•	Time observed	A	9	16:00 - 17:00 (8)	15:00 - 16:00 (7)	124:1	0.0000	33
•	•	•	•	•	•	•	•	Time observed	A	9	17:00 - 18:00 (9)	10:00 - 11:00 (5)	5:1	0.0032	33
•	•	•	•	•	•	•	•	Time observed	A	9	17:00 - 18:00 (9)	11:00 - 12:00 (6)	3:1	0.0259	33
•	•	•	•	•	•	•	•	Time observed	A	9	17:00 - 18:00 (9)	15:00 - 16:00 (7)	194:1	0.0000	33
Aspect	A	8	E (1)	NW (4)	3:1	0.0119	31	Aspect	A	8	E (1)	NW (4)	4:1	0.0056	33
Aspect	A	8	E (1)	S (5)	3:1	0.0288	31	Aspect	A	8	S (5)	E (1)	2:1	0.0412	33
Aspect	A	8	E (1)	SW (7)	3:1	0.0252	31	Aspect	A	8	N (2)	NW (4)	4:1	0.0035	33
Aspect	A	8	N (2)	NW (4)	3:1	0.0164	31	Aspect	A	8	S (5)	N (2)	3:1	0.0245	33
Aspect	A	8	N (2)	S (5)	2:1	0.0376	31	Aspect	A	8	NE (3)	NW (4)	6:1	0.0005	33
Aspect	A	8	N (2)	SW (7)	3:1	0.0314	31	Aspect	A	8	NE (3)	W (8)	2:1	0.0522	33
Aspect	A	8	SE (6)	NW (4)	5:1	0.0402	31	Aspect	A	8	S (5)	NW (4)	9:1	0.0000	33
Aspect	A	8	SE (6)	SW (7)	5:1	0.0551	31	Aspect	A	8	SE (6)	NW (4)	7:1	0.0018	33
•	•	•	•	•	•	•	•	Aspect	A	8	SW (7)	NW (4)	4:1	0.0089	33
•	•	•	•	•	•	•	•	Aspect	A	8	W (8)	NW (4)	3:1	0.0312	33
•	•	•	•	•	•	•	•	Aspect	A	8	S (5)	W (8)	4:1	0.0037	33
Distance from water	A	6	0 - 50 m (1)	501 - 1 000 m (4)	5:1	0.0093	31	Distance from water	A	6	51 - 250 m (2)	1 001 - 2 000 m (5)	2:1	0.0653	33
Distance from water	A	6	0 - 50 m (1)	1 001 - 2 000 m (5)	4:1	0.0582	31	Distance from water	A	6	251 - 500 m (3)	1 001 - 2 000 m (5)	3:1	0.0019	33
Distance from water	A	6	51 - 250 m (2)	501 - 1 000 m (4)	2:1	0.0478	31	Distance from water	A	6	501 - 1 000 m (4)	1 001 - 2 000 m (5)	2:1	0.0020	33
Distance from water	A	6	251 - 500 m (3)	501 - 1 000 m (4)	2:1	0.0239	31	•	•	•	•	•	•	•	•
Landscape position	C	3	Slope (1)	Valley (3)	3:1	0.0659	31	•	•	•	•	•	•	•	•
Tree canopy cover	A	4	0 - 10 % (1)	21 - 30 % (3)	8:1	0.0409	31	Tree canopy cover	A	4	0 - 10 % (1)	11 - 20 % (2)	3:1	0.0027	33
Tree canopy cover	A	4	11 - 20 % (2)	21 - 30 % (3)	6:1	0.0650	31	Tree canopy cover	A	4	21 - 30 % (3)	11 - 20 % (2)	15:1	0.0156	33
Bush canopy cover	B	2	> 10 % (2)	0 - 10 % (1)	4:1	0.0403	31	Bush canopy cover	B	2	> 10 % (2)	0 - 10 % (1)	6:1	0.0002	33
Woody veg. density	B	3	Medium (1)	Sparse (3)	3:1	0.0624	31	Woody veg. density	B	3	Medium (1)	Sparse (3)	3:1	0.0199	33
Woody veg. density	B	3	Medium (1)	Open (2)	2:1	0.0088	32	Woody veg. density	B	3	Open (2)	Sparse (3)	4:1	0.0048	33

Activity - walking

variable	group number	number of categories	category A	category B	A:B	probability	model number	variable	group number	number of categories	category A	category B	A:B	probability	model number
Habitat type	E	3	Drep sey (1)	MWH (2)	39:1	0.0343	34	Habitat type	E	3	MWP (3)	Drep sey (1)	12:1	0.0475	35
Habitat type	E	3	MWP (3)	MWH (2)	87:1	0.0051	34	•	•	•	•	•	•	•	•
Time observed	B	3	15:00 - 18:00 (3)	06:00 - 09:00 (1)	5:1	0.0240	34	Time observed	B	3	06:00 - 09:00 (1)	09:00 - 12:00 (2)	10:1	0.0102	36
Time observed	B	3	15:00 - 18:00 (3)	09:00 - 12:00 (2)	9:1	0.0444	34	Time observed	B	3	15:00 - 18:00 (3)	09:00 - 12:00 (2)	9:1	0.0423	36
•	•	•	•	•	•	•	•	Aspect	B	4	E (1)	N (2)	5:1	0.0334	36
•	•	•	•	•	•	•	•	Aspect	B	4	E (1)	S (3)	29:1	0.0149	35
•	•	•	•	•	•	•	•	Aspect	B	4	E (1)	W (4)	9:1	0.0291	36
Distance from water	B	5	> 1 000 m (5)	51 - 250 m (2)	10:1	0.0341	34	Distance from water	B	5	501 - 1 000 m (4)	0 - 50 m (1)	31:1	0.0194	35
•	•	•	•	•	•	•	•	Distance from water	B	5	501 - 1 000 m (4)	> 1 000 m (5)	7:1	0.0660	35
•	•	•	•	•	•	•	•	Grass cover	A	3	Dense (1)	Medium (2)	4:1	0.0310	35
•	•	•	•	•	•	•	•	Grass cover	A	3	Sparse (3)	Medium (2)	13:1	0.0625	35

WET SEASON								DRY SEASON							
variable	group number	number of categories	category A	category B	A:B	probability	model number	variable	group number	number of categories	category A	category B	A:B	probability	model number
Activity - resting															
Habitat type	E	3	MWP (3)	Drep Sey (1)	43:1	0.0579	37	Habitat type	E	3	Drep sey (1)	MWH (2)	51:1	0.0132	38
*	*	*	*	*	*	*	*	Habitat type	E	3	MWP (3)	Drep sey (1)	123:1	0.0063	38
*	*	*	*	*	*	*	*	Habitat type	E	3	MWP (3)	MWH (2)	6 258:1	0.0002	38
*	*	*	*	*	*	*	*	Aspect	B	4	E (1)	N (2)	11:1	0.0572	38
*	*	*	*	*	*	*	*	Distance from water	C	3	0 - 500 m (1)	> 1 000 m (3)	2 215:1	0.0129	38
*	*	*	*	*	*	*	*	Distance from water	C	3	501 - 1 000 m (2)	> 1 000 m (3)	5 692:1	0.0079	38
*	*	*	*	*	*	*	*	Landscape position	D	2	Slope (1)	Plain (2)	1 275:1	0.0010	38
*	*	*	*	*	*	*	*	Woody veg. density	B	3	Sparse (3)	Medium (1)	571:1	0.0272	38
*	*	*	*	*	*	*	*	Woody veg. density	B	3	Sparse (3)	Open (2)	20 200:1	0.0049	38
*	*	*	*	*	*	*	*	Grass cover	B	2	Medium (2)	Dense (1)	8:1	0.0399	38

on Lewa. The *Acacia drepanolobium - Acacia seyal* woodland in the southwest of Lewa is particularly favoured by large breeding herds of giraffe. Herds of up to 40 individuals were noted feeding for consecutive days in this plant community. The giraffe culling programme has also been conducted primarily in this plant community. Therefore the potential competition for food resources between the giraffe and the black rhinoceros in the culling area should be somewhat alleviated as long as giraffe numbers there are kept low.

The activity of the giraffe on Lewa does not appear to have any effect on its choice of habitat, although it is interesting to note that some giraffes were observed to rest only on the plains habitats. A giraffe does not necessarily lie down when it rests or ruminates, although if this were the case, then it would appear obvious to choose the flatter plains habitats, than the hills or slopes to do so. It was more likely to observe a giraffe resting on the mixed woodland plains, than in the mixed woodland hills (Odds ratio = 6 258:1 ; P = 0.0002). Breeding herds of giraffe are often restricted to the mixed *Acacia* plains, the mixed woodland plains and the gentle slopes. Young & Isbell (1991) also made similar observations elsewhere. Giraffe cows with young may feed in open areas because they provide better views of potential predators of their young. Pellew (1984) also claims that giraffe cows with young may prefer the more open habitats because they provide particularly nutritious foods. Young & Isbell (1991), however, found that giraffe cows leave their young in crèches in open habitats to allow them to feed in the woodlands. The giraffe bulls on Lewa especially utilised the *Acacia xanthophloea* riverine habitat during the dry season. Most of the browse there occurs above a height of 5 m, although the mature bulls can reach the lower branches of the *Acacia xanthophloea* trees. Giraffe bulls also feed from *Acacia xanthophloea* trees that had been pushed over by elephant bulls.

The giraffe on Lewa utilises habitats where the woody vegetation density is medium to open. During the dry season, giraffes were most often observed resting in habitats where the woody vegetation density was sparse (Odds ratio = 20 200:1 ; P = 0.0049). As mentioned previously, this is possibly as a defence against predators. On certain occasions, giraffes were observed lying down on the open grassland plains.

Habitats where the tree canopy cover is less than 10 % (Odds ratio = 2:1 ; P = 0.0042) and the bush canopy cover is greater than 10 % (Odds ratio = 4:1 ; P = 0.0007), are favoured during the dry season. When a giraffe browses during the dry season, an affinity is shown for habitats where the tree canopy cover is greater (Odds ratio = 15:1 ; P = 0.0156) than in the wet season. A greater tree canopy cover provides shade, especially during the dry season. Leuthold & Leuthold (1972) claim that almost 50 % of giraffe browsing is below 2 m. This may be the reason why the giraffe on Lewa prefers habitats with a greater percentage of bush canopy cover. Most *Acacia mellifera* and *Acacia drepanolobium* trees on Lewa have inverse giraffe browse-lines because the giraffe feeds on these trees from the top downwards, preventing them from growing taller. Young & Isbell (1991) also found that giraffe browsing usually keeps *Acacia drepanolobium* trees below a height of 2 m.

When a giraffe was seen ruminating, this was also regarded as resting. A giraffe ruminates whilst standing or lying down. During the dry season, most giraffes were observed ruminating whilst standing on the slopes. The bulls prefer utilising the upper, more densely vegetated slopes, whereas the cows prefer utilising the more gentle, open slopes. During the dry season, the giraffe was mostly observed on the east-facing slopes, whereas during the wet season, there is a preference for the southeast-facing slopes. Clear ecological separation occurs between the black rhinoceros that prefers the north-facing slopes, the elephant that prefers the south- and southwest-facing slopes, and the giraffe that prefers the east- and southeast-facing slopes.

No differences could be found between the occurrence of a giraffe and the distance from water at which it was found. Because of the abundance and distribution of water sources on Lewa, a giraffe was never observed more than 1 000 m away from water.

The habitat selection surveys were conducted from 06:00 to 10:00 and from 15:00 to 18:00. Therefore most observations were made during this time-span. The giraffe on Lewa demonstrates the typical ungulate pattern of feeding peaks during the early morning and late afternoon, usually resting during midday. During the dry season the giraffe was often noted feeding throughout the day, without a delay during midday. During this time, when less foliage and shoots are available, more time is spent feeding.

Population structure

The road transect technique used here to assess habitat selection is a repeatable game count and yielded repeatable results. According to Collinson (1985), a repeatable technique is precise but it may be inaccurate as the population size may be over- or underestimated when using it.

The black rhinoceros, elephant and giraffe populations on Lewa all consist of fewer than 40 % young animals (Figure 30). Bothma (1996) suggests that in most game populations 30 to 40 % of the population should consist of young animals. A balanced age structure must be maintained in any natural area so that the population remains productive. A change in the age structure over time can cause a change in the rate of the population growth (Grimsdell 1978). Depending on what the management objectives of the area are, the age structure of an animal population should also be closely monitored, so as to fulfil these objectives. On Lewa, the age structure of both the elephant and giraffe populations should be adjusted towards fewer young animals, so as to limit their productivity. Fertility in females in their first year is less than that in adult females. Therefore, to minimise the productivity in the giraffe population, the percentage of adult females should be decreased by culling or translocation. Young males, although sexually mature, seldom breed when there are older males in the population, therefore it is suggested that young males also be culled or translocated to minimise the productivity in the giraffe population on Lewa.

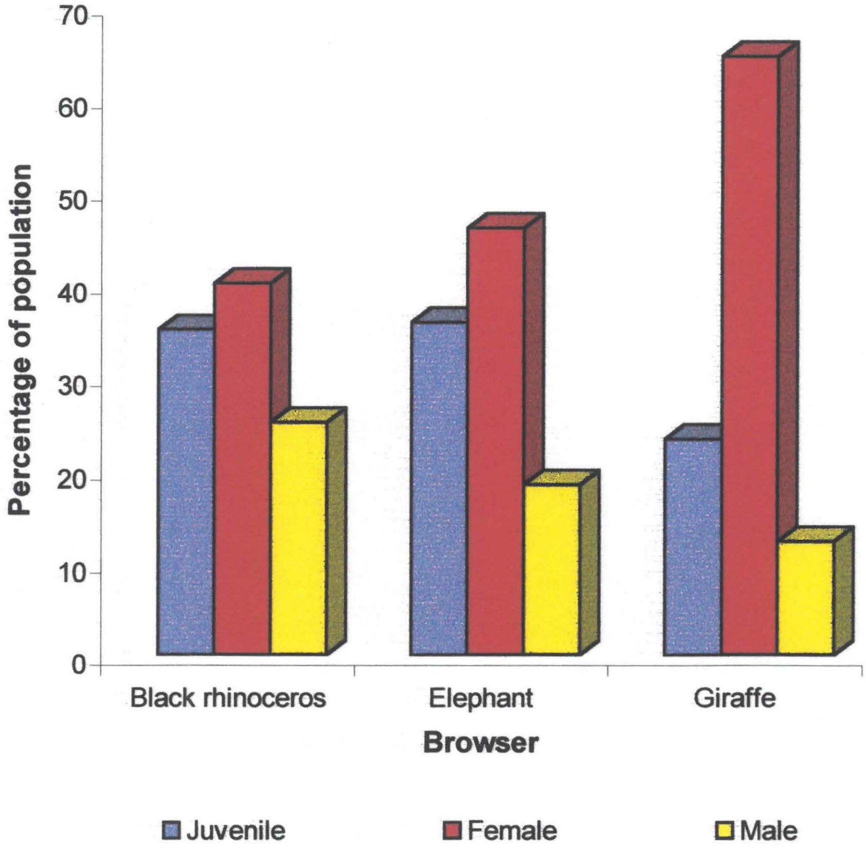

Figure 30 The broad age structure of the black rhinoceros, elephant and giraffe populations on the Lewa Wildlife Conservancy, Kenya, for the period April 1996 to April 1997.

Its sex ratio is the best indication of the breeding potential of a game population (Giles 1978). An imbalance in the sex ratio of animals often leads to a poor mating performance, especially in animal species where one male tries to maintain and serve a harem of 10 or more females while also trying to keep other males out of his territory and thus away from his breeding group (Bothma 1996). The sex ratio at birth of most game in natural conditions is 1:1 (Bothma 1996). An overabundance of females in the giraffe population on Lewa indicates an imbalance in the sex ratio. The sex ratio of the giraffe on Lewa is one male to 2.8 females. It is recommended that the sex ratio be rectified, so as to minimise the productivity of the giraffe population. As previously suggested, adult giraffe cows should be culled or translocated. A more realistic sex ratio of two males to one female is recommended. The sex ratio of the black rhinoceros on Lewa is one male to 1.1 females. To increase the productivity of the black rhinoceros population on Lewa, the number of cows should be increased. It is recommended that bulls be exchanged for cows from other rhinoceros sanctuaries in Kenya. The recommended sex ratio for the black rhinoceros on Lewa is one male to four females. A number of deaths have occurred in the female black rhinoceros population on Lewa. Some of these deaths are as a result of aggression shown by particular bulls. This aggression could possibly be caused by the limitation of space for these animals. These problem bulls should be translocated to other suitable protected areas in Kenya. The sex ratio for the elephant on Lewa is one male to 1.3 females. Twelve mature elephant bulls have recently been removed from Lewa. This may have a negative effect on the productivity of the elephant population. It should also help in preventing destruction pressure on the vegetation, especially in the riverine and swamp habitat. The elephant herds are not confined to Lewa and their sex ratio is therefore similar to what occurs in nature. With the removal of the 12 elephant bulls from the ranch, the sex ratio has been changed to a more realistic figure of one elephant bull to 10 elephant cows. Du Toit (1991) suggests that the sex ratio for elephants in a confined area should be one bull for each breeding herd comprising 6 to 10 elephants. The entry of large elephant herds onto Lewa and the period of time that these herds remain on Lewa will have to be controlled or limited so as to limit the impact that these animals are having on the vegetation.

The herd size of animals is determined by the type of habitat in which they occur. For example, plains game form larger herds than game that occur in denser habitats (Joubert 1995). The black rhinoceros is not a gregarious animal, but a female may move around with her calf and even an older calf too. Moreover, on Lewa two black rhinoceros sisters were often sighted together. The males were usually solitary. On numerous occasions five black rhinoceroses were seen feeding together for a few days, but then dispersed later. According to Estes (1995), elephant herds normally vary in size from 2 to 24, with herds of 9 to 11 individuals being typical. When the number of elephants in a family herd increases beyond 10, the herd tends to split up. On Lewa, the mean elephant herd size is seven animals. The giraffe on Lewa rarely group closely, except when browsing from the same tree. It was therefore difficult to determine how many individuals actually occurred in one herd. One record of 40 giraffe together was made, but the mean herd size calculated on Lewa is four giraffe. According to Skinner & Smithers (1990), there is not a set ratio of males to females in a herd of giraffe and the size of the herds varies greatly.

CONCLUSIONS

There is clear ecological separation between the browsers studied on Lewa. This is most evident in their seasonal choice of different habitats, although exceptions occur in the *Acacia drepanolobium - Acacia seyal* woodland and in the mixed woodland hills. The highest degree of ecological separation occurs during the dry season. The *Acacia drepanolobium - Acacia seyal* woodland has suffered severe browsing pressure by the giraffe, elephant and black rhinoceros. The giraffe and the elephant have been the main culprits, although the contribution of the black rhinoceros should not be ignored. During this study, the elephant only utilised this plant community for short periods of time. The woody vegetation decline in this plant community has led to the potential for competition between these browsers. The present giraffe culling programme should limit the competition for food resources between the black rhinoceros and the giraffe, particularly within this plant community if it is maintained and if the giraffe population is kept below 100 animals.

The mixed woodland hills sustain most of the browsers found on Lewa, especially during the dry season. During the wet season, most of the elephant herds migrate north, out of Lewa, thereby contributing to the ecological separation between the elephants and the other resident browsers on Lewa. The occupation of different habitat types in the same season, or the same habitat type in different seasons, is further evidence of the occurrence of ecological separation between these browsers. Ecological separation is also clear between the black rhinoceros and the giraffe, where the latter does not utilise the forest or forest verges. The black rhinoceros is also ecologically separated from both the elephant and the giraffe, in the aspect of the habitat and because the black rhinoceros prefers the north-facing slopes, the elephant prefer the south- and southwest-facing slopes, and the giraffe the east- and southeast-facing slopes.

It can be concluded that the optimum habitat for elephants is a large area with mixed woodland and grassland and an adequate supply of fresh water, together with large shady trees. Lewa fulfils all these requirements, and is essentially a haven for elephants.

At present the ecological capacity of Lewa for the elephant and giraffe during the dry season is exceeded. This has resulted in a decline of the woody vegetation resource. Unlike the elephant, which is both a grazer and a browser, depending on the season, the giraffe and black rhinoceros relies solely on woody vegetation for survival, although the black rhinoceros consumes a large variety of forbs. Numerous other browsers such as the eland, greater kudu, dikdik and gerenuk also utilise the woody vegetation on Lewa. Like the elephant, the eland is also a mixed feeder. Competition between the browser species for food resources is expected to be alleviated by their ecological separation, but on Lewa, the browser food resource is limited during the dry season. Therefore the potential for competition is real. The reduction of the stocking rate of the elephant, eland, giraffe and impala is therefore essential in terms of an overall browser management strategy.

Preference for different habitat types and seasonal variations in these preferences, together with the selection for specific environmental parameters all contribute to the ecological separation of the black rhinoceros, elephant and giraffe populations on Lewa. Although ecological separation does occur, the large number of giraffe and elephant present on Lewa creates an excessive demand for browse food resources, especially during the dry season. The threat of competition for food resources between the herbivores thus becomes real. Leuthold (1978) claims that actual competition occurs only when resources are in short supply. He also found ecological separation where the overlap in habitat preferences tended to be least in species with the greatest dietary overlap. Similarly, species that have overlapping food preferences tend to occupy different habitats, occupy the same habitats at different times, or feed at different height levels (Lamprey 1963). The overstocking of Lewa, particularly with elephant and giraffe has therefore clearly led to competition between the various browsers. The ecological separation evident among the three browsers studied would have probably permitted them to coexist in the same area, before the elephant and giraffe reached their dominant position and started altering the vegetation.

CHAPTER 6

FEEDING ECOLOGY

INTRODUCTION

To formulate a viable management plan for any species, its dietary requirements must be known. Selection of preferred plant species by herbivores is important, both in terms of habitat selection and interspecific competition between herbivores selecting for the same plant species. Not all food plants available to a herbivore are selected in equal quantities and some plants are completely ignored. According to Johnson (1980), plant species selection is fourth in the order of the hierarchy of habitat selection factors. A study of food plant selection by herbivores is therefore important from a management point of view because of the implications that it has for determining ecological capacity. It also helps one to know whether interspecific competition exists between herbivores or not.

Generally speaking interspecific competition between species is avoided in the evolutionary process by ecological separation (Joubert 1996). Leuthold (1978) states, however, that competition only occurs when the resources in question are in short supply. Browse availability studies on Lewa have confirmed the presence of a woody vegetation decline due to overstocking of the ranch with browsers such as the elephant and giraffe (Chapter 4). The potential for interspecific competition between the browsers on Lewa therefore exists and needs to be examined.

The feeding preferences of the black rhinoceros (Goddard 1968 & 1970; Emslie & Adcock 1994; Oloo *et al.* 1994), elephant (Laws 1970a; Guy 1976; Jachmann & Bell 1985; Viljoen 1990) and giraffe (Hall-Martin 1974b; Dagg & Foster 1976; Pellew 1983a, b & 1984; Owen-Smith 1985; Du Toit 1990; Furstenburg 1991; Kruger 1994) have been extensively studied in various parts of Africa. Various research attempts at identifying factors which might influence food selection, indicate that combinations of the following are likely:

- Secondary chemical compounds like tannins
- Mechanical defence mechanisms such as thorns
- Palatability and moisture content of plants
- Nutritional value of plants
- Availability of plants
- Structure of plants

Known conservation strategies for the black rhinoceros in Kenya include the translocation of these animals from unprotected areas to protected rhinoceros sanctuaries. Lewa is one of these protected sanctuaries. A study of the suitability of these areas for translocation depends on detailed knowledge of black rhinoceros food plants in their preferred natural habitats.

This study describes the results of the seasonal feeding ecology of the black rhinoceros, elephant and giraffe populations present on the Lewa Wildlife Conservancy. It focuses on plant species selection, plant part selection, the height of browsing and other factors which might influence such food selection. Competition between the browsers for the limited browse food resource is expected to occur, but this is also expected to be alleviated by some degree of ecological separation. Therefore the aim of this section was to study some aspects of this feeding competition, and the extent to which such competition may be avoided on Lewa. The results can then form the basis of a future browser management strategy as explained in Chapter 8.

METHODS

Collection of the data

In assessing the diet of a herbivore, three main methods can be used: examination of the stomach contents, examination of faecal material, and direct observation of feeding animals. The former two techniques are reliable and relatively accurate, but require a lot of expertise and equipment (Lamprey 1963). For this reason, the direct observation method was used on Lewa. A practical technique of indirect observation was also developed when observing the feeding habits of the black rhinoceros. This method was used when tracking a black rhinoceros in dense vegetation, or while back-tracking whenever it had stopped feeding and was found lying down.

Observations were made either on foot or from a vehicle, using 8 X 40 binoculars. Due to the myopia of a black rhinoceros, it could be followed upwind on foot at distances as close as 20 m. Individual or herds of elephants were followed on foot from further away, and also occasionally by a vehicle. Observations of giraffe were only made from inside a vehicle because they flee upon detecting any movement by a person on foot.

The data were recorded on a field data sheet (Appendix D) which itemised those variables that could influence the selection of food plants by the target browsers. The plants on which the herbivores browsed were identified either when the animal was actually feeding, or once it had moved on. When an animal was seen feeding on a plant for any given period of time, this incident was recorded as a feeding record and it counted as one observation. The plant fed on was called a feeding station for convenience of analysis. Two animals feeding from one plant counted as two observations. One animal feeding from a plant while standing in one spot, then turning to another nearby, and after a while returning to the original plant, was considered as three observations.

The data collection lasted from May 1996 to May 1997. Feeding records were gathered for the study of diurnal activity only. Data were analysed separately for the wet and dry seasons. Dry season data were defined as that collected from 1 May to 30 September and again from 1 February to 31 March. Wet season data were collected from 1 October to 31 January and again from 1 April to 30 April. A total of 2 829 feeding observations were made on Lewa during the study period. Of these, 893 were for the black rhinoceros, 913 for the elephant and 1 023 for the giraffe.

The following aspects were recorded at each sighting:

Animal:

- Black rhinoceros
- Elephant
- Reticulated giraffe

Date of observation:

The date of each observation was recorded to determine seasonal plant preferences.

Sex of the animal:

- Males - identified by distinct male characteristics.
- Females - identified by distinct female characteristics.

Plant species utilised:

At each feeding station, the plant species browsed upon was identified and recorded. Voucher specimens of plant species not identifiable in the range, were collected and accurately labelled and pressed for later identification.

Plant part utilised:

Individual plant parts or combinations of the following were recorded:

- Leaves
- Shoots
- Branches
- Bark
- Flowers
- Fruit

Height of utilisation:

The maximum and minimum height of utilisation was recorded in metres for each animal in order to determine the mean heights at which the browsers preferred to feed.

Structure of the feeding station:

- Height (m)
- Canopy diameter (m)
- Lowest available leaves (m)

Time spent at feeding station:

Feeding time was defined as beginning when the first bite was taken and ending when the animal pulled its head away from the plant involved.

Distance away from the nearest water:

The distance of each feeding station from the nearest water source was estimated. Options included the following:

- 0 - 50 m
- 51 - 250 m
- 251 - 500 m
- 501 - 1 000 m
- > 1 000 m

Wind speed:

Adapted from the Beaufort scale, wind speeds were recorded in the following categories:

- 0 - 2 knots (direction of wind shown by smoke)
- > 2 - 5 knots (wind felt on face, leaves rustle)
- > 5 - 9 knots (leaves in constant motion, wind extends light flag)
- > 9 - 13 knots (raises dust and loose paper, small branches moved)
- > 13 - 24 knots (small trees sway, crested wavelets on water, large branches move)

Cloud cover:

Categories used to describe the amount of cloud visible were divided into eighths and later converted to percentages.

- 0/8 - 2/8 = 0 - 25 %
- 3/8 - 4/8 = 26 - 50 %
- 5/8 - 6/8 = 51 - 75 %
- 7/8 - 8/8 = 76 - 100 %

Slope gradient:

A slope is an area that is inclined at an angle of more than 0°, but less than 45° from the horizontal (Vermaak 1996). The following categories were used:

- Flat - 0 - 3°
- Gradual - > 3 - 8°
- Average - > 8 - 16°
- Steep - > 16°

Aspect:

The aspect is the compass direction towards which a slope faces and is expressed as degrees relative to true North (Gabriel & Talbot 1984). The aspects N, NE, E, SE, S, SW, W or NW were determined using a compass.

Statistical analysis of the data

The feeding ecology data collected on Lewa were subjected to the unique and time-consuming categorical modeling procedure (CATMOD). A detailed analysis of the data was performed, obtaining meaningful, reliable results. Each observation entailed 13 variables, which in turn contained a number of sub-variables. The variables were submitted to the CATMOD procedure by the designated browser species and the season of observation. Models were then created using the CATMOD procedure (Table 12). The procedure followed has been described in detail in Chapter 5.

Table 12 Models used in the determination of the odds ratio's and probabilities for the feeding ecology of the black rhinoceros, elephant and giraffe populations on the Lewa Wildlife Conservancy, Kenya, from May 1996 to May 1997 by using the CATMOD procedure.

BROWSER	SEASON	MODEL NUMBER	MODEL													
Black rhinoceros bull	not specified	1	*	*	*	V6B	V7A		*	*	V11A	V12A	*	*	*	*
Black rhinoceros bull	wet	2	*	*	*	*	*	*	*	*	*	V12B	*	V14A	*	*
Black rhinoceros bull	dry	3	*	*	*	*	*	*	*	*	V11B	V12B	*	V14A	V15A	V16B
Black rhinoceros cow	not specified	4	V2D	V4C	V5C	V6A	V7A		*	*	V11A	V12A	*	V14A	V15A	V16B
Black rhinoceros cow	wet	5	*	V4C	V5C	V6B	*	*	*	*	V11B	V12B	*	V14A	V15A	V16B
Black rhinoceros cow	dry	6	V2D	*	V5C	V6B	*		*	*	V11B	V12B	*	V14A	V15A	*
Elephant bull	not specified	7	V2C	V4C	V5C	V6A	V7A		V9A	V10A	V11A	V12A	V13A	V14A	V15A	V16B
Elephant bull	wet	8	*	*	V5B	V6A	V7A		V9A	V10A	V11A	V12A	V13B	V14A	V15A	V16B
Elephant bull	dry	9	V2D	*	V5B	V6A	V7A		V9A	V10A	V11A	V12A	V13A	V14A	V15A	V16B
Elephant cow	not specified	10	*	*	V5B	V6A	V7A		V9A	V10B	V11A	V12A	V13A	V14A	V15A	V16B
Elephant cow	wet	11	*	*	V5B	V6B	V7A		V9A	V10B	V11A	V12A	V13B	V14A	V15A	V16B
Elephant cow	dry	12	*	*	V5B	V6A	V7A		V9B	V10C	V11A	V12A	V13C	V14A	V15A	V16B
Giraffe bull	not specified	13	V2C	*	*	V6B	V7A		V9A	V10A	V11A	V12A	V13A	V14A	V15A	V16B
Giraffe bull	wet	14	*	*	*	V6B	*		*	V10B	V11A	V12A	V13B	V14A	V15A	V16B
Giraffe bull	dry	15	V2C	*	*	V6B	V7A		V9A	V10B	V11A	V12A	V13B	V14A	V15A	V16B
Giraffe cow	not specified	16	V2C	*	*	V6A	V7A		V9B	V10B	V11A	V12A	V13C	V14A	V15A	V16B
Giraffe cow	wet	17	V2C	*	*	V6A	*		V9B	V10B	V11A	V12A	V13C	V14A	V15A	V16B
Giraffe cow	dry	18	V2C	*	*	V6A	V7A		V9B	V10C	V11A	V12A	V13C	V14A	V15A	V16B

Note: missing variables indicated by an asterisk (*)

RESULTS AND DISCUSSION

The results of the CATMOD analysis for the feeding preferences of the black rhinoceros, elephant and giraffe appear in Tables 13 to 22. Appendix E is the interpretation of the variables presented in Tables 13 to 22. Each data set was considered separately, and models were built with the maximum number of variables possible, until immediately prior to the collapse of the model. The interpretation of these models provided data specific to each individual browser.

Black rhinoceros

Selection of plant species

A total of 111 plant species from 39 families were browsed by the black rhinoceros on Lewa. The data were either collected during specific data collection periods or were recorded incidentally. This list of plant species falls within the range of plants utilised in studies in the Ngorongoro Crater (191 species), Tsavo National Park (102 species), the Masai-Mara region (70 species) and Ol Ari Nyiro Ranch, Kenya (103 species) (Goddard 1968 & 1970; Mukinya 1977; Oloo *et al.* 1994). Families having at least four representatives are the Acanthaceae, Amaranthaceae, Asteraceae, Capparaceae, Euphorbiaceae, Fabaceae, Malvaceae, Solanaceae, Tiliaceae, Verbenaceae and Vitaceae. The diversity of food plants browsed is greater during the wet season than during the dry season. Goddard (1970) suggested that the relative abundance and availability of legume species (Fabaceae) may be the best indicator of an optimal habitat for black rhinoceros. Taking into account the unidentified legume species consumed by the black rhinoceros on Lewa, leguminose flora form at least 40.5 % of the plant species in the diet of the black rhinoceros there. Furthermore, at least 30 species of leguminose flora are present on Lewa, making it an ideal habitat for the black rhinoceros.

Table 13 shows the relative frequency of the plants that were eaten by the black rhinoceros on Lewa, as categorised by season. As in previous studies elsewhere, *Acacia* species are the most abundant food plants, comprising 34 % of the plant species consumed by the black rhinoceros on Lewa during the wet season, and 47 % during the dry season. At least 20 plant species accounted for more than 1 % occurrence in the diet of the black rhinoceros during the wet season, but only 11 species did so during the dry season. The two plant species most commonly eaten during the wet *season* are *Acacia seyal* and *Acacia drepanolobium* which together account for 25 % of the black rhinoceros diet (Figure 31). During the dry season, the two plant species most commonly eaten are *Acacia drepanolobium* and *Acacia seyal* which together account for 43 % of the black rhinoceros diet (Figure 32). The relative importance of the various food plants of the black rhinoceros therefore differs between the wet and dry seasons on Lewa.

The preferred habitat of four black rhinoceros cows on Lewa was the *Acacia drepanolobium - Acacia seyal* woodland. Although these cows generally utilise the same ranges, their individual preferences

Table 13 The percentage occurrence of various plants in the seasonal diet of the black rhinoceros on the Lewa Wildlife Conservancy, Kenya, from May 1996 to May 1997 listed in descending order of use.

PLANT	WET SEASON (n = 577)	DRY SEASON (n = 334)
Acacia seyal	13.9	18.3
Acacia drepanolobium	11.8	24.9
Dyschoriste species	10.7	1.2
Hibiscus species	9.8	11.3
Unidentified grasses	8.9	7.5
Unidentified forbs	8.6	14.4
Asparagus species	4.8	0.3
Acacia mellifera	3.8	0.3
Maytenus senegalensis	3.3	0.3
Euclea divinorum	2.6	4.4
Cadaba farinosa	2.5	-
Acacia brevispica	2.4	-
Boscia species	2.4	3
Grewia species	2.3	0.6
Lycium shawii	2.3	0.3
Tinnea aethiopica	2.0	0.3
Carissa edulis	1.9	5.4
Lippia species	1.7	-
Rhus natalensis	1.7	0.9
Balanites aegyptiaca	1.3	2.1
Acacia tortilis	1.2	0.3
Acacia nilotica	1.0	2.4
Euphorbia species	0.9	0.6
Commiphora africana	0.8	-
Barleria species	0.5	-
Acacia xanthophloea	0.4	0.9
Acacia senegal	0.3	-
Acacia hockii	0.2	-
Datura stramonium	0.2	0.3
Total	100.0	100.0

Note: Dash indicates no record for the particular season.

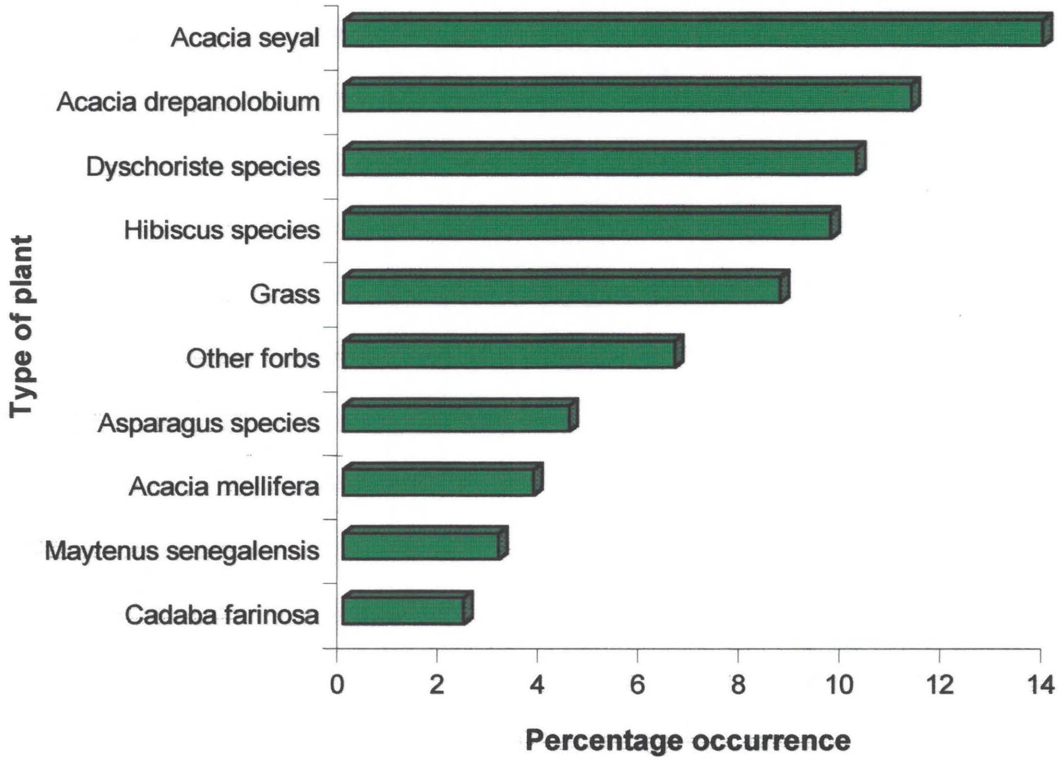

Figure 31 Percentage occurrence of 10 of the most commonly eaten types of plant in the diet of the black rhinoceros, in descending order of occurrence, on the Lewa Wildlife Conservancy, Kenya, during the wet season, from May 1996 to May 1997.

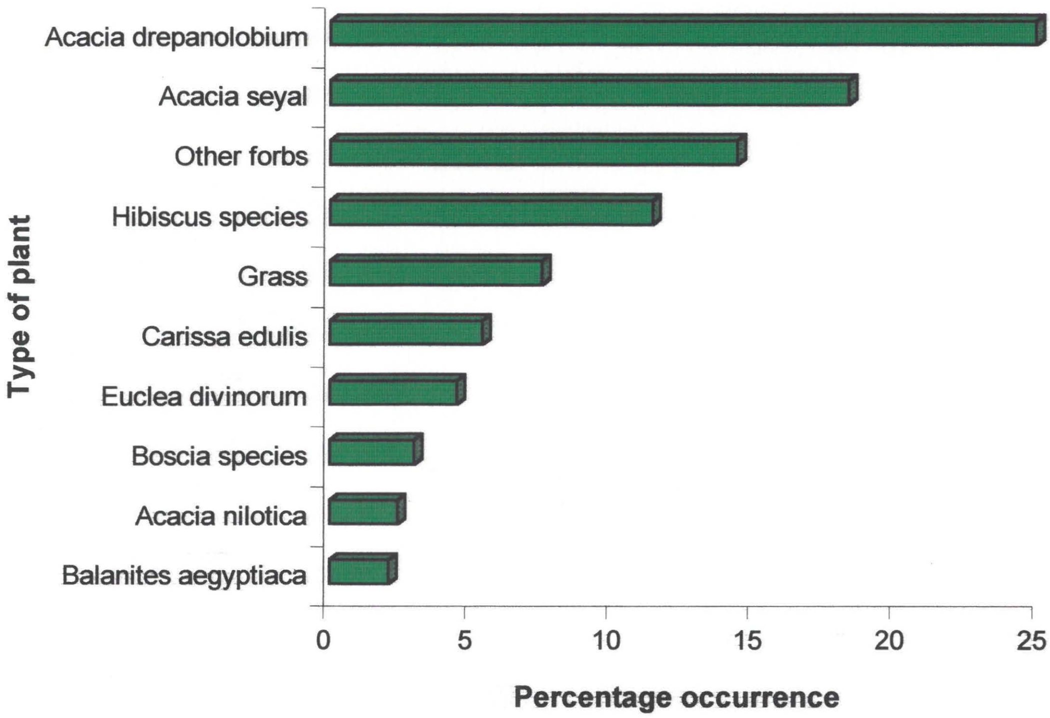

Figure 32 Percentage occurrence of 10 of the most commonly eaten types of plant in the diet of the black rhinoceros, in descending order of occurrence, on the Lewa Wildlife Conservancy, Kenya, during the dry season, from May 1996 to May 1997.

for food plants varied. *Acacia seyal*, followed by *Acacia drepanolobium*, are clearly the preferred food plants during both the wet and dry seasons for these black rhinoceros cows. It has been well documented that a black rhinoceros shows a marked preference for *Acacia* species throughout its distributional range (Kotze & Zacharias 1993; Emslie & Adcock 1994; Oloo *et al.* 1994), although they do have the ability to eat a wide variety of plants. Grasses and *Hibiscus* species also form a large part of the diet of these black rhinoceros cows on Lewa. Grasses constituted 15 % of the food plants in the diet of one of these cows during the wet season, and 10 % during the dry season. It is certainly not unusual on Lewa to observe a black rhinoceros eating grass, despite the belief by Emslie & Adcock (1994) that a black rhinoceros will only eat grass when under nutritional stress. The forb, *Datura stramonium,* is also eaten by the black rhinoceros on Lewa. Emslie & Adcock (1994) refer to studies done in Kwazulu-Natal, South Africa, where *Datura stramonium* was observed to grow in black rhinoceros dung piles, even though its seeds are narcotic. Oloo *et al.* (1994) also documented that the black rhinoceros feeds on *Datura stramonium.* Forbs therefore form a varying, but regular proportion of the diet of a black rhinoceros, and these plants are most important as food during the wet season flush.

Four male and one female black rhinoceros were observed browsing in the mixed woodland hills. A larger variety of food plants occurs in the mixed woodland hills than on the plains. Therefore the diet of these black rhinoceroses is different from that of the black rhinoceroses that occur in the *Acacia drepanolobium - Acacia seyal* woodland. *Commiphora africana* is an evergreen tree species which remains palatable throughout the year. It is readily eaten, especially by one of the males in whose diet it constituted 40 % of the plant species during the wet season. On the contrary, Goddard (1970) found that the black rhinoceros in the Tsavo National Park in Kenya did not eat *Commiphora* species at all, although they were present there. *Maytenus senegalensis* is also readily selected for by the black rhinoceros on Lewa that inhabit the mixed woodland hills. Emslie & Adcock (1994) believe that *Maytenus senegalensis* is not a preferred food plant for the black rhinoceros in Kwazulu-Natal, South Africa. On Lewa, the black rhinoceros seems to be a catholic, but opportunistic feeder, eating whatever is available. The shrub *Cadaba farinosa* constituted 42 % of the plant species in a female black rhinoceros' diet during the wet season. It furthermore appeared that she was very selective towards this shrub. The more common *Grewia* species, which also occur in her range, only formed a small part of her diet. There are clear individual food preferences between the black rhinoceros, although also an overall similarity as well. The reason why *Acacia tortilis* and *Acacia xanthophloea* are not more readily consumed by the black rhinoceros on Lewa, is probably related to the structure of these trees. Because most of their foliage is above 2 m in height it is therefore out of reach of a feeding black rhinoceros.

Two female and a male black rhinoceros were observed browsing in the forest verges and in the mixed woodland hills adjacent to the forest. The two females preferred to feed in the mixed woodland hills adjacent to the forest verges, where *Acacia drepanolobium* and a wide variety of forbs, particularly *Hibiscus* species, constitute the main part of their diet. *Dyschoriste* species are found mainly in the forest verges, where this forb constitutes 52 % of the plant species in the male's diet.

The black rhinoceros in these habitats were also observed grazing, although grass constituted less than 10 % of the food plants in their diet. *Carissa edulis* is an evergreen tree species, and is also readily eaten by the black rhinoceros that inhabit the forests and its verges. *Boscia coriacea*, which is also an evergreen species, is consumed during both the wet and the dry seasons. Goddard (1970), however, claims that these trees are rarely, if ever, used as a food source by black rhinoceros in the Tsavo National Park in Kenya.

Selection of plant parts

During both the wet and the dry season, the black rhinoceros cows on Lewa eat all parts of individual plants more often than eating only the leaves, branches or shoots (Table 14). Goddard (1970), Mukinya (1977) and Oloo *et al.* (1994) also noted this in the Tsavo National Park, the Masai-Mara region and on Ol Ari Nyiro Ranch, Kenya, respectively. During the dry season on Lewa, the bark of some trees is also eaten. The relative palatability of some of the food plants may differ between seasons. During the dry season, nutrients are translocated to the bark and branches, rather than to the shoots and leaves. This may explain why the black rhinoceros eats bark and branches more often during the dry season than during the wet season.

Method of feeding

By its feeding method, the black rhinoceros changes some aspects of its habitat in a characteristic manner. Schenkel & Schenkel-Hulliger (1969) recognised the effect of feeding by a black rhinoceros on the structure of an individual plant, and called it a “brush pattern”. When new shoots grow from the older branches, they are continually cut off again by feeding black rhinoceroses. This leaves a characteristic growth form (Figure 33). Browsing by elephants never causes the “brush pattern”. On Lewa the most obvious impact of the black rhinoceros on its habitat is the “brush pattern” found in many of the *Acacia mellifera* and *Boscia angustifolia* trees. Most of the twigs and branches are bitten off neatly (Figure 34). Occasionally the twigs and branches are severed, ending in a sharp spike (Figure 35). This is the result of biting with a twisting and pulling movement of the head. The feeding method of the black rhinoceros is also adapted to the respective type of food plant. When a black rhinoceros on Lewa feeds in habitats dominated by tall trees, it uses its horns to gain access to the higher branches. By hooking its front horn around the branch, it is pulled down sideways. Most often the branch is broken by this feeding method. The tree will not die, but its structure will be altered.

Browsing height

Throughout the year the black rhinoceros on Lewa prefers to browse on bushes and shrubs less than 1 m in height (Table 14). During the dry season, the black rhinoceros bulls on Lewa were more likely

Table 14 Odds ratio results and probabilities calculated for the feeding ecology of the black rhinoceros on the Lewa Wildlife Conservancy, Kenya, from May 1996 to May 1997, indicating their presence in category A, as opposed to category B, for the specific variable measured.

VARIABLE	GROUP NUMBER	NUMBER OF CATEGORIES	CATEGORY A	CATEGORY B	A:B	PROBABILITY	MODEL NUMBER
Black rhinoceros bulls							
Aspect	B	4	E (1)	S (3)	17:1	0.0000	1
Aspect	B	4	E (1)	W (4)	11:1	0.0000	1
Aspect	B	4	N (2)	S (3)	22:1	0.0000	1
Aspect	B	4	N (2)	W (4)	13:1	0.0000	1
Distance from water	A	5	251 - 500 m (3)	0 - 50 m (1)	7:1	0.0000	1
Distance from water	A	5	251 - 500 m (3)	51 - 250 m (2)	4:1	0.0000	1
Distance from water	A	5	251 - 500 m (3)	501 - 1 000 m (4)	23:1	0.0001	1
Distance from water	A	5	251 - 500 m (3)	> 1 000 m (5)	17:1	0.0000	1
Distance from water	A	5	501 - 1 000 m (4)	0 - 50 m (1)	3:2	0.0106	1
Distance from water	A	5	501 - 1 000 m (4)	51 - 250 m (2)	2:1	0.0294	1
Distance from water	A	5	501 - 1 000 m (4)	> 1 000 m (5)	3:1	0.0010	1
	B	3	Gradual (2)	Flat (1)	14:1	0.0000	1
	B	3	Average - steep (3)	Flat (1)	78:1	0.0000	1
Tree height	A	6	0 - 1 m (1)	> 1 - 2 m (2)	7:1	0.0000	1
Tree height	A	6	0 - 1 m (1)	> 2 - 3 m (3)	5:1	0.0000	1
Tree height	A	6	0 - 1 m (1)	> 3 - 4 m (4)	23:1	0.0000	1
Tree height	A	6	0 - 1 m (1)	> 4 - 5 m (5)	30:1	0.0001	1
Tree height	A	6	0 - 1 m (1)	> 5 m (6)	51:1	0.0008	1
Tree height	A	6	> 1 - 2 m (2)	> 3 - 4 m (4)	4:1	0.0108	1
Tree height	A	6	> 2 - 3 m (3)	> 3 - 4 m (4)	4:1	0.0036	1
Tree height	A	6	> 2 - 3 m (3)	> 4 - 5 m (5)	5:1	0.0368	1
Canopy diameter	A	6	0 - 1 m (1)	> 1 - 2 m (2)	2:1	0.0393	1
Canopy diameter	A	6	0 - 1 m (1)	> 2 - 3 m (3)	5:1	0.0011	1
Canopy diameter	A	6	> 1 - 2 m (2)	> 2 - 3 m (3)	3:1	0.0230	1
Canopy diameter	A	6	> 3 - 4 m (4)	> 2 - 3 m (3)	3:1	0.0148	1
Black rhinoceros cows							
Habitat type	D	4	*Drep sey* (1)	MAH (2)	405:1	0.0000	4
Habitat type	D	4	*Drep sey* (1)	MAP (3)	13:1	0.0000	4
Habitat type	D	4	*Drep sey* (1)	MWH (4)	152:1	0.0000	4
Habitat type	D	4	MAP (3)	MAH (2)	32:1	0.0000	4
Habitat type	D	4	MAP (3)	MWH (4)	12:1	0.0000	4
Plant species	B	12	*Acac dre* (1)	*Acac mel* (2)	146:1	0.0000	4
Plant species	B	13	*Acac dre* (1)	*Acac nil* (3)	8:1	0.0010	4
Plant species	B	12	*Acac dre* (1)	*Acac tor* (5)	65:1	0.0004	4
Plant species	B	12	*Acac dre* (1)	*Hibiscus* sp. (10)	20:1	0.0028	4
Plant species	B	12	*Acac dre* (1)	*Mayt sen* (11)	3:1	0.0192	4
Plant species	B	12	*Acac nil* (3)	*Acac mel* (2)	18:1	0.0136	4
Plant species	B	12	*Acac sey* (4)	*Acac mel* (2)	85:1	0.0001	4
Plant species	B	12	*Acac sey* (4)	*Acac nil* (3)	5:1	0.0197	4
Plant species	B	12	*Acac sey* (4)	*Acac tor* (5)	38:1	0.0026	4
Plant species	B	12	*Acac sey* (4)	*Hibiscus* sp. (10)	12:1	0.0154	4
Plant species	B	12	*Acac xan* (6)	*Acac mel* (2)	86:1	0.0010	4
Plant species	B	12	*Acac xan* (6)	*Acac tor* (5)	38:1	0.0083	4
Plant species	B	12	*Acac xan* (6)	*Hibiscus* sp. (10)	12:1	0.0489	4
Plant species	B	12	*Comm afr* (7)	*Acac mel* (2)	32:1	0.0133	4
Plant species	B	12	Forbs (8)	*Acac mel* (2)	164:1	0.0035	4
Plant species	B	12	Forbs (8)	*Acac tor* (5)	73:1	0.0159	4
Plant species	B	12	Grasses (9)	*Acac mel* (2)	39:1	0.0091	4
Plant species	B	12	*Mayt sen* (11)	*Acac mel* (2)	49:1	0.0007	4
Plant species	B	12	*Mayt sen* (11)	*Acac tor* (5)	22:1	0.0085	4
Plant part	B	7	br, ba (1)	le (5)	34:1	0.0000	4
Plant part	B	7	br, ba (1)	le, sh (6)	425:1	0.0000	4
Plant part	B	7	br, ba, le, sh (2)	le (5)	36:1	0.0000	4

Table 14 (continued)

VARIABLE	GROUP NUMBER	NUMBER OF CATEGORIES	CATEGORY A	CATEGORY B	A:B	PROBABILITY	MODEL NUMBER
Black rhinoceros cows (cont.)							
Plant part	B	7	br, ba, le, sh (2)	le, sh (6)	448:1	0.0000	4
Plant part	B	7	br, le (3)	le (5)	37:1	0.0000	4
Plant part	B	7	br, le (3)	le, sh (6)	459:1	0.0000	4
Plant part	B	7	br, le, sh (4)	br, ba (1)	4:1	0.0025	4
Plant part	B	7	br, le, sh (4)	br, ba, le, sh (2)	4:1	0.0306	4
Plant part	B	7	br, le, sh (4)	br, le (3)	4:1	0.0022	4
Plant part	B	7	br, le, sh (4)	le, sh (6)	1 813:1	0.0000	4
Plant part	B	7	br, le, sh (4)	br, ba, le, sh, fl, fr (7)	4:1	0.0399	4
Plant part	B	7	le (5)	br, le, sh (4)	145:1	0.0000	4
Plant part	B	7	le (5)	le, sh (6)	12:1	0.0017	4
Plant part	B	7	br, ba, le, sh, fl, fr (7)	le (5)	41:1	0.0000	4
Plant part	B	7	br, ba, le, sh, fl, fr (7)	le, sh (6)	516:1	0.0000	4
Aspect	A	8	E (1)	NE (3)	5:1	0.0125	4
Aspect	A	8	E (1)	S (5)	4:1	0.0236	4
Aspect	A	8	E (1)	SE (6)	40:1	0.0000	4
Aspect	A	8	N (2)	NE (3)	5:1	0.0027	4
Aspect	A	8	N (2)	S (5)	4:1	0.0103	4
Aspect	A	8	N (2)	SE (6)	45:1	0.0000	4
Aspect	A	8	N (2)	SW (7)	5:1	0.0386	4
Aspect	A	8	NE (3)	SE (6)	9:1	0.0126	4
Aspect	A	8	NW (4)	NE (3)	12:1	0.0006	4
Aspect	A	8	NW (4)	S (5)	10:1	0.0017	4
Aspect	A	8	NW (4)	SE (6)	107:1	0.0000	4
Aspect	A	8	NW (4)	SW (7)	11:1	0.0068	4
Aspect	A	8	S (5)	SE (6)	11:1	0.0046	4
Aspect	A	8	SW (7)	SE (6)	10:1	0.0211	4
Aspect	A	8	W (8)	NE (3)	4:1	0.0138	4
Aspect	A	8	W (8)	SE (6)	37:1	0.0000	4
Aspect	A	8	W (8)	S (5)	3:1	0.0265	4
Distance from water	A	5	251 - 500 m (3)	51 - 250 m (2)	4:1	0.0336	4
Distance from water	A	5	501 - 1 000 m (4)	0 - 50 m (1)	3:1	0.0572	4
Distance from water	A	5	501 - 1 000 m (4)	51 - 250 m (2)	9:1	0.0006	4
Distance from water	A	5	501 - 1 000 m (4)	251 - 500 m (3)	2:1	0.0487	4
Distance from water	A	5	501 - 1 000 m (4)	> 1 000 m (5)	3:1	0.0123	4
	B	3	Gradual (2)	Average - steep (3)	6:1	0.0078	4
Tree height	A	6	0 - 1 m (1)	> 1 - 2 m (2)	3:1	0.0021	4
Tree height	A	6	0 - 1 m (1)	> 2 - 3 m (3)	6:1	0.0004	4
Tree height	A	6	0 - 1 m (1)	> 3 - 4 m (4)	9:1	0.0002	4
Tree height	A	6	0 - 1 m (1)	> 4 - 5 m (5)	8:1	0.0204	4
Tree height	A	6	0 - 1 m (1)	> 5 m (6)	38:1	0.0018	4
Tree height	A	6	> 1 - 2 m (2)	> 3 - 4 m (4)	3:1	0.0586	4
Tree height	A	6	> 1 - 2 m (2)	> 5 m (6)	11:1	0.0292	4
Canopy diameter	A	6	> 1 - 2 m (2)	> 5 m (6)	12:1	0.0519	4
Canopy diameter	A	6	> 2 - 3 m (3)	0 - 1 m (1)	3:1	0.0597	4
Canopy diameter	A	6	> 2 - 3 m (3)	> 4 - 5 m (5)	7:1	0.0286	4
Canopy diameter	A	6	> 2 - 3 m (3)	> 5 m (6)	24:1	0.0130	4
Canopy diameter	A	6	> 3 - 4 m (4)	> 5 m (6)	16:1	0.0335	4
Wind speed	A	5	0 - 2 knots (1)	> 9 - 13 knots (4)	2:1	0.0000	4
Wind speed	A	5	> 2 - 5 knots (2)	0 - 2 knots (1)	1	0.0012	4
Wind speed	A	5	> 5 - 9 knots (3)	0 - 2 knots (1)	1	0.0054	4
Wind speed	A	5	> 9 - 13 knots (4)	> 5 - 9 knots (3)	1	0.0658	4
Cloud cover	B	4	0 - 25 % (1)	> 25 - 50 % (2)	3:1	0.0040	4
Cloud cover	B	4	0 - 25 % (1)	> 50 - 75 % (3)	2:1	0.0668	4
Cloud cover	B	4	0 - 25 % (1)	> 75 - 100 % (4)	3:1	0.0177	4

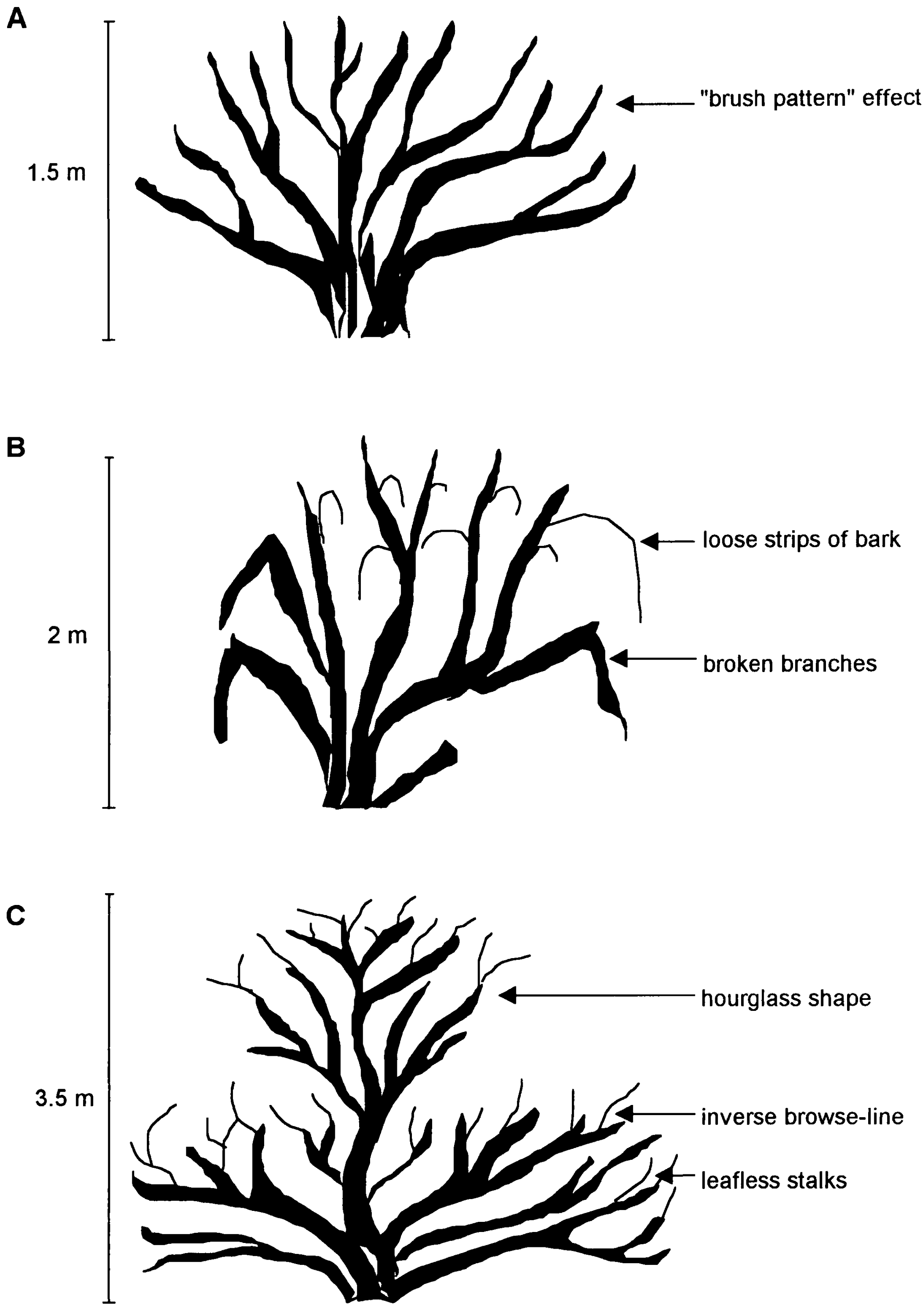

Figure 33 The effect of browsing on a shrub by a black rhinoceros (A), and on a tree by an elephant (B) and a giraffe (C).

Figure 34 The effect of black rhinoceros feeding on *Chenopodium album* on the Lewa Wildlife Conservancy. Notice that the stems are bitten off neatly, usually at a 45° angle.

Figure 35 A resultant sharp spike on an *Acacia drepanolobium* tree after a black rhinoceros had been feeding on it.

to browse on bushes and shrubs less than 1 m in height than on bushes and shrubs 1 to 2 m in height (Odds ratio = 3:1 ; P = 0.0496), 3 to 4 m in height (Odds ratio = 13:1 ; P = 0.0384) or greater than 4 m in height (Odds ratio = 18:1 ; P = 0.0364) (Table 16). During both the wet and the dry season, the black rhinoceros cows on Lewa browse on trees, bushes and shrubs up to 2 m in height, although during the dry season, the cows prefer to browse on bushes and shrubs less than 1 m in height (Tables 15 & 16). Kotze & Zacharias (1993) found that 86 % of the browse of a black rhinoceros in the Itala Game Reserve in South Africa was taken from small plants, less than 2.5 m in height. Oloo *et al.* (1994) found that the black rhinoceros on Ol Ari Nyiro Ranch in Kenya, feeds mostly in areas with a high density of low *Acacias*. Emslie & Adcock (1994) found that as *Acacias* get taller, their leaves become less palatable to a black rhinoceros. In the Hluhluwe-Umfolozi Park in South Africa, *Acacias* less than 1 m in height are highly preferred by the black rhinoceros. Joubert (1996) found that, although a black rhinoceros can browse at a height of approximately 1.2 m, its preferred browsing height is between 0.4 and 0.9 m. In terms of black rhinoceros habitat suitability, the marked selection preferences for trees and bushes less than 2 m in height indicate how important it is to maintain enough of these plants in a short growth stage on Lewa and to prevent them from maturing into taller trees.

During the wet season, the black rhinoceros on Lewa browses on trees and bushes with a canopy diameter of less than 4 m. It was more likely to observe a black rhinoceros bull browsing on trees and bushes with a canopy diameter of 0 to 1 m (Odds ratio = 16:1 ; P = 0.0095) or 3 to 4 m (Odds ratio = 12:1 ; P = 0.0194), than on trees and bushes with a canopy diameter greater than 4 m. Similarly, it was more likely to observe a black rhinoceros cow browsing on trees and bushes with a canopy diameter of 1 to 2 m (Odds ratio = 14:1 ; P = 0.0338) or 2 to 3 m (Odds ratio = 39:1 ; P = 0.0055), than on trees and bushes with a canopy diameter greater than 4 m (Table 15). During the dry season, however, a preference is shown for trees and bushes with a canopy diameter of greater than 4 m. It was more likely to observe a black rhinoceros bull browsing on trees and bushes with a canopy diameter greater than 4 m, than on trees and bushes with a canopy diameter of 1 to 2 m (Odds ratio = 8:1 ; P = 0.0702). Similarly, it was more likely to observe a black rhinoceros cow browsing on trees and bushes with a canopy diameter greater than 4 m, than on trees and bushes with a canopy diameter of 0 to 1 m (Odds ratio = 5:1 ; P = 0.0665) (Table 16). It therefore appears that the black rhinoceros on Lewa prefers to browse on trees and bushes with a small canopy diameter, but when food plant availability decreases during the dry season, trees and bushes with a larger canopy diameter are also selected. It is also possible that the black rhinoceros on Lewa seeks more shade during the dry season. Therefore it selects trees with a larger canopy diameter at this time. These results have an important bearing on the effect of habitat change, especially on the black rhinoceros population on Lewa. Trees and bushes that are in a short growth stage are essential black rhinoceros habitat components.

Table 15 Odds ratios and probabilities, categorised for the wet season, for the feeding ecology of the black rhinoceros on the Lewa Wildlife Conservancy, Kenya, from May 1996 to May 1997, indicating their presence in category A, as opposed to category B, for the specific variable measured.

VARIABLE	GROUP NUMBER	NUMBER OF CATEGORIES	CATEGORY A	CATEGORY B	A:B	PROBABILITY	MODEL NUMBER
Black rhinoceros bulls							
Canopy diameter	B	5	0 - 1 m (1)	> 4 m (5)	16:1	0.0095	2
Canopy diameter	B	5	> 1 - 2 m (2)	0 - 1 m (1)	3:1	0.0635	2
Canopy diameter	B	5	> 3 - 4 m (4)	> 4 m (5)	12:1	0.0194	2
Black rhinoceros cows							
Plant species	B	12	*Acac dre* (1)	*Acac mel* (2)	75:1	0.0030	5
Plant species	B	12	*Acac dre* (1)	*Acac nil* (3)	12:1	0.0483	5
Plant species	B	12	*Acac dre* (1)	*Acac tor* (5)	87:1	0.0017	5
Plant species	B	12	*Acac dre* (1)	*Comm afr* (7)	155:1	0.0000	5
Plant species	B	12	*Acac dre* (1)	*Hibiscus* sp. (10)	808:1	0.0000	5
Plant species	B	12	*Acac dre* (1)	*Mayt sen* (11)	16:1	0.0001	5
Plant species	B	12	*Acac nil* (3)	*Hibiscus* sp. (10)	66:1	0.0097	5
Plant species	B	12	*Acac sey* (4)	*Acac mel* (2)	157:1	0.0005	5
Plant species	B	12	*Acac sey* (4)	*Acac nil* (3)	25:1	0.0087	5
Plant species	B	12	*Acac sey* (4)	*Acac tor* (5)	180:1	0.0002	5
Plant species	B	12	*Acac sey* (4)	*Acac xan* (6)	25:1	0.0257	5
Plant species	B	12	*Acac sey* (4)	*Comm afr* (7)	322:1	0.0000	5
Plant species	B	12	*Acac sey* (4)	Grasses (9)	40:1	0.0307	5
Plant species	B	12	*Acac sey* (4)	*Hibiscus* sp. (10)	1 682:1	0.0000	5
Plant species	B	12	*Acac sey* (4)	*Mayt sen* (11)	33:1	0.0000	5
Plant species	B	12	*Acac xan* (6)	*Hibiscus* sp. (10)	67:1	0.0172	5
Plant species	B	12	Forbs (8)	*Acac mel* (2)	645:1	0.0044	5
Plant species	B	12	Forbs (8)	*Acac nil* (3)	104:1	0.0261	5
Plant species	B	12	Forbs (8)	*Acac tor* (5)	741:1	0.0026	5
Plant species	B	12	Forbs (8)	*Acac xan* (6)	104:1	0.0370	5
Plant species	B	12	Forbs (8)	*Comm afr* (7)	1 324:1	0.0004	5
Plant species	B	12	Forbs (8)	Grasses (9)	163:1	0.0344	5
Plant species	B	12	Forbs (8)	*Hibiscus* sp. (10)	6 916:1	0.0001	5
Plant species	B	12	Forbs (8)	*Mayt sen* (11)	136:1	0.0073	5
Plant species	B	12	*Mayt sen* (11)	*Comm afr* (7)	10:1	0.0109	5
Plant species	B	12	*Mayt sen* (11)	*Hibiscus* sp. (10)	51:1	0.0023	5
Plant part	B	7	br, ba (1)	le, sh (6)	90:1	0.0015	5
Plant part	B	7	br, ba, le, sh (2)	br, ba (1)	19:1	0.0287	5
Plant part	B	7	br, ba, le, sh (2)	le (5)	82:1	0.0183	5
Plant part	B	7	br, ba, le, sh (2)	le, sh (6)	1 710:1	0.0000	5
Plant part	B	7	br, le (3)	le, sh (6)	332:1	0.0000	5
Plant part	B	7	br, le, sh (4)	br, ba (1)	48:1	0.0000	5
Plant part	B	7	br, le, sh (4)	br, le (3)	13:1	0.0000	5
Plant part	B	7	br, le, sh (4)	le (5)	207:1	0.0006	5
Plant part	B	7	br, le, sh (4)	le, sh (6)	4 344:1	0.0000	5
Plant part	B	7	br, ba, le, sh, fl, fr (7)	br, ba (1)	26:1	0.0163	5
Plant part	B	7	br, ba, le, sh, fl, fr (7)	le (5)	111:1	0.0120	5
Plant part	B	7	br, ba, le, sh, fl, fr (7)	le, sh (6)	2 321:1	0.0000	5
Aspect	B	4	N (2)	E (1)	37:1	0.0000	5
Aspect	B	4	N (2)	S (3)	5:1	0.0139	5
Aspect	B	4	N (2)	W (4)	8:1	0.0011	5
Aspect	B	4	S (3)	E (1)	7:1	0.0246	5
Tree height	B	5	0 - 1 m (1)	> 2 - 3 m (3)	15:1	0.0011	5
Tree height	B	5	0 - 1 m (1)	> 3 - 4 m (4)	19:1	0.0035	5
Tree height	B	5	0 - 1 m (1)	> 4 m (5)	75:1	0.0001	5
Tree height	B	5	> 1 - 2 m (2)	> 2 - 3 m (3)	5:1	0.0159	5
Tree height	B	5	> 1 - 2 m (2)	> 3 - 4 m (4)	6:1	0.0319	5
Tree height	B	5	> 1 - 2 m (2)	> 4 m (5)	26:1	0.0020	5
Canopy diameter	B	5	> 1 - 2 m (2)	0 - 1 m (1)	4:1	0.0287	5
Canopy diameter	B	5	> 1 - 2 m (2)	> 4 m (5)	14:1	0.0338	5

Table 15 (continued)

VARIABLE	GROUP NUMBER	NUMBER OF CATEGORIES	CATEGORY A	CATEGORY B	A:B	PROBABILITY	MODEL NUMBER
Black rhinoceros cows (cont.)							
Canopy diameter	B	5	> 2 - 3 m (3)	0 - 1 m (1)	11:1	0.0102	5
Canopy diameter	B	5	> 2 - 3 m (3)	> 4 m (5)	39:1	0.0055	5
Wind speed	A	5	0 - 2 knots (1)	> 2 - 5 knots (2)	5:1	0.0129	5
Wind speed	A	5	0 - 2 knots (1)	> 9 - 13 knots (4)	9:1	0.0037	5
Wind speed	A	5	0 - 2 knots (1)	> 13 - 24 knots (5)	6:1	0.0706	5
Cloud cover	B	4	> 50 - 75 % (3)	0 - 25 % (1)	12:1	0.0355	5
Cloud cover	B	4	> 50 - 75 % (3)	> 25 - 50 % (2)	7:1	0.0039	5
Cloud cover	B	4	> 50 - 75 % (3)	> 75 - 100 % (4)	3:1	0.0441	5

Table 16 Odds ratios and probabilities, categorised for the dry season, for the feeding ecology of the black rhinoceroses on the Lewa Wildlife Conservancy, Kenya, from May 1996 to May 1997, indicating their presence in category A, as opposed to category B, for the specific variable

VARIABLE	GROUP NUMBER	NUMBER OF CATEGORIES	CATEGORY A	CATEGORY B	A:B	PROBABILITY	MODEL NUMBER
Black rhinoceros bulls							
Tree height	B	5	0 - 1 m (1)	> 1 - 2 m (2)	3:1	0.0496	3
Tree height	B	5	0 - 1 m (1)	> 3 - 4 m (4)	13:1	0.0384	3
Tree height	B	5	0 - 1 m (1)	> 4 m (5)	18:1	0.0364	3
Canopy diameter	B	5	0 - 1 m (1)	> 1 - 2 m (2)	5:1	0.0179	3
Canopy diameter	B	5	> 4 m (5)	> 1 - 2 m (2)	8:1	0.0702	3
Feeding Time	A	5	0 - 30 sec (1)	> 30 sec - 1 min (2)	5:1	0.0035	3
Feeding Time	A	5	0 - 30 sec (1)	> 1 - 3 min (3)	10:1	0.0028	3
Wind speed	A	5	0 - 2 knots (1)	> 13 - 24 knots (5)	6:1	0.0428	3
Wind speed	A	5	> 2 - 5 knots (2)	> 13 - 24 knots (5)	13:1	0.0020	3
Wind speed	A	5	> 5 - 9 knots (3)	> 13 - 24 knots (5)	14:1	0.0012	3
Wind speed	A	5	> 9 - 13 knots (4)	> 13 - 24 knots (5)	5:1	0.0421	3
Cloud cover	B	4	> 50 - 75 % (3)	0 - 25 % (1)	3:1	0.0199	3
Black rhinoceros cows							
Plant part	B	7	br, le (3)	le (5)	29:1	0.0000	6
Plant part	B	7	br, le (3)	le, sh (6)	415:1	0.0000	6
Plant part	B	7	br, le, sh (4)	le (5)	58:1	0.0000	6
Plant part	B	7	br, le, sh (4)	le, sh (6)	842:1	0.0000	6
Plant part	B	7	br, le, sh (4)	br, ba, le, sh, fl, fr (7)	4:1	0.0276	6
Plant part	B	7	le (5)	le, sh (6)	14:1	0.0010	6
Plant part	B	7	br, ba, le, sh, fl, fr (7)	le (5)	16:1	0.0007	6
Plant part	B	7	br, ba, le, sh, fl, fr (7)	le, sh (6)	229:1	0.0000	6
Aspect	B	4	E (1)	S (3)	3:1	0.0157	6
Aspect	B	4	N (2)	S (3)	6:1	0.0003	6
Aspect	B	4	W (4)	S (3)	4:1	0.0022	6
	B	3	Flat (1)	Gradual (2)	2:1	0.0308	6
	B	3	Flat (1)	Average - steep (3)	5:1	0.0186	6
Tree height	B	5	0 - 1 m (1)	> 1 - 2 m (2)	4:1	0.0002	6
Tree height	B	5	0 - 1 m (1)	> 2 - 3 m (3)	6:1	0.0003	6
Tree height	B	5	0 - 1 m (1)	> 3 - 4 m (4)	7:1	0.0008	6
Tree height	B	5	0 - 1 m (1)	> 4 m (5)	23:1	0.0003	6
Tree height	B	5	> 1 - 2 m (2)	> 4 m (5)	6:1	0.0282	6
Canopy diameter	B	5	> 4 m (5)	0 - 1 m (1)	5:1	0.0665	6
Feeding time	A	5	> 1 - 3 min (3)	> 30 sec - 1 min (2)	2:1	0.0298	6
Wind speed	A	5	0 - 2 knots (1)	> 2 - 5 knots (2)	3:1	0.0282	6
Wind speed	A	5	0 - 2 knots (1)	> 5 - 9 knots (3)	7:1	0.0002	6
Wind speed	A	5	0 - 2 knots (1)	> 9 - 13 knots (4)	8:1	0.0000	6
Wind speed	A	5	0 - 2 knots (1)	> 13 - 24 knots (5)	3:1	0.0141	6
Wind speed	A	5	> 2 - 5 knots (2)	> 9 - 13 knots (4)	3:1	0.0272	6
Wind speed	A	5	> 5 - 9 knots (3)	> 2 - 5 knots (2)	3:1	0.0633	6

Feeding time

During the dry season, the black rhinoceros cows on Lewa spend longer (1 to 3 minutes)(Odds ratio = 2:1 ; P = 0.0298) at feeding stations than do the bulls (0 to 30 seconds) (Odds ratio = 5:1 ; P = 0.0035 & Odds ratio = 10:1 ; P = 0.0028) (Table 16). This can be attributed to the fact that the bulls have larger ranges, and therefore spend less time at each feeding station. Oloo *et al.* (1994) found that a black rhinoceros on Ol Ari Nyiro Ranch in Kenya spends less time feeding on a given plant during the dry season than during the wet season. Because of insufficient data on the feeding time during the wet season in the current study, no statistical comparison could be made of the feeding times of the black rhinoceros between the seasons for Lewa. It is, however, presumed that the situation on Lewa will be similar to that found by Oloo *et al.* (1994) for Ol Ari Nyiro Ranch in Kenya, because either fewer palatable plants will be available during the dry season, or there will be a general decrease in the palatability of the selected plant parts.

Aspect and slope

The black rhinoceros bulls on Lewa prefer to browse on the east- and the north-facing slopes. It was more likely to observe a black rhinoceros bull browsing on the east-facing slopes, than on the south- (Odds ratio = 17:1 ; P = 0.0000) or on the west-facing (Odds ratio = 11:1 ; P = 0.0000) slopes. Similarly, it was more likely to observe a black rhinoceros bull browsing on the north-facing slopes, than on the south- (Odds ratio = 22:1 ; P = 0.0000) or on the west-facing (Odds ratio = 13:1 ; P = 0.0000) slopes (Table 14). A clear preference is shown for the gradual and the average to steep slopes over the flat plains. It was more likely to observe a black rhinoceros bull browsing on the gradual (Odds ratio = 14:1 ; P = 0.0000) or the average to steep slopes (Odds ratio = 78:1 ; P = 0.0000) than on the flat plains (Table 14).

During the wet season, the black rhinoceros cows on Lewa prefer to browse on the north-facing slopes. It was more likely to observe a black rhinoceros cow browsing on the north-facing slopes, than on the south- (Odds ratio = 5:1 ; P = 0.0139), east- (Odds ratio = 37:1 ; P = 0.0000) and west-facing (Odds ratio = 8:1 ; P = 0.0011) slopes (Table 15). During the dry season, however, the north-, east- and west-facing slopes were utilised. It was more likely to observe a black rhinoceros cow browsing on the north- (Odds ratio = 6:1 ; P = 0.0003), east- (Odds ratio = 3:1 ; P = 0.0157) or the west-facing (Odds ratio = 4:1 ; P = 0.0022) slopes, than on the south-facing slopes (Table 16). This indicates that the black rhinoceros cows utilise a larger area during the dry season, when food plants are less available, than during the wet season. The black rhinoceros cows on Lewa also prefer the flat plains to the gradual or the average to steep slopes.

Other factors

Both a male and a female black rhinoceros on Lewa feeds between 251 and 1 000 m away from water, although the bulls feed closer to water than do the cows (Table 14). It was more likely to observe a black rhinoceros bull feeding between 251 and 500 m away from water, than between 0 and 50 m (Odds ratio = 7:1 ; P = 0.0000), 51 and 250 m (Odds ratio = 4:1 ; P = 0.0000), 501 and 1 000 m (Odds ratio = 23:1 ; P = 0.0001) or greater than 1 000 m (Odds ratio = 17:1 ; P = 0.0000) away from water. It was more likely to observe a black rhinoceros cow feeding between 501 and 1 000 m away from water, than between 0 and 50 m (Odds ratio = 3:1 ; P = 0.0572), 51 and 250 m (Odds ratio = 9:1 ; P = 0.0006), 251 and 500 m (Odds ratio = 2:1 ; P = 0.0487) or greater than 1 000 m (Odds ratio = 3:1 ; P = 0.0123) from water. However, water sources are plentiful on Lewa, and therefore food plant selection by the black rhinoceros does not appear to be influenced by the proximity of water.

In terms of wind speed, the black rhinoceros on Lewa does not browse when the wind speed exceeds 13 knots. During the dry season, it was more likely to observe a black rhinoceros bull browsing when the wind speed was between 0 and 2 knots (Odds ratio = 6:1 ; P = 0.0428), > 2 and 5 knots (Odds ratio = 13:1 ; P = 0.0020), > 5 and 9 knots (Odds ratio = 14:1 ; P = 0.0012) or > 9 and 13 knots (Odds ratio = 5:1 ; P = 0.0421), than between 13 and 24 knots (Table 16). During the wet and the dry season, the black rhinoceros cows on Lewa prefer to browse when the wind speed is between 0 and 2 knots (Tables 15 & 16). Wind speed on Lewa is the strongest during the middle of the day, a time when the black rhinoceroses are already resting.

Because of a scarcity of data on cloud cover as a factor that might affect plant species selection by the black rhinoceros, no statistical comparison could be made between the seasons on Lewa. During the dry season, however, the black rhinoceros bulls were three times more likely to feed when the cloud cover was between 51 and 75 %, than between 0 and 25 % (P = 0.0199) (Table 16). During the wet season, the black rhinoceros cows were also more likely to feed when the cloud cover was between 51 and 75 %, than between 0 and 25 % (Odds ratio = 12:1 ; P = 0.0355), 26 and 50 % (Odds ratio = 7:1 ; P = 0.0039) or 76 and 100 % (Odds ratio = 3:1 ; P = 0.0441) (Table 15).

Elephant

Selection of plant species

A total of 122 plant species from 36 families were browsed by the elephants on Lewa during this study. As it was not always possible to identify the forbs that were eaten, their numbers must be underrepresented in the diet as recorded here. The total of 122 plant species eaten during the study period is therefore less than in other areas, where Douglas-Hamilton (1972) recorded over 134 species in the Lake Manyara National Park, Rushworth (1973) recorded 165 species in Hwange National Park and Guy (1976) recorded over 133 species in the Sengwa Area of Zimbabwe. Plant families having at least four representatives are the Acanthaceae, Amaranthaceae, Anacardiaceae, Asteraceae, Capparaceae, Euphorbiaceae, Fabiaceae, Lamiaceae, Malvaceae, Solanaceae, Tiliaceae and Thymelaeaceae. *Acacia* species comprise 32 % of the plant species consumed by the elephants on Lewa during wet season, and 70 % during the dry season. Leguminose flora constitute at least 50 % of the plant species in the diet of the elephants on Lewa. During times of drought, elephants are likely to reduce the browse and leguminose flora to a point where the black rhinoceros population on Lewa will be severely affected by competition from the elephants, especially for food plant resources.

Table 17 shows the relative frequencies of the plants that were eaten by the elephants on Lewa. At least 15 species account for more than 1 % occurrence in the diet of the elephants during the wet season, but only 11 species do so for the dry season. Grass and forb species are the two most commonly eaten types of food during the wet season, and account for 36 % of the plants in the elephants' diet (Figure 36). *Acacia mellifera* and *Acacia nilotica* are the two most commonly eaten plant species during the dry season, accounting for 36 % of the elephants' diet (Figure 37). *Acacia drepanolobium* is not a preferred food plant of the elephants on Lewa. It was more likely to observe an elephant browsing on *Acacia mellifera* (Odds ratio = 8:1 ; P = 0.0002), *Acacia nilotica* (Odds ratio = 10:1 ; P = 0.0000), *Acacia tortilis* (Odds ratio = 7:1 ; P = 0.0006), *Acacia xanthophloea* (Odds ratio = 7:1 ; P = 0.0026) or on a variety of forb species (Odds ratio = 147:1 ; P = 0.0003), than on an *Acacia drepanolobium* tree. *Maytenus senegalensis* and *Commiphora africana* are also preferred food plants of the elephants on Lewa. It was more likely to observe an elephant browsing on *Maytenus senegalensis*, than on *Acacia drepanolobium* (Odds ratio = 7:1 ; P = 0.0000) or on *Acacia seyal* (Odds ratio = 6:1 ; P = 0.0000). Similarly, it was more likely to observe an elephant browsing on *Commiphora africana*, than on *Acacia drepanolobium* (Odds ratio = 6:1 ; P = 0.0022) or on *Acacia seyal* (Odds ratio = 5:1 ; P = 0.0022).

The elephant on Lewa alters its feeding habits in relation to the prevalent season. A clear preference for grasses over browse is shown during the wet season. This preference is related to the high protein content of the grasses of Lewa at this time. Grasses constitute 24 % of the plants in the elephants' diet during the wet season, compared with 12.2 % during the dry season (Table 17). However, Buss (1961), McCullagh (1969) and Meissner (1991) have all recorded much higher percentages of grass in the diet of elephants during the wet season. This may indicate that the elephants on Lewa utilise the woody vegetation to a relatively high degree all year round, a situation if true, which will leave little time for its' regeneration during the wet season. Pressure is therefore placed on the woody vegetation throughout the year, thereby reducing the available browse and therefore the browsing capacity of Lewa. Elephants graze throughout the year, but they do so less during the dry season. This phenomenon is widely documented elsewhere (Williamson 1975; Ruggiero 1992; De Bruin 1995; Bowland & Yeaton 1997).

Table 17 The percentage occurrence of various plants in the seasonal diet of the elephant on the Lewa Wildlife Conservancy, Kenya, from may 1996 to May 1997 listed in descending order of use.

PLANT	WET SEASON (n = 504)	DRY SEASON (n = 477)
Unidentified grasses	24.0	12.2
Unidentified forbs	12.1	5.0
Cordia africana	10.3	0.4
Maytenus senegalensis	8.5	4.3
Acacia mellifera	7.7	18.9
Acacia nilotica	6.7	16.6
Acacia xanthophloea	5.8	4.6
Acacia tortilis	5.7	11.3
Commiphora africana	4.8	0.8
Grewia species	3.6	0.2
Acacia seyal	2.6	15.7
Acacia brevispica	2.2	-
Rhus natalensis	1.8	0.4
Acacia drepanolobium	1.2	2.5
Vangueria madagascariensis	1.0	-
Solanum species	0.8	0.2
Lycium shawii	0.2	0.2
Balanites aegyptiaca	0.2	0.2
Boscia species	0.2	5.5
Capparis tomentosa	0.2	1.0
Carissa edulis	0.2	-
Euclea divinorum	0.2	-
Total	100.0	100.0

Note: Dash indicates no record for the particular season.

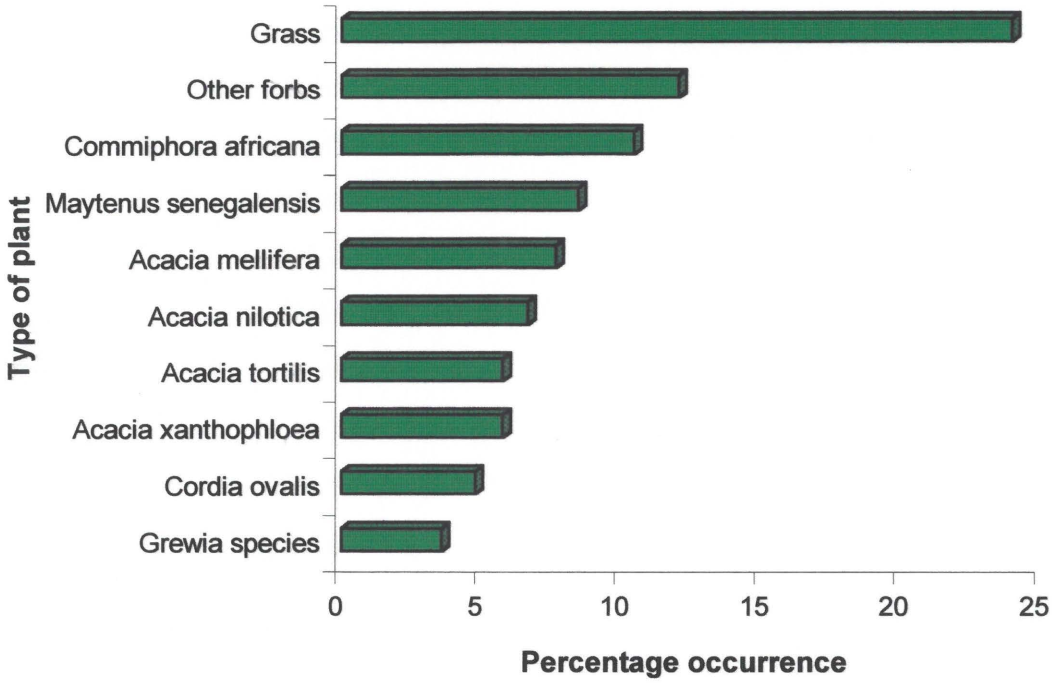

Figure 36 Percentage occurrence of 10 of the most commonly eaten types of plant in the diet of the elephant, in descending order of occurrence, on the Lewa Wildlife Conservancy, Kenya, during the wet season, from May 1996 to May 1997.

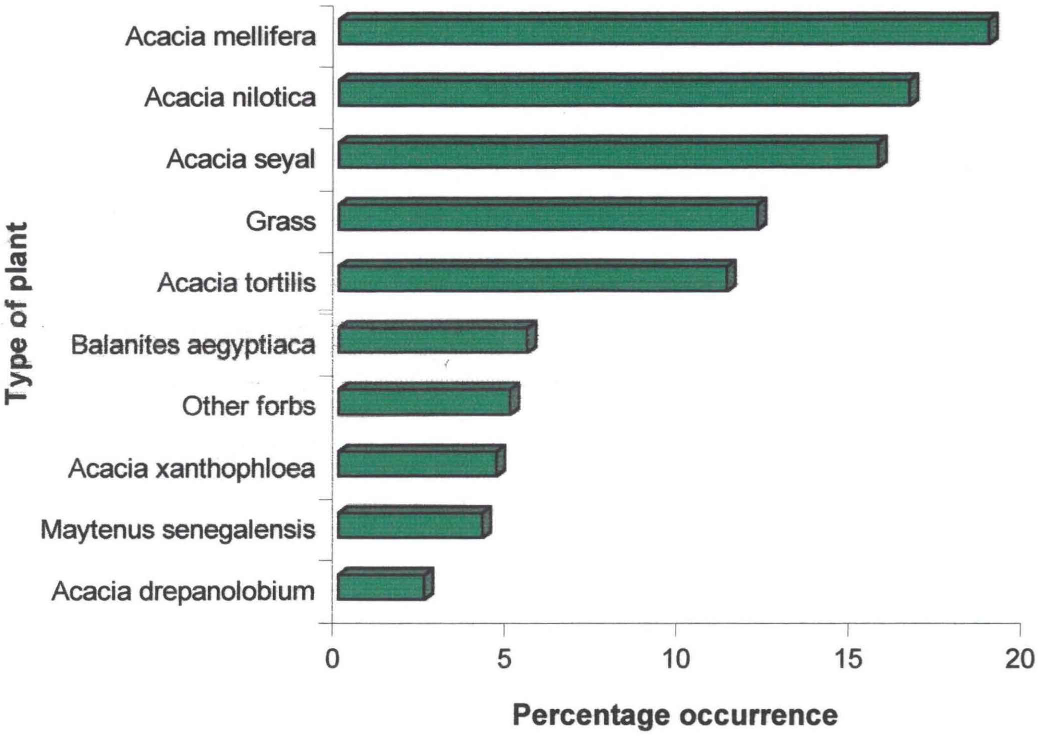

Figure 37 Percentage occurrence of 10 of the most commonly eaten types of plant in the diet of the elephant, in descending order of occurrence, on the Lewa Wildlife Conservancy, Kenya, during the dry season, from May 1996 to May 1997.

Table 18 Odds ratios and probabilities, categorised for the wet season, for the feeding ecology of the elephants on the Lewa Wildlife Conservancy, Kenya, from May 1996 to May 1997, indicating their presence in category A, as opposed to category B, for the specific variable measured.

VARIABLE	GROUP NUMBER	NUMBER OF CATEGORIES	CATEGORY A	CATEGORY B	A:B	PROBABILITY	MODEL NUMBER
Elephant bulls							
Plant part	A	8	br, ba (1)	le (6)	11:1	0.0098	5
Plant part	A	8	br, ba (1)	le, sh (7)	238:1	0.0000	5
Plant part	A	8	br, ba, le, sh (2)	le, sh (7)	97:1	0.0001	5
Plant part	A	8	br (3)	le (6)	10:1	0.0037	5
Plant part	A	8	br (3)	le, sh (7)	209:1	0.0000	5
Plant part	A	8	br, le (4)	le (6)	15:1	0.0001	5
Plant part	A	8	br, le (4)	le, sh (7)	312:1	0.0000	5
Plant part	A	8	br, le, sh (5)	le (6)	11:1	0.0007	5
Plant part	A	8	br, le, sh (5)	le, sh (7)	225:1	0.0000	5
Plant part	A	8	le (6)	le, sh (7)	21:1	0.0025	5
Plant part	A	8	br, ba, le, sh, fl, fr (8)	le (6)	11:1	0.0089	5
Plant part	A	8	br, ba, le, sh, fl, fr (8)	le, sh (7)	233:1	0.0000	5
Aspect	A	8	E (1)	N (2)	12:1	0.0059	5
Aspect	A	8	NE (3)	N (2)	9:1	0.0051	5
Aspect	A	8	NW (4)	N (2)	14:1	0.0099	5
Aspect	A	8	S (5)	N (2)	11:1	0.0025	5
Aspect	A	8	SE (6)	N (2)	23:1	0.0003	5
Aspect	A	8	SW (7)	N (2)	21:1	0.0022	5
Aspect	A	8	W (8)	N (2)	16:1	0.0002	5
Distance from water	A	5	0 - 50 m (1)	501 - 1 000 m (4)	11:1	0.0000	5
Distance from water	A	5	51 - 250 m (2)	501 - 1 000 m (4)	7:1	0.0003	5
Distance from water	A	5	251 - 500 m (3)	501 - 1 000 m (4)	6:1	0.0002	5
Distance from water	A	5	> 1 000 m (5)	501 - 1 000 m (4)	5:1	0.0109	5
	B	3	Flat (1)	Gradual (2)	7:1	0.0000	5
	B	3	Average - steep (3)	Gradual (2)	4:1	0.0007	5
Max height utilisation	A	6	> 2 - 3 m (3)	> 1 - 2 m (2)	2:1	0.0757	5
Lowest avail. leaves	B	5	> 4 m (5)	> 2 - 3 m (3)	33:1	0.0628	5
Feeding time	A	5	> 30 sec - 1 min (2)	> 1 - 3 min (3)	2:1	0.0512	5
Wind speed	A	5	0 - 2 knots (1)	> 5 - 9 knots (3)	4:1	0.0058	5
Wind speed	A	5	> 2 - 5 knots (2)	> 5 - 9 knots (3)	4:1	0.0031	5
Wind speed	A	5	> 9 - 13 knots (4)	> 5 - 9 knots (3)	4:1	0.0039	5
Wind speed	A	5	> 13 - 24 knots (5)	> 5 - 9 knots (3)	7:1	0.0073	5
Cloud cover	B	4	0 - 25 % (1)	> 25 - 50 % (2)	9:1	0.0006	5
Cloud cover	B	4	0 - 25 % (1)	> 50 - 75 % (3)	6:1	0.0087	5
Cloud cover	B	4	0 - 25 % (1)	> 75 - 100 % (4)	4:1	0.0339	5
Cloud cover	B	4	> 75 - 100 %	> 25 - 50 % (2)	2:1	0.0249	5
Elephant cows							
Plant part	A	8	br, ba (1)	br, le (4)	12:1	0.0370	11
Plant part	A	8	br, ba (1)	br, le, sh (5)	33:1	0.0035	11
Plant part	A	8	br, ba (1)	le (6)	1 141:1	0.0000	11
Plant part	A	8	br, ba (1)	le, sh (7)	9 183:1	0.0000	11
Plant part	A	8	br, ba (1)	br, ba, le, sh, fl, fr (8)	44:1	0.0045	11
Plant part	A	8	br, ba, le, sh (2)	br, le, sh (5)	6:1	0.0180	11
Plant part	A	8	br, ba, le, sh (2)	le, sh (7)	1 809:1	0.0000	11
Plant part	A	8	br, ba, le, sh (2)	br, ba, le, sh, fl, fr (8)	9:1	0.0341	11
Plant part	A	8	br (3)	br, le, sh (5)	5:1	0.0008	11
Plant part	A	8	br (3)	le (6)	170:1	0.0000	11
Plant part	A	8	br (3)	le, sh (7)	1 363:1	0.0000	11
Plant part	A	8	br (3)	br, ba, le, sh, fl, fr (8)	7:1	0.0200	11
Plant part	A	8	br, le (4)	br, le, sh (5)	3:1	0.0084	11
Plant part	A	8	br, le (4)	le (6)	98:1	0.0000	11
Plant part	A	8	br, le (4)	le, sh (7)	792:1	0.0000	11
Plant part	A	8	br, le, sh (5)	le (6)	35:1	0.0002	11

Table 18 (continued)

VARIABLE	GROUP NUMBER	NUMBER OF CATEGORIES	CATEGORY A	CATEGORY B	A:B	PROBABILITY	MODEL NUMBER
Elephant cows (cont.)							
Plant part	A	8	br, le, sh (5)	le, sh (7)	280:1	0.0000	11
Plant part	A	8	br, ba, le, sh, fl, fr (8)	le (6)	26:1	0.0051	11
Plant part	A	8	br, ba, le, sh, fl, fr (8)	le, sh (7)	209:1	0.0001	11
Distance from water	A	5	251 - 500 m (3)	0 - 50 m (1)	3:1	0.0443	11
Distance from water	A	5	> 1 000 m (5)	0 - 50 m (1)	3:1	0.0513	11
	B	3	Gradual (2)	Flat (1)	11:1	0.0000	11
	B	3	Average - steep (3)	Flat (1)	55:1	0.0000	11
	B	3	Average - steep (3)	Gradual (2)	5:1	0.0000	11
Canopy diameter	A	6	> 5 m (6)	0 - 1 m (1)	5:1	0.0611	11
Canopy diameter	A	6	> 5 m (6)	> 1 - 2 m (2)	4:1	0.0680	11
Canopy diameter	A	6	> 5 m (6)	> 2 - 3 m (3)	7:1	0.0221	11
Canopy diameter	A	6	> 5 m (6)	> 3 - 4 m (4)	5:1	0.0247	11
Feeding time	A	5	> 30 sec - 1 min (2)	0 - 30 sec (1)	3:1	0.0308	11
Feeding time	A	5	> 1 - 3 min (3)	0 - 30 sec (1)	2:1	0.0615	11
Feeding time	A	5	> 10 min (5)	0 - 30 sec (1)	5:1	0.0447	11
Wind speed	A	5	> 9 - 13 knots (4)	0 - 2 knots (1)	3:1	0.0353	11
Wind speed	A	5	> 13 - 24 knots (5)	0 - 2 knots (1)	6:1	0.0128	11
Wind speed	A	5	> 13 - 24 knots (5)	> 2 - 5 knots (2)	4:1	0.0486	11
Cloud cover	B	4	> 25 - 50 % (2)	0 - 25 % (1)	671:1	0.0000	11
Cloud cover	B	4	> 25 - 50 % (2)	> 75 - 100 % (4)	4:1	0.0038	11
Cloud cover	B	4	> 50 - 75 % (3)	0 - 25 % (1)	318:1	0.0002	11
Cloud cover	B	4	> 75 - 100 % (4)	0 - 25 % (1)	173:1	0.0004	11

Table 19 Odds ratios and probabilities, categorised for the dry season, for the feeding ecology of the elephants on the Lewa Wildlife Conservancy, Kenya, from May 1996 to May 1997, indicating their presence in category A, as opposed to category B, for the specific variable measured.

VARIABLE	GROUP NUMBER	NUMBER OF CATEGORIES	CATEGORY A	CATEGORY B	A:B	PROBABILITY	MODEL NUMBER
Elephant bulls							
Plant part	A	8	br, ba (1)	le (6)	6:1	0.0177	9
Plant part	A	8	br, ba (1)	le, sh (7)	43:1	0.0004	9
Plant part	A	8	br, ba (1)	br, ba, le, sh, fl, fr (8)	77:1	0.0000	9
Plant part	A	8	br, ba, le, sh (2)	br, ba (1)	6:1	0.0324	9
Plant part	A	8	br, ba, le, sh (2)	br (3)	7:1	0.0002	9
Plant part	A	8	br, ba, le, sh (2)	br, le (4)	20:1	0.0000	9
Plant part	A	8	br, ba, le, sh (2)	br, le, sh (5)	9:1	0.0000	9
Plant part	A	8	br, ba, le, sh (2)	le (6)	241:1	0.0000	9
Plant part	A	8	br, ba, le, sh (2)	le, sh (7)	427:1	0.0000	9
Plant part	A	8	br, ba, le, sh (2)	br, ba, le, sh, fl, fr (8)	36:1	0.0000	9
Plant part	A	8	br (3)	br, le (4)	3:1	0.0317	9
Plant part	A	8	br (3)	le (6)	34:1	0.0002	9
Plant part	A	8	br (3)	le, sh (7)	60:1	0.0000	9
Plant part	A	8	br (3)	br, ba, le, sh, fl, fr (8)	5:1	0.0245	9
Plant part	A	8	br, le (4)	le (6)	12:1	0.0069	9
Plant part	A	8	br, le (4)	le, sh (7)	21:1	0.0000	9
Plant part	A	8	br, le, sh (5)	le (6)	27:1	0.0004	9
Plant part	A	8	br, le, sh (5)	le, sh (7)	48:1	0.0000	9
Plant part	A	8	br, le, sh (5)	br, ba, le, sh, fl, fr (8)	4:1	0.0478	9
Plant part	A	8	br, ba, le, sh, fl, fr (8)	le, sh (7)	12:1	0.0034	9
Aspect	A	8	NE (3)	E (1)	14:1	0.0000	9
Aspect	A	8	NE (3)	N (2)	4:1	0.0428	9
Aspect	A	8	NE (3)	NW (4)	26:1	0.0000	9
Aspect	A	8	NE (3)	S (5)	8:1	0.0041	9
Aspect	A	8	NE (3)	SE (6)	13:1	0.0004	9
Aspect	A	8	NE (3)	W (8)	13:1	0.0000	9
Aspect	A	8	SW (7)	E (1)	17:1	0.0000	9
Aspect	A	8	SW (7)	N (2)	13:1	0.0000	9
Aspect	A	8	SW (7)	S (5)	4:1	0.0390	9
Aspect	A	8	SW (7)	SE (6)	5:1	0.0208	9
Aspect	A	8	SW (7)	W (8)	4:1	0.0353	9
Distance from water	A	5	0 - 50 m (1)	251 - 500 m (3)	5:1	0.0071	9
Distance from water	A	5	0 - 50 m (1)	501 - 1 000 m (4)	4:1	0.0243	9
Distance from water	A	5	0 - 50 m (1)	> 1 000 m (5)	59:1	0.0000	9
Distance from water	A	5	51 - 250 m (2)	251 - 500 m (3)	4:1	0.0113	9
Distance from water	A	5	51 - 250 m (2)	501 - 1 000 m (4)	3:1	0.0409	9
Distance from water	A	5	51 - 250 m (2)	> 1 000 m (5)	54:1	0.0000	9
Distance from water	A	5	251 - 500 m (3)	> 1 000 m (5)	12:1	0.0017	9
Distance from water	A	5	501 - 1 000 m (4)	> 1 000 m (5)	16:1	0.0002	9
	B	3	Gradual (2)	Flat (1)	3:1	0.0537	9
Max height utilisation	A	6	> 1 - 2 m (2)	> 3 - 4 m (4)	7:1	0.0701	9
Max height utilisation	A	6	> 2 - 3 m (3)	> 3 - 4 m (4)	11:1	0.0261	9
Min height utilisation	B	5	0 - 1 m (1)	> 3 - 4 m (4)	705:1	0.0074	9
Min height utilisation	B	5	> 1 - 2 m (2)	> 3 - 4 m (4)	1 234:1	0.0032	9
Min height utilisation	B	5	> 2 - 3 m (3)	> 3 - 4 m (4)	397:1	0.0158	9
Min height utilisation	B	5	> 4 m (5)	> 3 - 4 m (4)	5 172:1	0.0021	9
Tree height	A	6	> 5 m (6)	> 3 - 4 m (4)	7:1	0.0375	9
Lowest avail. leaves	A	6	> 3 - 4 m (4)	0 - 1 m (1)	67:1	0.0557	9
Lowest avail. leaves	A	6	> 3 - 4 m (4)	> 1 - 2 m (2)	106:1	0.0195	9
Lowest avail. leaves	A	6	> 3 - 4 m (4)	> 2 - 3 m (3)	139:1	0.0265	9
Lowest avail. leaves	A	6	> 3 - 4 m (4)	> 4 - 5 m (5)	691:1	0.0067	9
Lowest avail. leaves	A	6	> 5 m (6)	0 - 1 m (1)	210:1	0.0215	9
Lowest avail. leaves	A	6	> 5 m (6)	> 1 - 2 m (2)	219:1	0.0064	9
Lowest avail. leaves	A	6	> 5 m (6)	> 2 - 3 m (3)	1 088:1	0.0011	9
Lowest avail. leaves	A	6	> 5 m (6)	> 4 - 5 m (5)	331:1	0.0058	9

Table 19 (continued)

VARIABLE	GROUP NUMBER	NUMBER OF CATEGORIES	CATEGORY A	CATEGORY B	A:B	PROBABILITY	MODEL NUMBER
Elephant bulls (cont.)							
Feeding time	A	5	> 10 min (5)	0 - 30 sec (1)	3:1	0.0793	9
Feeding time	A	5	> 10 min (5)	> 3 - 10 min (4)	2:1	0.0669	9
Wind speed	A	5	0 - 2 knots (1)	> 2 - 5 knots (2)	17:1	0.0001	9
Wind speed	A	5	0 - 2 knots (1)	> 5 - 9 knots (3)	12:1	0.0000	9
Wind speed	A	5	0 - 2 knots (1)	> 9 - 13 knots (4)	5:1	0.0038	9
Wind speed	A	5	0 - 2 knots (1)	> 13 - 24 knots (5)	4:1	0.0131	9
Wind speed	A	5	> 9 - 13 knots (4)	> 2 - 5 knots (2)	4:1	0.0269	9
Wind speed	A	5	> 9 - 13 knots (4)	> 5 - 9 knots (3)	4:1	0.0165	9
Wind speed	A	5	> 13 - 24 knots (5)	> 2 - 5 knots (2)	3:1	0.0350	9
Wind speed	A	5	> 13 - 24 knots (5)	> 5 - 9 knots (3)	3:1	0.0226	9
Elephant cows							
Plant part	A	8	br, ba (1)	br, ba, le, sh (2)	6:1	0.0030	12
Plant part	A	8	br, ba (1)	br, le, sh (5)	6:1	0.0025	12
Plant part	A	8	br, ba (1)	le (6)	336:1	0.0000	12
Plant part	A	8	br, ba (1)	le, sh (7)	614:1	0.0000	12
Plant part	A	8	br, ba (1)	br, ba, le, sh, fl, fr (8)	8:1	0.0035	12
Plant part	A	8	br, ba, le, sh (2)	le (6)	56:1	0.0000	12
Plant part	A	8	br, ba, le, sh (2)	le, sh (7)	102:1	0.0000	12
Plant part	A	8	br (3)	br, ba, le, sh (2)	6:1	0.0000	12
Plant part	A	8	br (3)	le (6)	325:1	0.0000	12
Plant part	A	8	br (3)	le, sh (7)	594:1	0.0000	12
Plant part	A	8	br (3)	br, ba, le, sh, fl, fr (8)	8:1	0.0006	12
Plant part	A	8	br, le (4)	br, ba, le, sh (2)	3:1	0.0040	12
Plant part	A	8	br, le (4)	br, le, sh (5)	3:1	0.0020	12
Plant part	A	8	br, le (4)	le (6)	170:1	0.0000	12
Plant part	A	8	br, le (4)	le, sh (7)	311:1	0.0000	12
Plant part	A	8	br, le (4)	br, ba, le, sh, fl, fr (8)	4:1	0.0165	12
Plant part	A	8	br, le, sh (5)	le (6)	54:1	0.0000	12
Plant part	A	8	br, le, sh (5)	le, sh (7)	98:1	0.0000	12
Plant part	A	8	br, ba, le, sh, fl, fr (8)	le (6)	41:1	0.0002	12
Plant part	A	8	br, ba, le, sh, fl, fr (8)	le, sh (7)	75:1	0.0000	12
Aspect	A	8	N (2)	NE (3)	5:1	0.0006	12
Aspect	A	8	S (5)	E (1)	3:1	0.0466	12
Aspect	A	8	S (5)	NE (3)	6:1	0.0017	12
Aspect	A	8	SE (6)	E (1)	6:1	0.0002	12
Aspect	A	8	SE (6)	N (2)	3:1	0.0248	12
Aspect	A	8	SE (6)	NE (3)	3:1	0.0000	12
Aspect	A	8	SE (6)	NW (4)	7:1	0.0018	12
Aspect	A	8	SE (6)	SW (7)	7:1	0.0032	12
Aspect	A	8	SE (6)	W (8)	4:1	0.0034	12
Aspect	A	8	W (8)	NE (3)	4:1	0.0131	12
Distance from water	A	5	51 - 250 m (2)	0 - 50 m (1)	3:1	0.0366	12
Distance from water	A	5	51 - 250 m (2)	251 - 500 m (3)	3:1	0.0133	12
Distance from water	A	5	51 - 250 m (2)	501 - 1 000 m (4)	6:1	0.0004	12
Distance from water	A	5	51 - 250 m (2)	> 1 000 m (5)	4:1	0.0149	12
	B	3	Gradual (1)	Flat (1)	5:1	0.0000	12
	B	3	Average - steep (3)	Flat (1)	4:1	0.0017	12
Max height utilisation	B	5	0 - 1 m (1)	> 4 m (5)	36:1	0.0161	12
Max height utilisation	B	5	> 1 - 2 m (2)	> 4 m (5)	46:1	0.0074	12
Max height utilisation	B	5	> 2 - 3 m (3)	> 4 m (5)	38:1	0.0103	12
Max height utilisation	B	5	> 3 - 4 m (4)	> 4 m (5)	42:1	0.0049	12
Tree height	A	6	> 3 - 4 m (4)	> 5 m (6)	4:1	0.0673	12
Canopy diameter	A	6	> 1 - 2 m (2)	> 2 - 3 m (3)	2:1	0.0273	12
Lowest avail. leaves	C	3	> 1 - 2 m (2)	0 - 1 m (1)	2:1	0.0397	12
Lowest avail. leaves	C	3	> 2 m (3)	0 - 1 m (1)	12:1	0.0016	12
Lowest avail. leaves	C	3	> 2 m (3)	> 1 - 2 m (2)	5:1	0.0326	12

Table 19 (continued)

VARIABLE	GROUP NUMBER	NUMBER OF CATEGORIES	CATEGORY A	CATEGORY B	A:B	PROBABILITY	MODEL NUMBER
Elephant cows (cont.)							
Feeding time	A	5	> 30 sec - 1 min (2)	0 - 30 sec (1)	3:1	0.0066	12
Feeding time	A	5	> 1 - 3 min (3)	0 - 30 sec (1)	3:1	0.0223	12
Feeding time	A	5	> 3 - 10 min (4)	0 - 30 sec (1)	3:1	0.0088	12
Wind speed	A	5	> 2 - 5 knots (2)	0 - 2 knots (1)	14:1	0.0018	12
Wind speed	A	5	> 5 - 9 knots (3)	0 - 2 knots (1)	36:1	0.0000	12
Wind speed	A	5	> 5 - 9 knots (3)	> 2 - 5 knots (2)	3:1	0.0242	12
Wind speed	A	5	> 5 - 9 knots (3)	> 13 - 24 knots (5)	3:1	0.0011	12
Wind speed	A	5	> 9 - 13 knots (4)	0 - 2 knots (1)	23:1	0.0001	12
Wind speed	A	5	> 9 - 13 knots (4)	> 13 - 24 knots (5)	2:1	0.0326	12
Wind speed	A	5	> 13 - 24 knots (5)	0 - 2 knots (1)	12:1	0.0024	12
Cloud cover	B	4	> 75 - 100 % (4)	0 - 25 % (1)	3:1	0.0404	12
Cloud cover	B	4	> 75 - 100 % (4)	> 25 - 50 % (2)	4:1	0.0075	12
Cloud cover	B	4	> 75 - 100 % (4)	> 50 - 75 % (3)	4:1	0.0245	12

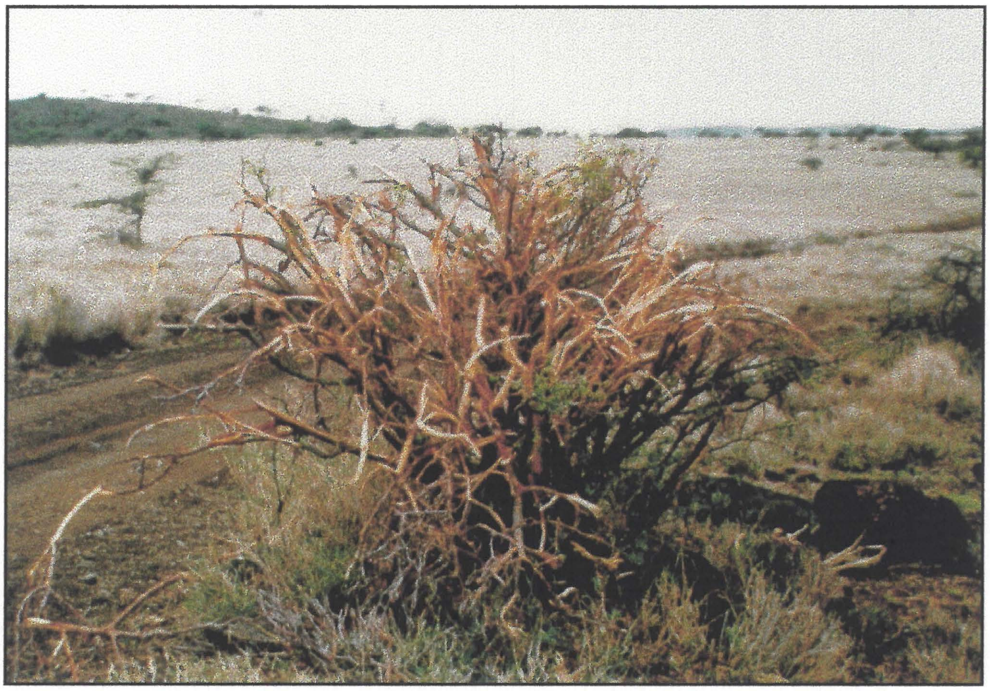

Figure 38 An *Acacia mellifera* tree which has been denuded of bark and with loose strips of bark hanging from the branches, after an elephant had been feeding from it.

Selection of plant parts

Laws (1970b) states that elephants take bark as a form of roughage when feeding on large quantities of young grass. McCullagh (1969) found that bark contains a high percentage of calcium, which the elephants search for during the dry season. The elephant bulls on Lewa consume more bark during the dry season, than during the wet season (Tables 18 & 19), possibly because of the increased translocation of nutrients to the bark and branches at this time of the year. This may also be a form of ecological separation between the elephant and the black rhinoceros on Lewa, especially during the dry season. The elephant cows, however, feed on bark during both the wet and the dry season. It was more likely to observe an elephant cow feeding on a combination of bark and branches during the wet season, than on leaves only (Odds ratio = 1 141:1 ; P = 0.0000) or on leaves and shoots only (Odds ratio = 9 183:1 ; P = 0.0000) (Table 18). When eaten by elephants, most browse is taken in the form of leafy branches, especially during the wet season. The elephant cows on Lewa were more likely to browse on leafy branches, than on leaves only (Odds ratio = 98:1 ; P = 0.0000) or on leaves and shoots only (Odds ratio = 792:1 ; P = 0.0000). Similarly, the elephant bulls were also more likely to browse on leafy branches, than on leaves only (Odds ratio = 15:1 ; P = 0.0001) or on leaves and shoots only (Odds ratio = 312:1 ; P = 0.0000) (Table 18).

Method of feeding

The feeding method of an elephant is different to that of the black rhinoceros. When browsing, the elephants on Lewa strip the leaves and the ends of the twigs off with their trunks, or break off smaller branches by bending them over a tusk. Bushes and trees are then denuded of bark, often with strips of loose bark hanging from the branches (Figures 33 and 38). Mostly, the feeding methods of elephants do not cause the die-off of the woody vegetation, but rather alters its structure (Schenkel & Schenkel-Hulliger 1969). On Lewa, most of the bushes show signs of coppicing after having been browsed on by elephants. This makes their foliage more accessible to other browsers such as the black rhinoceros. However, other feeding methods of elephants, such as ringbarking, uprooting and trampling, can cause the die-off of woody vegetation. An investigation into the death of *Acacia xanthophloea* trees on Lewa showed that 77 % of the trees have died as a result of uprooting by elephants, and that 33 % have died as a result of being broken off at their base. Many of the living *Acacia xanthophloea* trees on Lewa show signs of elephant damage to their bark. The uprooting of many *Commiphora* species by the elephants on Lewa has resulted in the death of some of these trees. Trampling is another form of vegetation destruction by the elephants on Lewa, as it is elsewhere in their range. This form of destruction mainly affects the grass layer near water points. It is concluded that the impact of elephants on the bush vegetation of Lewa is not as heavy as it is on the large trees.

Browsing height

The elephants on Lewa have definite feeding height preferences. The feeding height of the elephants on Lewa ranges from ground level to higher than 5 m. In the *Acacia xanthophloea* forests, the bulls mostly browse on trees taller than 5 m (Odds ratio = 7:1 ; P = 0.0375). During the wet season, the preferred maximum height of utilisation of trees by the elephant bulls, is between 2 and 3 m (Odds ratio = 2:1 ; P = 0.0757) (Table 18). During the dry season, the bulls utilise trees at most heights, browsing least at the > 3 to 4 m height interval (Table 19). The elephant cows prefer to utilise trees that are > 3 to 4 m high (Odds ratio = 4:1 ; P = 0.0673). During the dry season, the preferred maximum height of utilisation of trees by the elephant cows on Lewa, is < 4 m (Table 19). Guy (1976) found that the elephants in the Sengwa Area of Zimbabwe, prefer to feed below a height of 2 m. Jachmann & Bell (1985) found that the elephants in the Kasungu National Park in Malawi, prefer to feed at a height of between 1 and 2 m above the ground. The elephant bulls on Lewa push over *Acacia xanthophloea* trees, both for food and as form of social display. In doing so, a high degree of selection is observed for trees taller than the height at which the elephants normally prefer to feed. It is evident that tall trees whose major portion of their canopy leaves are out of reach of a feeding elephant, are pushed over by the bulls. This destruction is not altogether a negative aspect, as other browsers are then often able to feed on the trees that are pushed over by the elephant bulls.

Selection for trees of different canopy diameter was also observed. The elephant bulls select trees with a canopy diameter of < 3 m. It was more likely to observe a bull browsing on trees, bushes and shrubs with a canopy diameter of 0 to 1 m (Odds = 3:1 ; P = 0.0153), > 1 to 2 m (Odds = 2:1 ; P = 0.0578) or > 2 to 3 m (Odds = 2:1 ; P = 0.0153), than with a canopy diameter of > 5 m. The elephant cows on Lewa select trees with a greater canopy diameter during the wet season than during the dry season (Tables 18 and 19). This simply is the result of a greater abundance of foliage at this time, which provides greater shade. Besides abundant food and water, suitable shade is a major elephant habitat component.

During the wet season, the elephant bulls on Lewa select trees which have their lowest available leaves above 4 m high (Odds = 33:1 ; P = 0.0628) (Table 18). During the dry season, however, the bulls select trees with their lowest available leaves between 3 and 4 m high and above 5 m high (Table 19). In other words, when food plant availability on Lewa decreases during the dry season, the feeding level spectrum of the elephants increases. The elephant cows on Lewa select trees with their lowest available leaves > 2 to 3 m. It was more likely to observe an elephant cow browsing on trees with their lowest available leaves > 2 to 3 m, than between 0 and 1 m (Odds ratio = 5:1 ; P = 0.0101), > 1 to 2 m (Odds ratio = 3:1 ; P = 0.0572) or > 3 to 4 m (Odds ratio = 20:1 ; P = 0.0297). It would therefore appear that the elephant cows on Lewa browse at height levels that appear to be most convenient for them.

Feeding time

During the dry season, the elephant bulls on Lewa spend longer at a feeding station than do the cows (Table 19). Guy (1976) also noted this phenomenon in Zimbabwe. During the wet season, however, the cows spend longer at a feeding station than the bulls (Table 18). Groups of up to five elephants were often observed spending more than 10 minutes stripping the bark and leaves of *Acacia mellifera* trees until there was no foliage left and the bark was in shreds (Figure 38). The maximum time that an elephant spent feeding on one individual plant was of an *Acacia xanthophloea* tree that was fed on for 100 minutes. The plant species that elephants spend the longest time feeding on are *Acacia xanthophloea* and *Acacia nilotica*. During the wet season, elephants spend up to an hour grazing, but then they return to the woodlands to browse. It was also noted that the juvenile elephants spend a shorter time at each feeding station than the adult elephants.

Aspect and slope

During the wet season, the elephant bulls that remain on Lewa utilise all the aspects, except for the north-facing slopes (Table 18). The reason for this is that the grassy plains, which are utilised more during this time of the year, do not occur on north-facing aspects. During the dry season, the bulls feed on the southwest- and the northeast-facing slopes. The gradual slopes are preferred to the flat plains (Odds ratio = 3:1 ; P = 0.0537) (Table 19). The elephant cows on Lewa prefer to feed on the southeast-facing slopes during the dry season. Few data were gathered for the wet season when the breeding herds of elephants migrate north out of Lewa. The elephant cows prefer the gradual (Odds ratio = 5:1 ; P = 0.0000) and the average to steep slopes (Odds ratio = 4:1 ; P = 0.0017) to the flat plains.

Other factors

During the dry season, the elephants on Lewa are found closer to water than during the wet season (Tables 18 & 19). These results are supported by the bulk of literature on this topic (Viljoen & Bothma 1990; Dublin 1996; Bhima 1998). Food selection by the elephants on Lewa, however, does not appear to be influenced by the availability and proximity of water, because permanent water sources are abundant on Lewa.

No significant differences exist between browsing intensity at various classes of wind speed. It can therefore be assumed that wind speed has little, if any, effect on food plant selection and the feeding times of the elephants present on Lewa.

Because of a small sample size, no comparison could be made on the effect of cloud cover on the feeding times of the elephant bulls. During the dry season, a cloud cover of between 76 and 100 %, however, does lead to longer feeding times by the elephant cows than during the wet season on Lewa (Table 19).

Giraffe

Selection of plant species

A total of 21 plant species from 13 families were browsed by the giraffe during the present study on Lewa. However, this is most likely an underestimate, because many forbs and young seedlings are eaten whole, leaving no evidence of their use by giraffes. Studies in the Tsavo, Kidepo and Serengeti National Parks reveal that the giraffe there browsed 66, 39 and 45 plant species respectively (Leuthold & Leuthold 1972; Field & Ross 1976; Pellew 1984).

Table 20 shows the relative frequencies of the plants known to be eaten by the giraffe on Lewa. During the wet and the dry season, *Acacia drepanolobium*, *Acacia tortilis* and *Acacia seyal* are the most frequently eaten plant species (Figures 39 and 40). *Acacia* species comprise 76 % of the observations of plant species consumed by the giraffe on Lewa during the wet season, and 84 % during the dry season. Taking into account the unidentified legume species consumed by the giraffe, leguminose flora constitute at least 80 % of the observations of plant species in the diet of the giraffe on Lewa. There are no marked seasonal differences in the utilisation of plant species, although more evergreen species are eaten during the dry season (Table 20). Two of the browse species that frequently occur in the diet of the giraffe, also occur frequently in the diet of the elephant on Lewa during the dry season. They are *Acacia seyal* and *Acacia tortilis*. Similarly, two of the browse species that occur frequently in the diet of the giraffe, are the most frequently consumed plant species in the diet of the black rhinoceros on Lewa. They are *Acacia seyal* and *Acacia drepanolobium*.

Selection of plant parts

The giraffe on Lewa browses mainly on the twigs, leaves and shoots of the trees present. When available, inflorescences and fruit are also taken. This plant part selection is widely documented for giraffes in Africa (Leuthold & Leuthold 1972; Moss 1975; Pellew 1984; Bergström 1992; Kruger 1994). In Kenya, it has been shown that the giraffe has a high protein intake (Field & Blankenship 1973). According to Pellew (1984), new shoots have a high protein content, but this only lasts for the first few days after sprouting. It also explains why a giraffe moves from tree to tree to select the new shoots when they are available. In the present study, there was a particular preference for young leaves and shoot tips, especially of the *Acacia* species. Pellew (1984) found that the giraffe concentrates its feeding on plant species with the greatest new shoot growth. This implies that seasonal changes in the diet of the giraffe may be associated with changes in the phenology of the plant species involved (Hall-Martin 1974b; Sauer, *et al.* 1977; Kruger 1994).

Table 20 The percentage occurrence of various plants in the seasonal diet of the giraffe on the Lewa Wildlife Conservancy, Kenya, from May 1996 to May 1997 listed in descending order of use.

PLANT	WET SEASON (n = 400)	DRY SEASON (n = 641)
Acacia tortilis	24.6	15.1
Acacia drepanolobium	23.2	23.9
Acacia seyal	14.0	30.7
Maytenus senegalensis	9.7	3.1
Acacia xanthophloea	8.5	5.8
Balanites aegyptiaca	4.5	1.9
Acacia nilotica	4.3	6.4
Cordia africana	3.2	1.9
Boscia species	2.0	3.6
Commiphora africana	1.8	0.8
Carissa edulis	1.2	0.6
Acacia mellifera	1.0	3.3
Unidentified forbs	0.8	1.1
Hibiscus species	0.7	-
Lycium shawii	0.3	0.2
Grewia species	0.2	-
Achyranthes aspera	-	0.4
Capparis tomentosa	-	0.3
Euclea divinorum	-	0.2
Scutia myrtina	-	0.2
Solanum species	-	0.5
Total	100.0	100.0

Note: Dash indicates no record for the particular season.

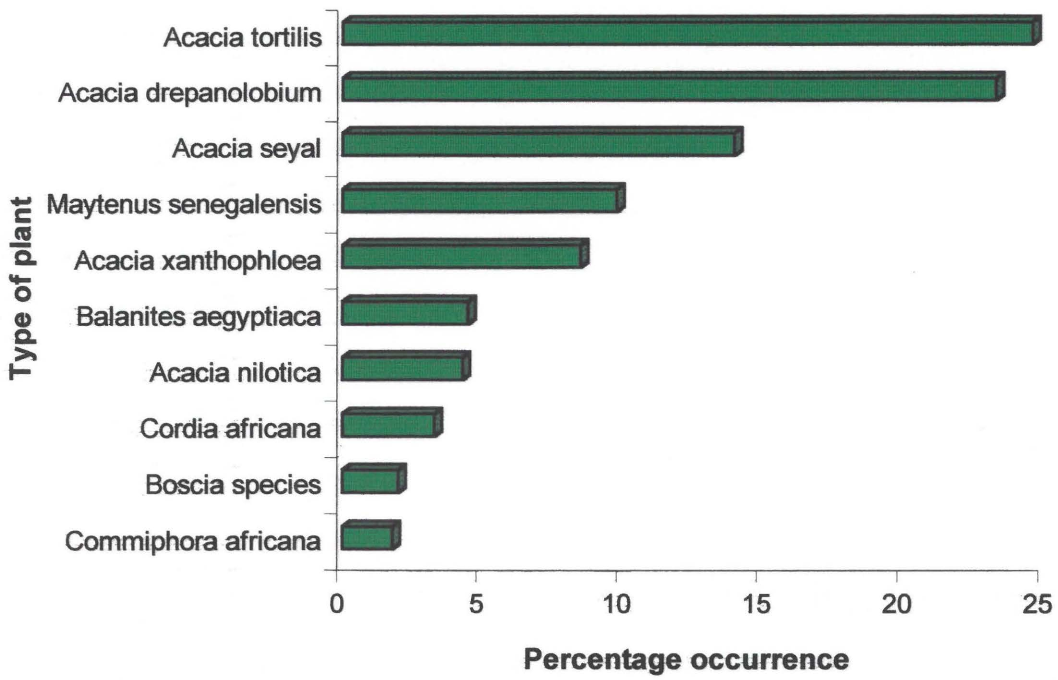

Figure 39 Percentage occurrence of 10 of the most commonly eaten types of plant in the diet of the giraffe, in descending order of occurrence, on the Lewa Wildlife Conservancy, Kenya, during the wet season, from May 1996 to May 1997.

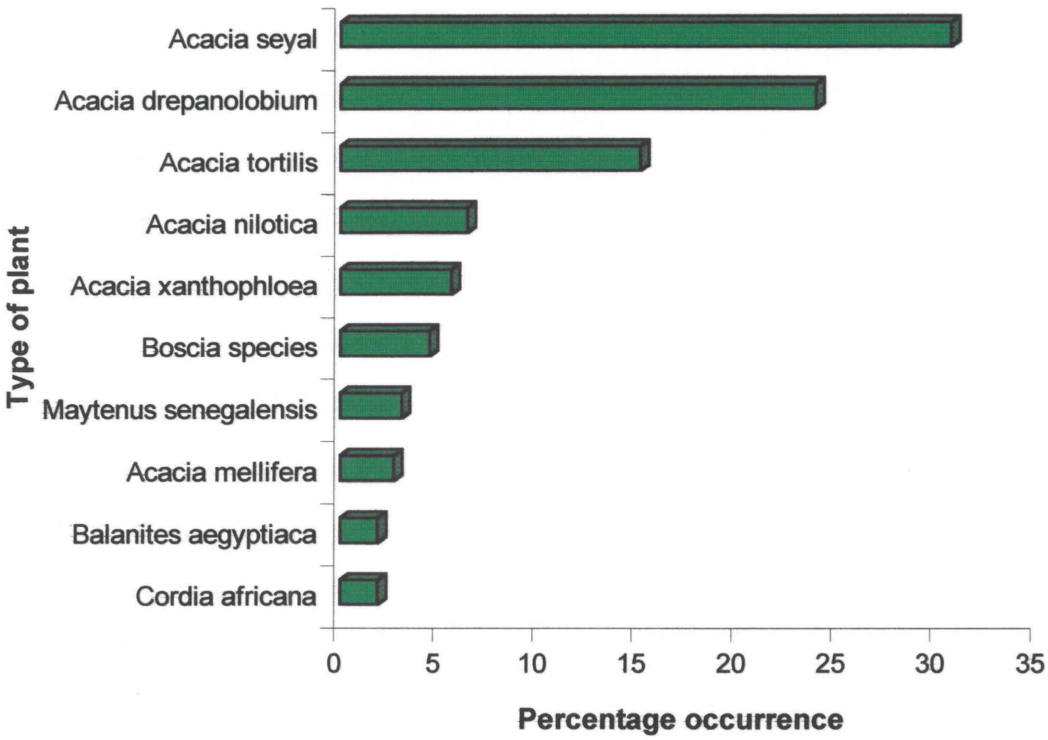

Figure 40 Percentage occurrence of 10 of the most commonly eaten types of plant in the diet of the giraffe, in descending order of occurrence, on the Lewa Wildlife Conservancy, Kenya, during the dry season, from May 1996 to May 1997.

Table 21 Odds ratios and probabilities, categorised for the wet season, for the feeding ecology of the giraffes on the Lewa Wildlife Conservancy, Kenya, from May 1996 to May 1997, indicating their presence in category A, as opposed to category B, for the specific variable measured.

VARIABLE	GROUP NUMBER	NUMBER OF CATEGORIES	CATEGORY A	CATEGORY B	A:B	PROBABILITY	MODEL NUMBER
Giraffe bulls							
Aspect	B	4	E (1)	N (2)	18:1	0.0000	14
Aspect	B	4	E (1)	W (4)	8:1	0.0060	14
Aspect	B	4	S (3)	N (2)	26:1	0.0000	14
Aspect	B	4	S (3)	W (4)	11:1	0.0009	14
	B	3	Flat (1)	Gradual (2)	14:1	0.0000	14
	B	3	Flat (1)	Average - steep (3)	5:1	0.0001	14
Min height utilisation	B	5	> 2 - 3 m (3)	0 - 1 m (1)	4:1	0.0275	14
Min height utilisation	B	5	> 2 - 3 m (3)	> 1 - 2 m (2)	3:1	0.0222	14
Min height utilisation	B	5	> 3 - 4 m (4)	0 - 1 m (1)	14:1	0.0001	14
Min height utilisation	B	5	> 3 - 4 m (4)	> 1 - 2 m (2)	12:1	0.0000	14
Min height utilisation	B	5	> 3 - 4 m (4)	> 2 - 3 m (3)	4:1	0.0197	14
Min height utilisation	B	5	> 4 m (5)	0 - 1 m (1)	17:1	0.0008	14
Min height utilisation	B	5	> 4 m (5)	> 1 - 2 m (2)	14:1	0.0006	14
Tree height	A	6	> 3 - 4 m (4)	> 2 - 3 m (3)	4:1	0.0146	14
Tree height	A	6	> 5 m (6)	> 2 - 3 m (3)	5:1	0.0414	14
Tree height	A	6	> 5 m (6)	> 4 - 5 m (5)	6:1	0.0237	14
Canopy diameter	A	6	0 - 1 m (1)	> 2 - 3 m (3)	4:1	0.0417	14
Canopy diameter	A	6	0 - 1 m (1)	> 3 - 4 m (4)	6:1	0.0020	14
Canopy diameter	A	6	0 - 1 m (1)	> 4 - 5 m (5)	4:1	0.0330	14
Canopy diameter	A	6	0 - 1 m (1)	> 5 m (6)	34:1	0.0000	14
Canopy diameter	A	6	> 1 - 2 m (2)	> 3 - 4 m (4)	6:1	0.0148	14
Canopy diameter	A	6	> 1 - 2 m (2)	> 5 m (6)	19:1	0.0001	14
Canopy diameter	A	6	> 2 - 3 m (3)	> 5 m (6)	8:1	0.0205	14
Canopy diameter	A	6	> 3 - 4 m (4)	> 5 m (6)	5:1	0.0318	14
Canopy diameter	A	6	> 4 - 5 m (5)	> 5 m (6)	9:1	0.0022	14
Lowest avail. leaves	B	5	> 3 - 4 m (4)	0 - 1 m (1)	25:1	0.0051	14
Lowest avail. leaves	B	5	> 3 - 4 m (4)	> 1 - 2 m (2)	15:1	0.0245	14
Lowest avail. leaves	B	5	> 3 - 4 m (4)	> 2 - 3 m (3)	16:1	0.0131	14
Lowest avail. leaves	B	5	> 3 - 4 m (4)	> 4 m (5)	20:1	0.0057	14
Feeding time	A	5	> 3 - 10 min (4)	> 30 sec - 1 min (2)	2:1	0.0651	14
Feeding time	A	5	> 3 - 10 min (4)	> 1 - 3 min (3)	2:1	0.0365	14
Wind speed	A	5	> 2 - 5 knots (2)	0 - 2 knots (1)	8:1	0.0006	14
Wind speed	A	5	> 5 - 9 knots (3)	0 - 2 knots (1)	11:1	0.0002	14
Wind speed	A	5	> 9 - 13 knots (4)	0 - 2 knots (1)	6:1	0.0057	14
Wind speed	A	5	> 13 - 24 knots (5)	0 - 2 knots (1)	70:1	0.0000	14
Wind speed	A	5	> 13 - 24 knots (5)	> 2 - 5 knots (2)	8:1	0.0001	14
Wind speed	A	5	> 13 - 24 knots (5)	> 5 - 9 knots (3)	6:1	0.0006	14
Wind speed	A	5	> 13 - 24 knots (5)	> 9 - 13 knots (4)	11:1	0.0001	14
Cloud cover	B	4	0 - 25 % (1)	> 25 - 50 % (2)	18:1	0.0000	14
Cloud cover	B	4	0 - 25 % (1)	> 50 - 75 % (3)	10:1	0.0001	14
Cloud cover	B	4	0 - 25 % (1)	> 75 - 100 % (4)	906:1	0.0000	14
Cloud cover	B	4	> 25 - 50 % (2)	> 75 - 100 % (4)	51:1	0.0000	14
Cloud cover	B	4	> 50 - 75 % (3)	> 75 - 100 % (4)	90:1	0.0000	14
Giraffe cows							
Habitat type	C	6	MAP (3)	Drep sey (1)	11:1	0.0072	17
Habitat type	C	6	MWH (4)	Drep sey (1)	82:1	0.0000	17
Habitat type	C	6	MWH (4)	MAH (2)	18:1	0.0204	17
Habitat type	C	6	MWH (4)	MAP (3)	7:1	0.0000	17
Habitat type	C	6	MWH (4)	MWP (5)	6:1	0.0006	17
Habitat type	C	6	MWH (4)	RIV (6)	15:1	0.0000	17
Habitat type	C	6	MWP (5)	Drep sey (1)	14:1	0.0047	17
Aspect	A	8	N (2)	E (1)	10:1	0.0000	17
Aspect	A	8	N (2)	NE (3)	23:1	0.0000	17

Table 21 (continued)

VARIABLE	GROUP NUMBER	NUMBER OF CATEGORIES	CATEGORY A	CATEGORY B	A:B	PROBABILITY	MODEL NUMBER
Giraffe cows (cont.)							
Aspect	A	8	N (2)	W (8)	8:1	0.0001	17
Aspect	A	8	S (5)	E (1)	11:1	0.0000	17
Aspect	A	8	S (5)	NE (3)	25:1	0.0000	17
Aspect	A	8	S (5)	SE (6)	3:1	0.0104	17
Aspect	A	8	S (5)	W (8)	9:1	0.0000	17
Aspect	A	8	SE (6)	E (1)	5:1	0.0016	17
Aspect	A	8	SE (6)	NE (3)	10:1	0.0001	17
Aspect	A	8	SW (7)	E (1)	10:1	0.0004	17
Aspect	A	8	SW (7)	NE (3)	22:1	0.0000	17
	B	3	Flat (1)	Average - steep (3)	3:1	0.0167	17
	B	3	Gradual (2)	Average - steep (3)	6:1	0.0000	17
Max height utilisation	B	5	> 1 - 2 m (2)	0 - 1 m (1)	7:1	0.0023	17
Max height utilisation	B	5	> 2 - 3 m (3)	0 - 1 m (1)	9:1	0.0047	17
Max height utilisation	B	5	> 3 - 4 m (4)	0 - 1 m (1)	20:1	0.0016	17
Max height utilisation	B	5	> 4 m (5)	0 - 1 m (1)	68:1	0.0010	17
Max height utilisation	B	5	> 4 m (5)	> 1 - 2 m (2)	10:1	0.0341	17
Max height utilisation	B	5	> 4 m (5)	> 2 - 3 m (3)	8:1	0.0584	17
Min height utilisation	B	5	0 - 1 m (1)	> 3 - 4 m (4)	14:1	0.0030	17
Min height utilisation	B	5	0 - 1 m (1)	> 4 m (5)	13:1	0.0356	17
Min height utilisation	B	5	> 1 - 2 m (2)	> 3 - 4 m (4)	13:1	0.0019	17
Min height utilisation	B	5	> 1 - 2 m (2)	> 4 m (5)	12:1	0.0346	17
Min height utilisation	B	5	> 2 - 3 m (3)	> 3 - 4 m (4)	13:1	0.0013	17
Min height utilisation	B	5	> 2 - 3 m (3)	> 4 m (5)	12:1	0.0379	17
Tree height	A	6	0 - 1 m (1)	> 5 m (6)	46:1	0.0018	17
Tree height	A	6	> 1 - 2 m (2)	> 5 m (6)	35:1	0.0006	17
Tree height	A	6	> 2 - 3 m (3)	> 5 m (6)	41:1	0.0002	17
Tree height	A	6	> 3 - 4 m (4)	> 5 m (6)	24:1	0.0008	17
Tree height	A	6	> 4 - 5 m (5)	> 5 m (6)	25:1	0.0003	17
Canopy diameter	A	6	> 4 - 5 m (5)	> 1 - 2 m (2)	2:1	0.0662	17
Lowest avail. leaves	C	3	> 2 m (3)	> 1 - 2 m (2)	5:1	0.0458	17
Feeding time	A	5	0 - 30 sec (1)	> 3 - 10 min (4)	5:1	0.0004	17
Feeding time	A	5	0 - 30 sec (1)	> 10 min (5)	11:1	0.0026	17
Feeding time	A	5	> 30 sec - 1 min (2)	> 3 - 10 min (4)	3:1	0.0056	17
Feeding time	A	5	> 30 sec - 1 min (2)	> 10 min (5)	8:1	0.0096	17
Feeding time	A	5	> 1 - 3 min (3)	> 3 - 10 min (4)	4:1	0.0001	17
Feeding time	A	5	> 1 - 3 min (3)	> 10 min (5)	11:1	0.0016	17
Wind speed	A	5	> 5 - 9 knots (3)	0 - 2 knots (1)	5:1	0.0001	17
Wind speed	A	5	> 5 - 9 knots (3)	> 2 - 5 knots (2)	3:1	0.0012	17
Wind speed	A	5	> 5 - 9 knots (3)	> 13 - 24 knots (5)	4:1	0.0056	17
Wind speed	A	5	> 9 - 13 knots (4)	0 - 2 knots (1)	3:1	0.0061	17
Cloud cover	B	4	0 - 25 % (1)	> 75 - 100 % (4)	5:1	0.0239	17
Cloud cover	B	4	> 25 - 50 % (2)	> 50 - 75 % (3)	2:1	0.0066	17
Cloud cover	B	4	> 25 - 50 % (2)	> 75 - 100 % (4)	12:1	0.0000	17
Cloud cover	B	4	> 50 - 75 % (3)	> 75 - 100 % (4)	6:1	0.0001	17

Table 22 Odds ratios and probabilities, categorised for the dry season, for the feeding ecology of the giraffes on the Lewa Wildlife Conservancy, Kenya, from May 1996 to May 1997, indicating their presence in category A, as opposed to category B, for the specific variable measured.

VARIABLE	GROUP NUMBER	NUMBER OF CATEGORIES	CATEGORY A	CATEGORY B	A:B	PROBABILITY	MODEL NUMBER
Giraffe bulls							
Habitat type	C	6	MAH (2)	Drep sey (1)	4:1	0.0007	15
Habitat type	C	6	MAH (2)	MWH (4)	7:1	0.0000	15
Habitat type	C	6	MAP (3)	Drep sey (1)	2:1	0.0164	15
Habitat type	C	6	MAP (3)	MWH (4)	4:1	0.0001	15
Habitat type	C	6	MWP (5)	MWH (4)	4:1	0.0130	15
Habitat type	C	6	RIV (6)	Drep sey (1)	4:1	0.0025	15
Habitat type	C	6	RIV (6)	MWH (4)	7:1	0.0000	15
Aspect	B	4	S (3)	E (1)	3:1	0.0001	15
Aspect	B	4	S (3)	N (2)	4:1	0.0000	15
Aspect	B	4	W (4)	E (1)	3:1	0.0041	15
Aspect	B	4	W (4)	N (2)	3:1	0.0007	15
Distance from water	A	5	0 - 50 m (1)	501 - 1 000 m (4)	4:1	0.0060	15
Distance from water	A	5	51 - 250 m (2)	0 - 50 m (1)	2:1	0.0577	15
Distance from water	A	5	51 - 250 m (2)	501 - 1 000 m (4)	7:1	0.0000	15
Distance from water	A	5	251 - 500 m (3)	501 - 1 000 m (4)	6:1	0.0000	15
Distance from water	A	5	> 1 000 m (5)	501 - 1 000 m (4)	5:1	0.0000	15
	B	3	Gradual (2)	Flat (1)	2:1	0.0045	15
	B	3	Average - steep (3)	Flat (1)	3:1	0.0030	15
Max height utilisation	A	6	> 1 - 2 m (2)	0 - 1 m (1)	10:1	0.0041	15
Max height utilisation	A	6	> 2 - 3 m (3)	0 - 1 m (1)	19:1	0.0006	15
Max height utilisation	A	6	> 2 - 3 m (3)	> 1 - 2 m (2)	2:1	0.0512	15
Max height utilisation	A	6	> 3 - 4 m (4)	0 - 1 m (1)	16:1	0.0028	15
Max height utilisation	A	6	> 4 - 5 m (5)	0 - 1 m (1)	146:1	0.0000	15
Max height utilisation	A	6	> 4 - 5 m (5)	> 1 - 2 m (2)	15:1	0.0001	15
Max height utilisation	A	6	> 4 - 5 m (5)	> 2 - 3 m (3)	8:1	0.0024	15
Max height utilisation	A	6	> 4 - 5 m (5)	> 3 - 4 m (4)	9:1	0.0002	15
Max height utilisation	A	6	> 5 m (6)	0 - 1 m (1)	146:1	0.0002	15
Max height utilisation	A	6	> 5 m (6)	> 1 - 2 m (2)	15:1	0.0139	15
Max height utilisation	A	6	> 5 m (6)	> 3 - 4 m (4)	9:1	0.0386	15
Min height utilisation	B	5	> 3 - 4 m (4)	0 - 1 m (1)	6:1	0.0055	15
Min height utilisation	B	5	> 3 - 4 m (4)	> 1 - 2 m (2)	5:1	0.0094	15
Min height utilisation	B	5	> 3 - 4 m (4)	> 2 - 3 m (3)	7:1	0.0013	15
Min height utilisation	B	5	> 4 m (5)	0 - 1 m (1)	7:1	0.0598	15
Min height utilisation	B	5	> 4 m (5)	> 2 - 3 m (3)	7:1	0.0515	15
Tree height	A	6	0 - 1 m (1)	> 2 - 3 m (3)	5:1	0.0512	15
Tree height	A	6	0 - 1 m (1)	> 4 - 5 m (5)	6:1	0.0570	15
Canopy diameter	A	6	> 1 - 2 m (2)	0 - 1 m (1)	2:1	0.0062	15
Canopy diameter	A	6	> 2 - 3 m (3)	0 - 1 m (1)	2:1	0.0344	15
Canopy diameter	A	6	> 3 - 4 m (4)	0 - 1 m (1)	3:1	0.0075	15
Canopy diameter	A	6	> 3 - 4 m (4)	> 5 m (6)	3:1	0.0754	15
Lowest avail. leaves	B	5	0 - 1 m (1)	> 2 - 3 m (3)	4:1	0.0501	15
Lowest avail. leaves	B	5	0 - 1 m (1)	> 4 m (5)	7:1	0.0475	15
Lowest avail. leaves	B	5	> 1 - 2 m (2)	> 2 - 3 m (3)	5:1	0.0307	15
Lowest avail. leaves	B	5	> 1 - 2 m (2)	> 4 m (5)	8:1	0.0327	15
Feeding time	A	5	0 - 30 sec (1)	> 1 - 3 min (3)	3:1	0.0009	15
Feeding time	A	5	0 - 30 sec (1)	> 3 - 10 min (4)	4:1	0.0000	15
Feeding time	A	5	0 - 30 sec (1)	> 10 min (5)	35:1	0.0000	15
Feeding time	A	5	> 30 sec - 1 min (2)	> 3 - 10 min (4)	3:1	0.0031	15
Feeding time	A	5	> 30 sec - 1 min (2)	> 10 min (5)	22:1	0.0000	15
Wind speed	A	5	0 - 2 knots (1)	> 2 - 5 knots (2)	2:1	0.0242	15
Wind speed	A	5	0 - 2 knots (1)	> 9 - 13 knots (4)	3:1	0.0025	15
Wind speed	A	5	0 - 2 knots (1)	> 13 - 24 knots (5)	3:1	0.0006	15
Wind speed	A	5	> 5 - 9 knots (3)	> 13 - 24 knots (5)	2:1	0.0373	15

Table 22 (continued)

VARIABLE	GROUP NUMBER	NUMBER OF CATEGORIES	CATEGORY A	CATEGORY B	A:B	PROBABILITY	MODEL NUMBER
Giraffe cows							
Habitat type	C	6	Drep sey (1)	MAH (2)	7:1	0.0000	18
Habitat type	C	6	Drep sey (1)	MWH (4)	2:1	0.0075	18
Habitat type	C	6	Drep sey (1)	MWP (5)	8:1	0.0000	18
Habitat type	C	6	Drep sey (1)	RIV (6)	22:1	0.0000	18
Habitat type	C	6	MAH (2)	RIV (6)	4:1	0.0070	18
Habitat type	C	6	MAP (3)	MAH (2)	7:1	0.0000	18
Habitat type	C	6	MAP (3)	MWH (4)	3:1	0.0031	18
Habitat type	C	6	MAP (3)	MWP (5)	8:1	0.0000	18
Habitat type	C	6	MAP (3)	RIV (6)	24:1	0.0000	18
Habitat type	C	6	MWH (4)	MAH (2)	3:1	0.0040	18
Habitat type	C	6	MWH (4)	MWP (5)	3:1	0.0085	18
Habitat type	C	6	MWH (4)	RIV (6)	9:1	0.0000	18
Habitat type	C	6	MWP (5)	RIV (6)	3:1	0.0340	18
Aspect	A	8	E (1)	N (2)	3:1	0.0007	18
Aspect	A	8	E (1)	NE (3)	6:1	0.0001	18
Aspect	A	8	E (1)	NW (4)	4:1	0.0027	18
Aspect	A	8	E (1)	W (8)	16:1	0.0000	18
Aspect	A	8	N (2)	W (8)	5:1	0.0008	18
Aspect	A	8	NW (4)	W (8)	4:1	0.0042	18
Aspect	A	8	S (5)	W (8)	10:1	0.0000	18
Aspect	A	8	S (5)	N (2)	2:1	0.0164	18
Aspect	A	8	S (5)	NE (3)	4:1	0.0013	18
Aspect	A	8	S (5)	NW (4)	2:1	0.0343	18
Aspect	A	8	SE (6)	W (8)	9:1	0.0000	18
Aspect	A	8	SW (7)	NE (3)	3:1	0.0235	18
Aspect	A	8	SW (7)	W (8)	9:1	0.0000	18
Distance from water	A	5	0 - 50 m (1)	251 - 500 m (3)	3:1	0.0007	18
Distance from water	A	5	0 - 50 m (1)	501 - 1 000 m (4)	4:1	0.0001	18
Distance from water	A	5	0 - 50 m (1)	> 1 000 m (5)	5:1	0.0003	18
Distance from water	A	5	51 - 250 m (2)	251 - 500 m (3)	2:1	0.0505	18
Distance from water	A	5	51 - 250 m (2)	501 - 1 000 m (4)	2:1	0.0051	18
Distance from water	A	5	51 - 250 m (2)	> 1 000 m (5)	3:1	0.0065	18
	B	3	Flat (1)	Gradual (2)	4:1	0.0000	18
	B	3	Average - steep (3)	Gradual (2)	2:1	0.0318	18
Max height utilisation	B	5	> 1 - 2 m (2)	0 - 1 m (1)	25:1	0.0000	18
Max height utilisation	B	5	> 2 - 3 m (3)	0 - 1 m (1)	73:1	0.0000	18
Max height utilisation	B	5	> 2 - 3 m (3)	> 1 - 2 m (2)	3:1	0.0007	18
Max height utilisation	B	5	> 3 - 4 m (4)	0 - 1 m (1)	252:1	0.0000	18
Max height utilisation	B	5	> 3 - 4 m (4)	> 1 - 2 m (2)	10:1	0.0000	18
Max height utilisation	B	5	> 3 - 4 m (4)	> 2 - 3 m (3)	3:1	0.0019	18
Max height utilisation	B	5	> 3 - 4 m (4)	> 4 m (5)	7:1	0.0007	18
Max height utilisation	B	5	> 4 m (5)	0 - 1 m (1)	34:1	0.0001	18
Min height utilisation	C	4	0 - 1 m (1)	> 1 - 2 m (2)	2:1	0.0173	18
Min height utilisation	C	4	0 - 1 m (1)	> 3 m (4)	16:1	0.0000	18
Min height utilisation	C	4	> 1 - 2 m (2)	> 3 m (4)	8:1	0.0003	18
Min height utilisation	C	4	> 2 - 3 m (3)	> 3 m (4)	8:1	0.0003	18
Tree height	A	6	0 - 1 m (1)	> 1 - 2 m (2)	4:1	0.0114	18
Tree height	A	6	0 - 1 m (1)	> 2 - 3 m (3)	4:1	0.0069	18
Tree height	A	6	0 - 1 m (1)	> 3 - 4 m (4)	11:1	0.0001	18
Tree height	A	6	0 - 1 m (1)	> 4 - 5 m (5)	5:1	0.0099	18
Tree height	A	6	0 - 1 m (1)	> 5 m (6)	8:1	0.0076	18
Tree height	A	6	> 1 - 2 m (2)	> 3 - 4 m (4)	3:1	0.0017	18
Tree height	A	6	> 2 - 3 m (3)	> 3 - 4 m (4)	3:1	0.0038	18
Canopy diameter	A	6	> 5 m (6)	> 3 - 4 m (4)	3:1	0.0161	18
Feeding time	A	5	0 - 30 sec (1)	> 1 - 3 min (3)	2:1	0.0429	18
Feeding time	A	5	0 - 30 sec (1)	> 3 - 10 min (4)	3:1	0.0001	18

Table 22 (continued)

VARIABLE	GROUP NUMBER	NUMBER OF CATEGORIES	CATEGORY A	CATEGORY B	A:B	PROBABILITY	MODEL NUMBER
Giraffe cows (cont.)							
Feeding time	A	5	0 - 30 sec (1)	> 10 min (5)	33:1	0.0000	18
Feeding time	A	5	> 30 sec - 1 min (2)	> 3 - 10 min (4)	2:1	0.0098	18
Feeding time	A	5	> 30 sec - 1 min (2)	> 10 min (5)	22:1	0.0000	18
Feeding time	A	5	> 1 - 3 min (3)	> 3 - 10 min (4)	2:1	0.0096	18
Feeding time	A	5	> 1 - 3 min (3)	> 10 min (5)	20:1	0.0000	18
Feeding time	A	5	> 3 - 10 min (4)	> 10 min (5)	10:1	0.0004	18
Wind speed	A	5	> 2 - 5 knots (2)	0 - 2 knots (1)	6:1	0.0000	18
Wind speed	A	5	> 2 - 5 knots (2)	> 5 - 9 knots (3)	2:1	0.0231	18
Wind speed	A	5	> 2 - 5 knots (2)	> 9 - 13 knots (4)	2:1	0.0270	18
Wind speed	A	5	> 2 - 5 knots (2)	> 13 - 24 knots (5)	2:1	0.0329	18
Wind speed	A	5	> 5 - 9 knots (3)	0 - 2 knots (1)	3:1	0.0095	18
Wind speed	A	5	> 9 - 13 knots (4)	0 - 2 knots (1)	3:1	0.0053	18
Wind speed	A	5	> 13 - 24 knots (5)	0 - 2 knots (1)	3:1	0.0022	18
Cloud cover	B	4	> 50 - 75 % (3)	0 - 25 % (1)	5:1	0.0000	18
Cloud cover	B	4	> 50 - 75 % (3)	> 25 - 50 % (2)	4:1	0.0000	18
Cloud cover	B	4	> 75 - 100 % (4)	0 - 25 % (1)	4:1	0.0038	18
Cloud cover	B	4	> 75 - 100 % (4)	> 25 - 50 % (2)	3:1	0.0069	18

Figure 41 A pair of giraffe on the Lewa Wildlife Conservancy browsing on an *Acacia mellifera* tree from the top, therefore keeping the tree from growing taller. This effect on the woody vegetation is not necessarily a disadvantage, as these trees are maintained at an accessible height for other browsers such as the black rhinoceros.

The giraffe on Lewa does not have large-scale seasonal migrations. Within individual ranges, however, seasonal movements do occur. These can possibly be attributed to seasonal changes in the distribution of the available browse. There is a general tendency for the giraffe cows with calves on Lewa to utilise the open *Acacia* - dominated plains during both the wet and dry season. However, during the wet season, the giraffe often also browse on the upper slopes of the mixed woodland hills. It was more likely to observe a giraffe cow browsing in the mixed woodland hills, than on the mixed *Acacia* plains (Odds ratio = 7:1 ; P = 0.0000) or on the mixed woodland plains (Odds ratio = 6:1 ; P = 0.0006) (Table 21). During the dry season, large herds of giraffe move into the *Acacia drepanolobium* - *Acacia seyal* woodland and also onto the mixed *Acacia* plains. It was seven times more likely to observe a giraffe cow browsing in the *Acacia drepanolobium* - *Acacia seyal* woodland or on the mixed Acacia plains, than in the mixed Acacia hills (P = 0.0000) (Table 22). The giraffe bulls, however, prefer the riverine habitat during the dry season, when the browse biomass in the mixed woodland hills declines (Odds ratio = 7:1 ; P = 0.0000). The choice by the giraffe of different habitats in which to feed, therefore reflects the differential seasonal production of browse material on Lewa.

Method of feeding

A giraffe has two feeding methods. The first is stripping, where the giraffe wraps its tongue around a branch and then strips the leaves off by jerking its head. In consequence, long leafless stalks are left sticking out from the tree or bush (Figure 33). The second is picking, where individual leaves and shoots are picked off from among the thorns of a plant (Kruger 1994). By selecting primarily for the young shoots and leaves of trees, the giraffe on Lewa alters the structure of the woody vegetation by inhibiting the regeneration of these growing parts. The trees therefore become stunted because of the continual removal of their growing meristems. The impact of giraffe feeding on Lewa can be seen as a browse-line on many trees. On tall trees like *Acacia tortilis*, the giraffe cuts the foliage at an even height above the ground, giving them a flat bottom. Many of the taller *Acacia mellifera* trees on Lewa also have an hourglass shape (Figure 21). The lower part of the tree is rounded, whereas the branches above are able to grow and spread out. The middle section has been browsed out. During the dry season, the giraffe browses heavily on the evergreen tree species, such as *Boscia angustifolia* and *Balanites aegyptiaca,* resulting in their characteristic inverse browse-lines. The giraffes feed on these trees from the top, therefore keeping them from growing taller (Figure 41). This effect on the woody vegetation is not necessarily a disadvantage, as these trees are maintained at an accessible height for other browsers, such as the black rhinoceros.

Browsing height

The giraffe is generally said to feed mainly on trees and shrubs that are too tall for the smaller browsers. Therefore, there is no competition for browse with the giraffe (Darling 1960; Leuthold 1978). Observations on Lewa, however, showed that this assumption is only partly true. The data indicate that the giraffe on Lewa have definite feeding height preferences, some of which are also used by the other browsers present. The giraffe cows prefer to feed at a height of between 1 and 4 m. Seasonal feeding height preferences do not differ for the giraffe cows on Lewa. Interspecific competition between the black rhinoceros and the giraffe on Lewa therefore does occur to some degree. Seasonal tree height preferences do differ, however, for the giraffe cows. During the wet season, trees of up to 5 m tall are selected (Table 21). During the dry season, however, trees of up to 3 m tall are selected, although bushes less than l m tall are preferred (Table 22). *Acacia mellifera* and *Boscia angustifolia* have low growth forms that allow a giraffe to feed on them from above. Similar observations have been made elsewhere (Lamprey 1963; Leuthold & Leuthold 1972; Moss 1975; Furstenburg 1991; Kruger 1994). It was more likely to observe a giraffe cow on Lewa browsing on bushes of 0 to 1 m tall, than on trees of > 1 to 2 m (Odds ratio = 4:1 ; P = 0.0114), > 2 to 3 m (Odds ratio = 4:1 ; P = 0.0069), > 3 to 4 m (Odds ratio = 11:1 ; P = 0.0001), > 4 to 5 m (Odds ratio = 5:1 ; P = 0.0099) or greater than 5 m (Odds ratio = 8:1 ; P = 0.0076) tall. The evergreen trees and bushes present on Lewa are *Balanites aegyptiaca*, *Boscia angustifolia*, *Boscia coriacea*, *Carissa edulis* and *Euclea divinorum*. These plant species are kept predominantly to a height of less than 1 m by giraffe, elephant and black rhinoceros browsing. During the dry season, these plant species are all favoured by the giraffe, but particularly so the *Boscia* species.

The giraffe bulls on Lewa prefer to browse at a height of above 3 m. Seasonal feeding height preferences do not differ for the giraffe bulls, although the bulls can feed above 5 m high, whereas the cows prefer to feed below a height of 4 m. Seasonal tree height preferences, however, do differ for the giraffe bulls. During the wet season, the bulls browse on trees taller than 3 m (Table 21), whereas during the dry season, bushes less than 1 m tall are preferred (Table 22).

The giraffe on Lewa was also observed to feed on trees that have a greater canopy diameter during the dry season, than the wet season. During the dry season, the giraffe cows select trees with a canopy diameter of greater than 5 m, as opposed to a canopy diameter of 3 to 4 m (Odds ratio = 3:1 ; P = 0.0161) (Table 22). A larger canopy diameter also provides shade for the giraffe during the dry season.

Feeding time

No significant differences could be found between the mean feeding time of giraffe cows on Lewa between the dry and the wet season. The cows spend less than 3 minutes at a feeding station (Tables 21 and 22). The maximum time that a giraffe cow was observed to feed on one individual *Acacia mellifera* tree, was 18 minutes. Seasonal difference in time spent feeding is only significant for the giraffe bulls, who spend between 3 and 10 minutes at a feeding station during the wet season (Table 21), but less than 1 minute during the dry season (Table 22). Pellew (1981) found that giraffe bulls in the Serengeti National Park in Tanzania are more mobile during the dry season than during the wet season. This is the result of a search for females in oestrus. The same reason probably applies to the shorter feeding times shown by the giraffe bulls on Lewa during the dry season.

Aspect and slope

During the wet season, giraffe bulls browse mainly on the south- and the east-facing slopes. Areas with a flat gradient are selected above those with gradual or average to steep slopes. It was more likely to observe a giraffe bull browsing in a flat area, than on a gradual slope (Odds ratio = 14:1 ; P = 0.0000) or on an average to steep slope (Odds ratio = 5:1 ; P = 0.0001) (Table 21). During the dry season, the giraffe bulls browse mainly on the south- and the west-facing slopes. Areas with a gradual and average to steep gradient are selected at this time of the year (Table 22). During the wet season, the giraffe cows concentrate on the north-, south-, southwest- and the southeast-facing slopes (Table 21). During the dry season, however, their distribution expands, probably in their search for a better browse resource elsewhere on Lewa. At that time of the year, the giraffe cows utilise the north-, south-, east-, northwest-, southwest- and the southeast-facing slopes (Table 22).

Other factors

The distance away from water at which a giraffe feeds has no influence on its feeding ecology. During the dry season when the giraffe on Lewa concentrates its feeding activities in the valleys and the riverine habitat, a given individual is naturally closer to water. The abundance of water sources on Lewa does not necessitate the concentration of giraffe around water, especially during the dry season. Moss (1975) moreover suggests that giraffes get their moisture from the vegetation on which they feed. This happens when browsing early in the morning when a giraffe will take in much of the dew collected on the leaves. Furthermore, the natural moisture content of the vegetation seems to supply the giraffe with adequate metabolic water. The tender twigs of *Acacia drepanolobium* are also known to contain 74 % water (Moss 1975), and this is a resource that is possibly used abundantly by the giraffe on Lewa.

Wind speed has no influence on the feeding ecology of the giraffe on Lewa. Moreover, Kruger (1994) found that the feeding time of a giraffe in the Kalahari Gemsbok National Park in South Africa increases with a decrease in cloud cover. This was also observed on Lewa, particularly with giraffe bulls (Odds ratio = 7:1 ; P = 0.0000).

CONCLUSIONS

The food plants consumed by most herbivorous species are probably not only determined by feeding preferences, but also by what is available (Lamprey 1963). On Lewa, this proved to be the case, especially with the black rhinoceros. The elephant also displays this during the wet season, when a large proportion of its diet consists of grasses. There is considerable overlap between the various browsers in terms of food plants and plant parts used, and the factors which influence the feeding ecology of the various browsers on Lewa. It is therefore clear that the ecological separation of these browsers is only partly achieved through food plant selection. Seasonal variations in the browsing height of the giraffe also have the effect of reducing overlap in browse use with the black rhinoceros during the dry season, a time when browsable food is in relatively short supply. Apart from the general competition for food plants, facilitation of food by one species for another also occurs. The black rhinoceros and giraffe often feed on trees that are pushed over by the elephants.

Seasonal movements by the elephant in particular, but also by the giraffe, alleviate competition for food plants between the browsers on Lewa to a certain extent. The elephants that remain on Lewa during the wet season consume an abundance of grasses. The giraffes that concentrate in the valleys and riverine habitats during the dry season create a form of ecological separation from the black rhinoceros. The overlap in diet between the elephant and black rhinoceros is more profound during the dry than the wet season. The black rhinoceros on Lewa eats little grass in comparison with the elephant there. As a consequence, the black rhinoceros may suffer severely from competition with the giraffe and the elephant, especially during the dry season.

Although there is some ecological separation between the black rhinoceros, elephant and giraffe on Lewa, the large number of giraffes and elephants present create an excessive demand for browsable food resources, especially during the dry season. Throughout the year, the elephant compete directly with the giraffe and the black rhinoceros on Lewa. Large herds of eland also contribute to this competition. During the dry season when plant production is low, this competition must reach significant levels. The continued survival of browsers on Lewa, but particularly of the black rhinoceros depends primarily on the future development and maintenance of an abundant woody vegetation resource. The following management actions designed to prevent further substantial vegetation changes should therefore be considered: Firstly, based on the browsing capacity of Lewa, the number of elephants and giraffes, but also of the eland and impala that enter Lewa should be monitored and closely controlled. Secondly, the effects of fire on the germination, regeneration and survival of the young seedlings and forbs has to be studied and quantified.

Based on the data gathered on Lewa the main food plants of the black rhinoceros are *Acacia drepanolobium*, *Acacia seyal*, *Hibiscus* species and many unidentified forb species. All the parts of individual plants are eaten more often than only the leaves, branches or shoots. The browsing height and the feeding time also influences the feeding ecology of the black rhinoceros on Lewa. A preference is shown for immature plants, indicating the importance of the vegetation structure on the habitat suitability for the black rhinoceros. One must, however, not think statically about habitat suitability, but be aware of how vegetation dynamics, and especially structural changes in the vegetation can affect the habitat suitability and its browsing capacity for the black rhinoceros. Shorter feeding times were recorded for the black rhinoceros during the dry season, as opposed to the wet season. This suggests the availability of fewer palatable plants, or a decrease in the palatability of selected plant parts during the dry season.

The main browsable food plants of the elephant on Lewa are *Acacia mellifera*, *Acacia nilotica*, *Acacia seyal*, *Acacia tortilis* and many unidentified forb species. The elephant alters its feeding habits in relation to the season, grazing considerably more during the wet than during the dry season. Most browse is taken in the form of leafy branches, although bark is eaten as a form of roughage during the wet and the dry season. The elephant shows definite feeding height preferences on Lewa. The elephant bulls prefer to feed between a height of 2 to 3 m, and cows at heights of > 3 to 4 m. In the *Acacia xanthophloea* forests, the elephant bulls select trees taller than the height at which they prefer to feed. These trees are pushed over to get at the browse. The elephant bulls also spend longer at a feeding station than do the cows. The availability and proximity of water on Lewa has little, if any effect on the feeding ecology of the elephants. A cloud cover of more than 76 % leads to longer feeding times by the elephant cows.

The main food plants of the giraffe on Lewa are *Acacia drepanolobium*, *Acacia seyal* and *Acacia tortilis*. The choice by the giraffe of different habitats in which to feed, reflects the differential seasonal production of browse material on Lewa. The giraffe on Lewa has a definite feeding height preference. The cows feed between a height of 1.5 and 3 m, and the bulls above 3 m. The giraffe bulls have shorter feeding times during the dry season, possibly as a result of the search for females in oestrus at this time. The availability and proximity of water, and wind speed have no influence on the feeding ecology of the giraffe on Lewa. A decrease in cloud cover, however, corresponds with an increase in feeding time, particularly by the giraffe bulls.

CHAPTER 7

THE IMPACT OF BROWSING ON THE REGENERATION AND RECRUITMENT OF *ACACIA XANTHOPHLOEA* IN THE RIVERINE HABITATS

INTRODUCTION

The major impact that herbivores have on their habitat is through the modification of the vegetation. Typically, a balanced relationship exists between the herbivore and its food source, and if the former is removed the vegetation will react to the alleviation of this pressure (Delany 1982).

The mature *Acacia xanthophloea* trees in the riverine habitats on Lewa produce large quantities of seed, but the number of established seedlings currently found in these habitats is not enough to maintain this species. Even during the wet season heavy seedling mortality occurs on Lewa. This suggests that factors other than the rainfall are influencing seedling mortality. The large number of elephants that have access to Lewa, but no longer pass through it as was done in earlier years, has resulted in the widespread destruction of mature canopy woodland, particularly in the *Acacia xanthophloea* riverine habitats. The destructive feeding habits of elephants and its prevention of the regeneration of woody vegetation have been widely documented throughout Africa (Eggeling 1947; Spinage & Guinness 1971; Belsky 1984; Lewis 1987; Tchamba & Mahamat 1992; Tchamba 1993). The present condition of the woody vegetation on Lewa is a clear indication that the browser stocking rate exceeds the browsing capacity of the area. Moreover, the high browser stocking rate may be the crucial factor in the lack of regeneration and recruitment of *Acacia xanthophloea* seedlings on Lewa.

There appears to be no real recruitment or regeneration of *Acacia xanthophloea* seedlings in the riverine habitats on Lewa. The seedlings that do germinate do not grow into mature *Acacia xanthophloea* trees. The management team on Lewa has speculated that this lack of regeneration is due to selective browsing by the elephant, giraffe and impala populations in the area. One aim of this study was to quantify the impact that these browsers have on the regeneration and recruitment of *Acacia xanthophloea* seedlings and juvenile *Acacia xanthophloea* trees in the riverine habitats on Lewa. A second aim was to identify other animals on Lewa that may also be having an impact on this riverine vegetation.

METHODS

Five exclusion plots were created within the riverine habitats on Lewa. The plots were 100 X 60 m each. Two of these plots were total exclusion plots, fencing out the elephant, giraffe and impala, two excluded only the elephant and giraffe, and one was a control, allowing access to all animals.

- Total exclusion plots (A and B)
  All animals were fenced out with a mesh fence 1 m high. Two electric wire strands 1 and 1.5 m above the ground, respectively, ensured that no animals entered the exclusion plot. The aim of these plots was to establish the natural growth patterns of the *Acacia xanthophloea* seedlings without subjection to browsing.
- Elephant & Giraffe exclosures (Aa and Bb)
  Two electric wire strands 2 and 2.2 m above the ground, respectively, ensured that no elephants or giraffes entered the plots. The aim of these plots was to quantify the impact that the impala has on the regeneration of the *Acacia xanthophloea* seedlings within the plots.
- Control plot (C)
  This plot was unfenced, and allowed access to all animals. The aim of this plot was to quantify the impact that the browsers were having on the regeneration and recruitment of the *Acacia xanthophloea* seedlings in an unfenced area.

Ten *Acacia xanthophloea* seedlings and trees were marked within each plot, with the exception of the control plot C where 15 trees were marked and total exclusion plot A where five trees were marked. Each tree was marked by placing a large flat stone on which a number was painted near it (Figure 42). Three shoots on each individual tree were also tagged with a strip of tinfoil with a number for further identification (Figure 43). Tagging of shoots was random, but all were within 1.5 m of ground level for easy access. At each measurement a standardised diagram of each tagged shoot was drawn from which any new shoot growth occurring during the following month was identified by comparison with that of the previous month. Monthly growth or length increments were thus measured for each tagged shoot.

A field data sheet was used to record the height of each tree, the stem diameter of each tree, and the shoot length of the tagged shoots (Appendix F). The trees and seedlings were monitored once a month, over a period of 11 months, from June 1996 to April 1997. The rainfall received during the study period was also recorded.

RESULTS

The rainfall recorded during the study period was received during the following months: June (118 mm), July (24 mm), October (52 mm), November (75 mm), March (19 mm) and April (319 mm).

Total exclusion plot A

In total exclusion plot A only five trees were monitored because of a lack of young trees and seedlings. A maximum total shoot growth of 106.7 mm was measured over a period of 11 months

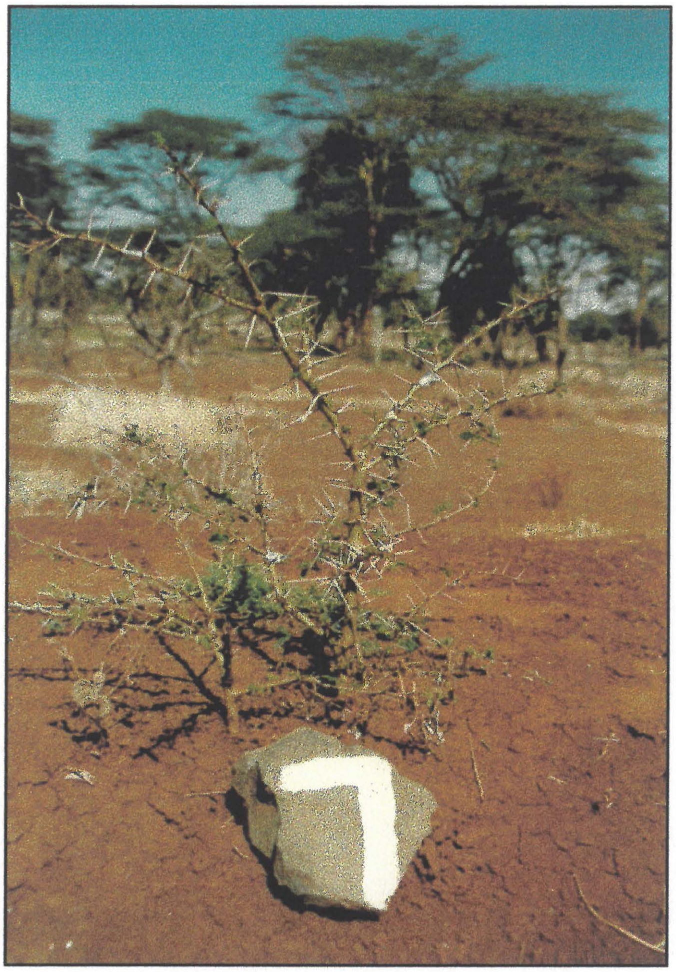

Figure 42 Each *Acacia xanthophloea* tree or seedling in the exclusion plots in the riverine habitats were marked by placing a flat stone near the tree, on which a number was painted.

Figure 43 Three shoots on each individual *Acacia xanthophloea* seedling in the riverine habitats on the Lewa Wildlife Conservancy were tagged with tinfoil with a number for further identification.

(Figure 44). During December a maximum shoot growth of 184.6 mm was measured. The rapid shoot growth in July and from October to November is attributed to the rains received during these months. The relatively slow shoot growth in the months following the rains is indicative of the slower growth during the dry season. Despite the rains received in March and April, there was a decline in shoot growth, but particularly so in April. Because of the small sample size of trees within this exclusion plot, the death of any shoots will create a large deviation in the curve. Three shoots died in April, explaining the dip in the curve of shoot growth for the month of April. The cause of death of these shoots could not be established.

Total exclusion plot B

A maximum shoot growth of 288.4 mm was measured over a period of 11 months (Figure 45). The rapid shoot growth from June to August, October to November and March to April is attributed to the rains received during these months. Although no rain was received in September and in February, an increase in the shoot growth is still evident. A herd of impala entered the exclusion plot on two occasions, once in December and again in January. The negative shoot growth in January is a combination of the lack of rains in December and in January and the browsing pressure exerted by these impala in November.

Elephant and giraffe exclusion plot Aa

A maximum shoot growth of 46.5 mm was measured over a period of 11 months (Figure 46). The rapid shoot growth during July, and again from October to November and in April, is attributed to the rains received during these months. In April 1997, Lewa received 319 mm of rain, whereas a far lower rainfall was recorded for the other wet months. The rapid increase in shoot growth in February could perhaps be because of the stimulatory effect that browsing has on trees. Another reason for the rapid shoot growth in February, before the rainy season, might also be the *Acacia's* ability to sense rain (Pellew 1983a). This aspect is discussed in another section. The negative shoot growth from the end of November to the beginning of February coincided with the dry season and also the browsing pressure exerted by the impala during this time of the year. Despite the fact that Lewa received rain in March, a negative shoot growth occurred during that month. This is possibly due to the heavy browsing impact of the impala from late November to early February. The shoots in plot Aa grew more slowly than those in plot Bb. More impala were observed in the area where plot Aa was situated and therefore the browsing pressure there was greater than in plot Bb. During March, after the rains, a count of the seedlings less than 50 mm in height, revealed that germination of *Acacia xanthophloea* seedlings had occurred. The count also revealed many seedlings of greater than 150 mm in height. No seedlings between 50 and 150 mm in height could be found.

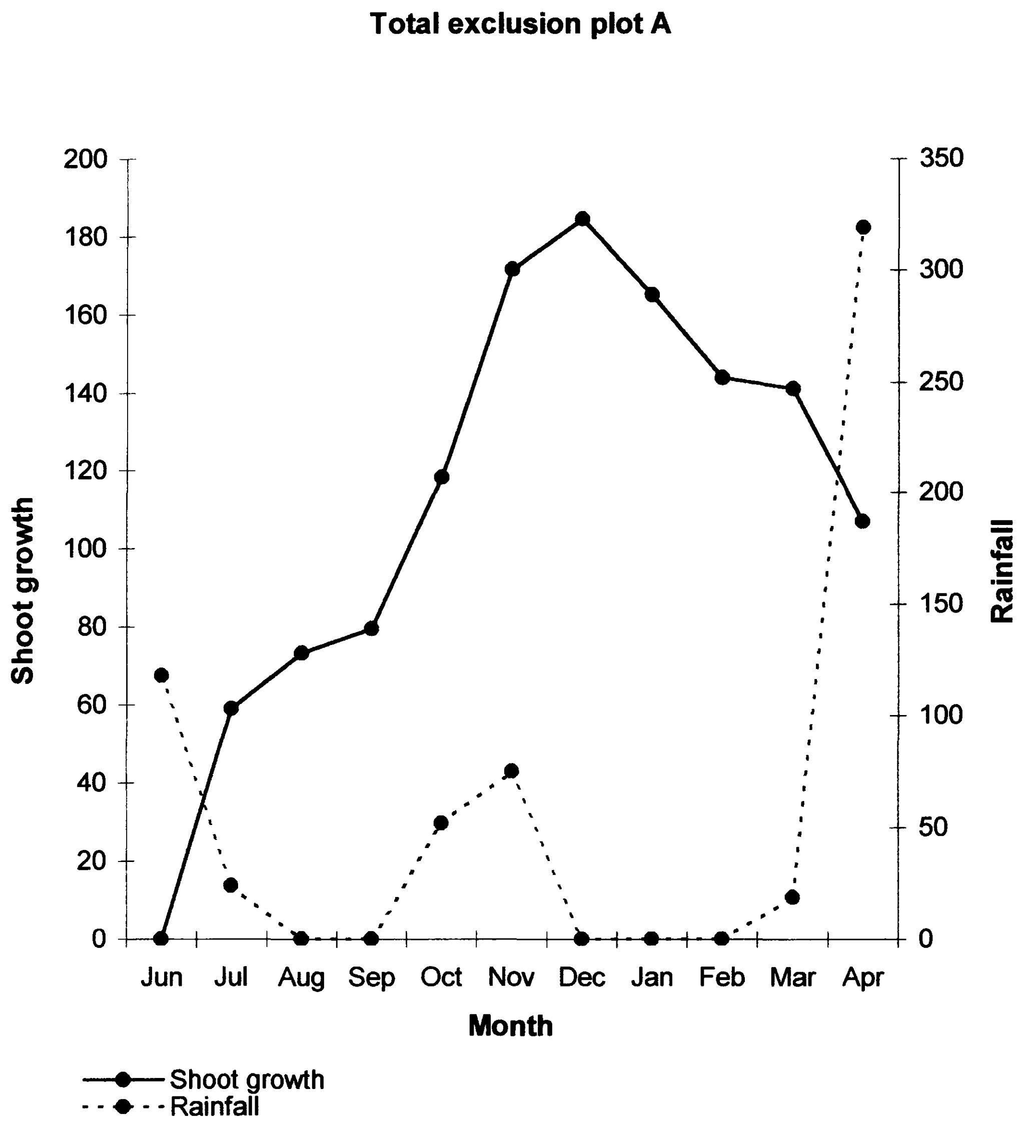

Figure 44 The effect of rainfall (mm) on the shoot growth (mm) of the *Acacia xanthophloea* seedlings in total exclusion plot A, on the Lewa Wildlife Conservancy, Kenya, from June 1996 to April 1997. The effect was most conspicuous for the months of July, October and November as a response to the rainfall received during those months.

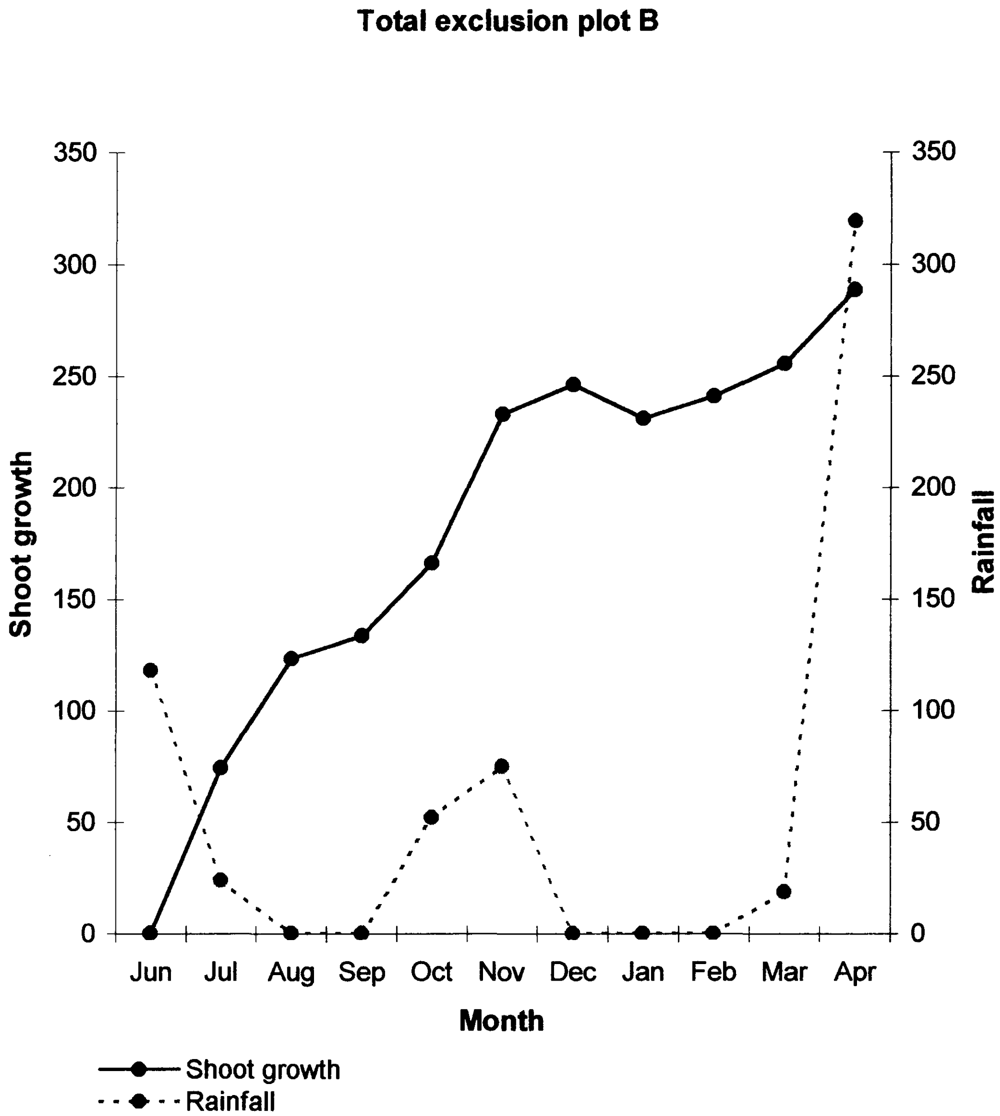

Figure 45 The effect of rainfall (mm) on the shoot growth (mm) of the *Acacia xanthophloea* seedlings in total exclusion plot B, on the Lewa Wildlife Conservancy, Kenya, from June 1996 to April 1997. The effect was most conspicuous for the months of July to August, October to November and from March to April. This is as a response to the rainfall received during these months.

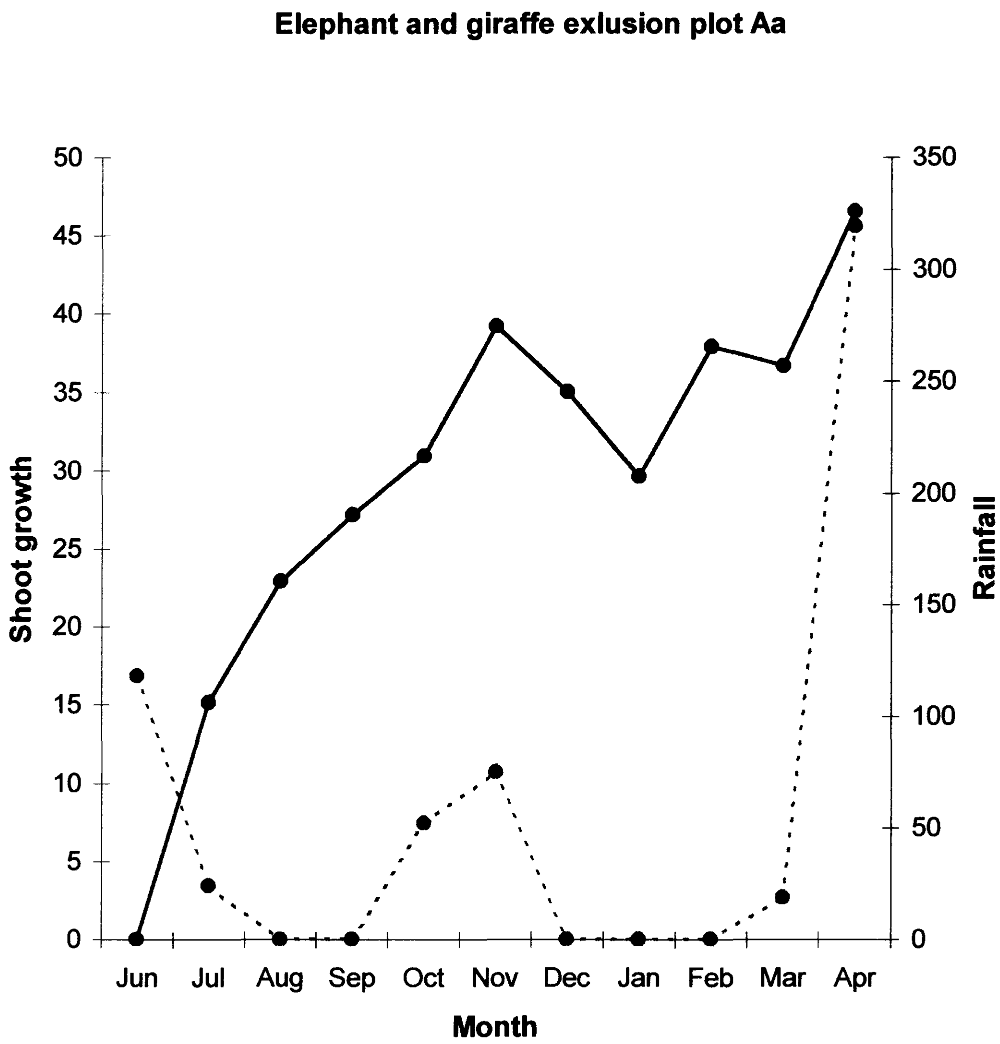

Figure 46 The effect of rainfall (mm) on the shoot growth (mm) of the *Acacia xanthophloea* seedlings in the elephant and giraffe exclusion plot Aa, on the Lewa Wildlife Conservancy, Kenya, from June 1996 to April 1997. The effect was most conspicuous for the months of July, November and April as a response to rainfall received during these months.

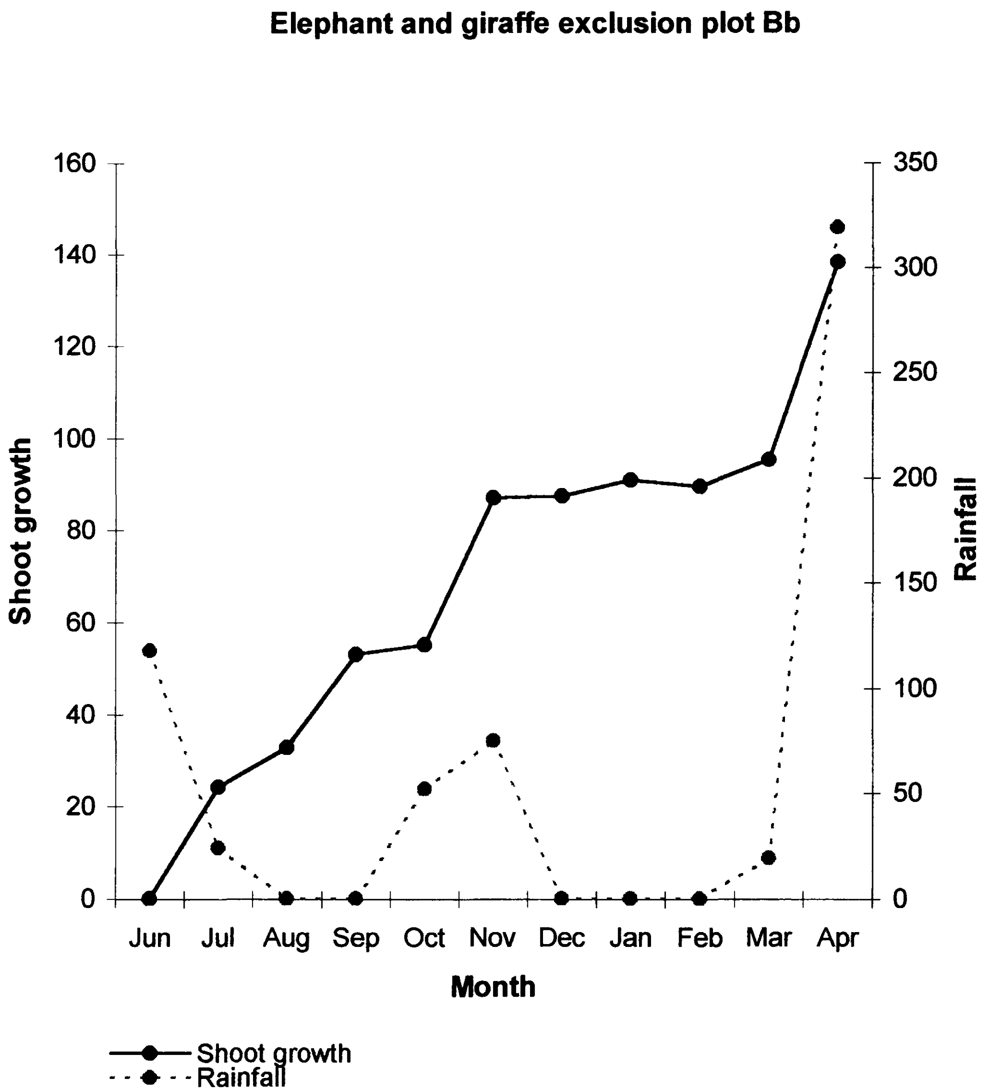

Figure 47 The effect of rainfall (mm) on the shoot growth (mm) of the *Acacia xanthophloea* seedlings in the elephant and giraffe exclusion plot Bb, on the Lewa Wildlife Conservancy, Kenya, from June 1996 to April 1997. The effect was most conspicuous for the months of July, November and April as a response to the rainfall received during these months.

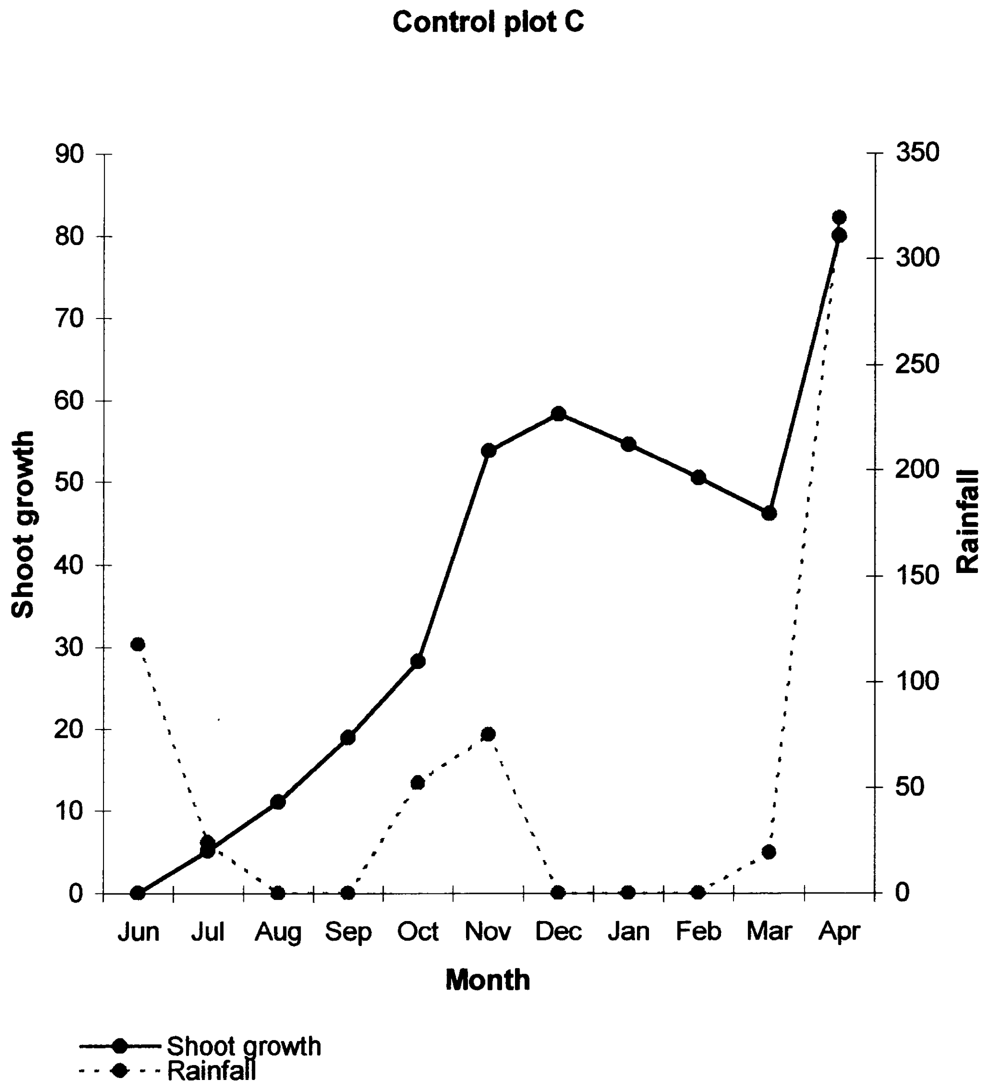

Figure 48 The effect of rainfall (mm) on the shoot growth (mm) of the *Acacia xanthophloea* seedlings in control plot C, on the Lewa Wildlife Conservancy, Kenya, from June 1996 to April 1997. The rapid shoot growth in November and in April is attributed to the rainfall received during these months.

Elephant and giraffe exclusion plot Bb

A maximum shoot growth of 138.2 mm was measured over a period of 11 months (Figure 47). The rapid shoot growth in July, November and again in April is attributed to the rains received during these months. No negative shoot growth occurred in plot Bb. This is as a result of fewer impala in the area where the plot was situated. There was, nevertheless, a browsing impact from the impala. This can be seen in the slow growth rate of the shoots from early August to late October, and from December to March.

Control plot C

A maximum shoot growth of 79.9 mm was measured over a period of 11 months (Figure 48). The rapid shoot growth in November and in April, is attributed to the rains received during these months. The negative shoot growth, from December to March, is attributed to heavy browsing by the elephants. Over the 4-month period from December to March a herd of elephant bulls frequented the area in which control plot C occurred. Four young trees were broken off at the base of their stems, but in April, once the elephants had moved off from the area, these trees started to coppice and regeneration started taking place. None of the trees were uprooted. There were signs of giraffe browsing on the mature *Acacia xanthophloea* trees, but not on the seedlings. Despite the impact of the elephant bulls in control plot C, a net increase in shoot length was found.

DISCUSSION

Total exclusion plots A and B both showed the most shoot growth when compared to plots Aa, Bb and control plot C. This is noticeable on the y-axis of each graph (Figures 44 to 48). The variable shoot growth of each plot is also an indication of the impact that the browsers have had on the trees within the experimental plots. The trees in the total exclusion plots A and B had the fastest shoot growth as a result of being protected from browsing. It therefore appears that seedlings and young trees that are protected entirely from browsing, will have a better chance of establishing and growing into mature adult trees. Young trees and seedlings that are subjected to browsing pressure from an early age, will mature into adult trees, but at a slower rate than those that are protected from browsing. However, it is the level of browsing pressure exerted upon the young trees and seedlings and the amount of rainfall that is received, which will eventually dictate whether a seedling will survive and mature into an adult tree.

Trees in the elephant and giraffe exclusion plots Aa and Bb showed a moderate shoot growth, when compared with those in the total exclusion plots A and B. This growth pattern is the result of the browsing impact and pressure exerted by the impala, especially during the dry season. The trees on plot Aa indicate a slower shoot growth than plot Bb, which is a result of the greater impala impact in the area where plot Aa is situated. Lewa is presently overstocked with impala and these animals have a negative impact on the regeneration and recruitment of the *Acacia xanthophloea* seedlings and young trees. A game count in 1996 revealed that an estimated 600 impala were present on Lewa. It has been recommended that this population be reduced (Chapter 4). This reduction will have a positive effect on the regeneration and recruitment of the *Acacia xanthophloea* trees and seedlings. Browsers other than the impala that may also contribute to the defoliation of the *Acacia xanthophloea* seedlings and trees in plots Aa and Bb on Lewa are the eland, dikdik and domestic goats. It has also been recommended that the stocking rate of the eland on Lewa be reduced in an effort to reduce the competition between the various browsers and also to alleviate the browsing pressure on the vegetation of Lewa, especially in the riverine areas. It is also recommended that all domestic goats and cattle be kept away from the riverine areas, as these animals can have a negative impact on the *Acacia xanthophloea* seedlings by trampling and defoliation.

Although accessible to all the game in the area, control plot C showed a net increase in shoot length over the period of 11 months. During the dry season, the elephant bulls had a negative impact on the growth of the young trees and seedlings, from the beginning of December to March. Browsing pressure from the giraffe was not evident, although their contribution should not be ignored. The feeding methods of the giraffe can be destructive on the growth of young trees and seedlings. The destructive feeding tendencies of both the giraffe and impala have been widely documented (Dunham 1980; Pellew 1984; Cooper 1985; Du Toit 1988; Du Toit, Bryant & Frisby 1990). It is therefore recommended to reduce the numbers of elephant and giraffe on Lewa. This should encourage the regeneration and recruitment of the young trees and seedlings. The resident elephant bulls on Lewa spend most of their time feeding in the *Acacia xanthophloea* forests in the riverine habitats. Shade is an important elephant attractant and it is provided well by the *Acacia xanthophloea* trees on Lewa. A continuous water supply is also provided in the riverine habitats. Therefore the elephant bulls have little need to venture far from these habitats, other than during the musthe. During January 1997, 12 elephant bulls were removed from Lewa. This removal, together with the recommended reduction of impala and giraffe on Lewa, including the riverine areas, should encourage the recruitment and regeneration of the *Acacia xanthophloea* trees and seedlings.

It cannot be assumed that the browsing pressure on the *Acacia xanthophloea* trees and seedlings is solely exerted by the elephant, giraffe and impala. Nevertheless, there is evidence that the damage caused to the trees in control plot C, was from a number of elephant bulls. In the elephant and giraffe exclusion plots Aa and Bb, the effects of other resident animals such as the eland, greater kudu, dik-dik, Grant's gazelle and waterbuck, cannot be ignored. Domestic goats also frequent the riverine habitats and they will have a major impact on the seedlings. A study conducted in the Sudan by Obeid & Seif El Din (1970) already concluded that regeneration of *Acacia senegal* was negligible in areas frequently occupied by goats. They also found that a high density of *Acacia senegal* was maintained with complete protection from goat browsing, but allowing cattle grazing. The impact of browsing on *Acacia* seedlings by animals other than elephants and giraffes has been widely documented (Knapp 1977; Miller, Kinnaird & Cummins 1982; Belsky 1984; Prins & Van der Jeugd 1993).

In the present study, the seedling count performed in plot Aa revealed a lack of seedlings less than 150 mm in height. A few seedlings of less than 50 mm in height were, however, found which indicates that some germination and recruitment has occurred. The lack of seedlings less than 150 mm in height can be attributed to three factors: 1. It is possible that the majority of these seedlings were overlooked during the count, as a result of the occurrence of a dense undergrowth in March when the seedling count took place. 2. The selective feeding by the impala, eland and even the warthog, may account for the lack of seedlings. 3. The competition from the existing vegetation for survival may also be detrimental. The latter aspect is discussed in more detail in a subsequent section in this chapter.

In plots Aa, B and Bb there was an increase in shoot growth three weeks before the onset of the rainy season. This could possibly be because of the conspicuous late dry-season flush which is a peculiar feature of *Acacia* ecology. Milton (1987) observed a rapid extension of *Acacia karroo* shoots in the Nylsvley Nature Reserve, South Africa, approximately 6 weeks before the rains. Pellew (1983a) found that the leaf-flush of *Acacia tortilis* occurs before that of *Acacia senegal* and *Acacia hockii*. Examination of the *Acacia xanthophloea* flush on Lewa shows that both new shoots and leaves are produced by the trees. Pellew (1983a) found that only new leaves are produced and that shoot production is delayed until the first heavy rain. However, a flush of new shoots and leaves was not found in control plot C in the present study. The elephant activity in this plot at the time may be the reason why no flush was evident. The dry-season flush of the *Acacia xanthophloea* trees may therefore be a direct result of the unreliability of the rains on Lewa. The timing of the dry-season flush on Lewa coincides with the heaviest browsing pressures on the woody vegetation. If the rains were late, then this browsing may remove the regeneration and debilitate the tree or seedling. The need to reduce the stocking rate of browsers on Lewa, especially in the riverine habitats, is therefore essential. However, Pellew (1984) suggests that *Acacia* species have evolved a high tolerance to losses such as defoliation at a critical time of the year.

Factors that affect the regeneration and recruitment of *Acacia xanthophloea*

The following section deals with various factors that affect the regeneration and recruitment of seedlings and young trees. Some of the factors mentioned below may contribute more than other factors to the lack of regeneration and recruitment of the *Acacia xanthophloea* seedlings on Lewa. The extent and influence of a few of these factors on the regeneration and recruitment of the *Acacia xanthophloea* seedlings on Lewa fell beyond the scope of this study and may not be contributing factors at all, but are worthy of being mentioned.

Fire

Fire can have a positive and a negative effect on the regeneration and recruitment of seedlings. *Acacia* seeds have a hard testa which breaks open with the heat generated from a fire, allowing germination to occur. Seedlings that have been exposed to heavy browsing seldom survive the effects of a fire (Spinage & Guinness 1971; Lewis 1987; Belsky 1984).

Moisture and irradiance

Previous research indicates that seedling germination is dependent upon the frequency and intensity of rainfall, besides factors such as heat and light (Seif El Din & Obeid 1971a; Smith & Goodman 1986). O'Connor (1995) found that *Acacia karroo* seedling establishment is low in seasons with a rainfall of less than 500 mm. This may also be true for Lewa where *Acacia xanthophloea* seedling establishment only seems to occur in those seasons when the rainfall exceeds 500 mm. Smith & Goodman (1986) suggest that reductions in irradiance could limit seedling establishment. Moreover, O'Connor (1995) found that shading increased the density of surviving *Acacia karroo* seedlings. This beneficial effect of shade is attributed to improved soil moisture conditions. Seif El Din & Obeid (1971a) support the findings of O'Connor (1995).

Competition from established vegetation

Limited seedling regeneration and recruitment occurs under competition from established vegetation (Seif El Din & Obeid 1971a; Smith & Goodman 1986; Prins & Van der Jeugd 1993; Dangerfield, Perkins & Kaunda 1996). Douglas-Hamilton (1972) found that *Acacia* seeds do not germinate well under adult *Acacia* trees. Germination of *Acacia xanthophloea* seedlings is occurring on Lewa, but a general lack of seedlings and especially those between 50 and 150 mm in height, indicates that besides being browsed, the seedlings may be suffering from competition from established vegetation. Competition from weed species may be of particular importance. Darwin (1859) pointed out that the early seedling phases of a plant are usually the most at risk and that the seedlings suffer most when germinating in ground already thickly populated with other plants. Seif El Din & Obeid (1971b) also found that the mortality of *Acacia senegal* seedlings is highest when they are browsed when between 2 and 7 weeks old.

Large browsers

The density of large browsers has a significant effect on the regeneration and recruitment of *Acacia xanthophloea* seedlings. A significant positive change in the structure of the riverine vegetation on Lewa could ensue if the recommended stocking rate of large browsers is adhered to. A decrease in the stocking rate of these browsers will alleviate the pressure on the riverine vegetation and allow the establishment and regeneration of seedlings to take place. An increase in the number of *Acacia xanthophloea* seedlings will contribute largely to the structural changes within the riverine habitats on Lewa. Dangerfield *et al.* (1996) state that heavy browsing may prevent shrubs from reaching maturity and seed set, ultimately affecting recruitment. Moreover, compensation or allocation to protection by a plant in response to browsing might affect its competitive ability, and subsequent reproductive potential.

Other animals

Numerous other animal species that are often overlooked also affect the regeneration and recruitment of seedlings. For example, Miller (1995) found that rodents gnawing on seeds is beneficial to seed germination. On the other hand, rodents may also predate on the seeds of *Acacia* species. The possible role of rodents in the regeneration and recruitment of *Acacia xanthophloea* seedlings on Lewa has not yet been established. Other animals present in the riverine habitats on Lewa are monkeys, baboons, tree hyraxes, guineafowls and warthogs. It is possible that these animals also predate on the seeds of *Acacia xanthophloea* trees, thereby reducing the recruitment potential of the seedlings. Large herds of eland, impala and waterbuck, all capable of pulling out and trampling young seedlings, also often utilise the riverine habitats on Lewa. Bruchid beetle larvae consume seed contents, usually rendering seeds non-viable (Miller 1995). However, the passage of bruchid infested seeds through an ungulate gut decreases the effects of bruchid infestation, possibly by killing bruchid larvae within the seeds and selectively destroying those seeds which have been weakened by tunnelling larvae. The extent to which bruchid infestation of *Acacia xanthophloea* seeds occurs on Lewa, was beyond the scope of this study. Termites and ants are also known to bury the seeds of *Acacia* species. Miller (1994) conducted a study in the Nylsvley Nature Reserve in South Africa, and found that 97.5 % of *Acacia nilotica* seeds and 92.8 % of *Acacia tortilis* seeds were destroyed by burial by termites and ants. Decomposers may also soften buried seeds which are then mostly destroyed.

Continued overbrowsing

The effects of overbrowsing on the regeneration of vegetation are widely documented (Seif El Din & Obeid 1971b; Belsky 1984; Lewis 1987; Milton 1988; Prins & Van der Jeugd 1993; Dangerfield *et al.* 1996). Browsing, however, also has a stimulating effect on forage production (Crawley 1983; Pellew 1983a; Du Toit *et al.* 1990). On Lewa, the exclusion plots all showed a net increase in shoot length over an 11 - month period. This supports the results of Crawley (1983) and Pellew (1983a) who stated that browsing or pruning stimulates shoot production. However, the effects of overbrowsing in the exclusion plots on Lewa are clearly visible because the increase in shoot length was greatly reduced in control plot C which was accessible to all the browsers. It was also clear in plot Aa where there was often a concentration of impala. Overbrowsing in the *Acacia xanthophloea* forests on Lewa can therefore be attributed to the combined effect of the elephant, eland, giraffe and impala populations resident there, and occasionally also to the presence of domestic goats and cattle in the riverine habitats.

Management recommendations

Several recommendations can be made to improve the regeneration of the *Acacia xanthophloea* forests on Lewa:

1. Reduce the numbers of elephant, giraffe and impala in the overall area. The elephant and impala graze more often during the wet than the dry season. Therefore the browsing pressure on the *Acacia xanthophloea* trees and seedlings is not as heavy then as what it is during the dry season. Although the giraffe does not graze, it spends most of its time on the open plains and in the hills of Lewa during the wet season. Therefore, during the growing season the *Acacia xanthophloea* trees and seedlings will be given a chance to establish and regenerate before the onset of the browsing pressure in the dry season.

2. Detailed monitoring of the number of elephants that enter Lewa will assist in determining periods of high elephant density, pressure and impact on the riverine habitats. It is crucial to identify those elephant bulls that cause most of the destruction in the riverine habitats. Depending on the logistics and funding available, such elephant bulls will have to be removed far enough away from Lewa to stop then from returning later.

3. Increase the sample size of the trees within the monitoring plots and establish more monitoring plots. Furthermore, all the total exclusion plots should be protected from use by any browsing game. The mesh fence surrounding the total exclusion plots should be at least 2 m high, with two electric strands, one 0.3 m and another 1.5 m above the ground. These plots should also be monitored every month by the same person for a period of at least two years.

4. The existing elephant and giraffe exclusion fences that surround some of the riverine habitats on Lewa are of paramount importance in assisting the regeneration and recruitment of *Acacia xanthophloea* trees and seedlings. It is recommended that these fences be extended to include more of the riverine habitats on Lewa.

CONCLUSIONS

The monthly growth increment of the shoots of the *Acacia xanthophloea* trees and seedlings in the exclusion plots on Lewa all indicated an overall growth. The stem diameter and tree height measurements were not indicative of the browsing impact and pressure by the elephants, giraffes and impala on the regeneration and recruitment of the *Acacia xanthophloea* trees and seedlings.

The present browser stocking rate is the primary cause of the lack of regeneration and recruitment of *Acacia xanthophloea* seedlings in the riverine habitats on Lewa. A reduction in the present stocking rate of browsers is paramount if regeneration were to occur. Factors other than the high browser stocking rate are, however, also presumed to have an effect on the regeneration and recruitment of *Acacia xanthophloea* seedlings, but the extent and the influence of these factors were beyond the scope of this study.

The preservation of the riverine habitats on Lewa should be a conservation and management priority. It can only be achieved through the combined control of elephant densities and those of the other major browser species on Lewa. Continuation of monitoring of the impact that the browsers are having on the riverine vegetation is essential to establish a viable management plan that will benefit both the regeneration of the vegetation and the browsers on Lewa.

CHAPTER 8

WILDLIFE MANAGEMENT RECOMMENDATIONS

INTRODUCTION

Ecological studies form a vital part of any wildlife management programme. Thomson (1992) explains wildlife management in the light of two concepts; conservation and preservation. The objective of conservation management is the sustainable use of animals that are not listed as endangered or vulnerable by the International Union for the Conservation of Nature and Natural Resources (IUCN) for the benefit of man. This is the ultimate objective of managing all renewable natural resources. The objective of preservation, on the other hand, is to protect those animal species that are listed as endangered or vulnerable. When this objective has been achieved, the animal population must then be placed under conservation management. In this sense, preservation management is the antithesis of conservation management.

Both conservation and preservation management form part of Lewa's present management programme. Preservation management is applied to the black and white rhinoceros and to Grevy's zebra on Lewa. The need to protect these species so as to ensure their population increase, is one of the primary aims of Lewa. The status of these animal populations can change, for the better, over time, if appropriate preservation management strategies are successfully applied. Conservation management is essentially being applied to all the other animal species on Lewa. The controlled sustainable utilisation of wildlife can have a high recreational and educational value, and may be utilised in conjunction with consumptive methods (Garaï 1998). The use of any wildlife resource on Lewa, however, should be based on the results of detailed studies such as the present one and that of Botha (1999). When combined with continuous future monitoring, the results of such ecological studies will determine the extent of the allowable use of the wildlife resources on Lewa.

Sustainable utilisation of wildlife can be consumptive or non-consumptive (Thomson 1992). Both forms of sustainable utilisation form part of Lewa's present management programme. Translocation and culling of certain animal species are the two forms of consumptive sustainable utilisation that occur currently on Lewa, as does eco-tourism as a form of non-consumptive sustainable utilisation. Hunting and live animal sales are other forms of consumptive sustainable utilisation, but because of the current government legislation, they cannot form part of any management programme on a reserve or national park in Kenya. Hunting, according to Thomson (1992), is the most financially beneficial and cost-effective form of wildlife use, when compared with other forms of consumptive-use. Live animal sales usually provide the next most profit. On Lewa, the latter form of consumptive sustainable utilisation has been partly achieved by swopping animals with other wildlife areas in Kenya, although financial benefits are limited in the short term. According to Thomson (1992), the sale of game products from culled animals is the least gainful of the three utilisation options. It is, nevertheless, reasonably profitable, provided that there is a market for the commodities produced. The sale of meat from culled animals on Lewa occurs locally, within the boundaries of Kenya. At the time of this study, a market for the sale of skins from culled animals on Lewa was being investigated. Lewa benefits from a substantial annual income from eco-tourism as a form of non-consumptive sustainable utilisation. However, non-consumptive sustainable utilisation does not preclude the need for some form of consumptive sustainable utilisation. The former is therefore an additional form of use and not an alternative one.

According to Mentis & Collinson (1979) management is futile if unambiguous goals are not defined. Ultimately, the goals of Lewa are to provide protection for the black and white rhinoceros and the Grevy's zebra. This is aimed at maintaining a steady increase in the growth rates of these animal populations. The maintenance of animal and plant species diversity, in conjunction with the protection of the available natural resources, particularly the vegetation, are other important goals on Lewa.

Lewa currently gains much of its annual revenue from tourism. The aesthetic value of large herbivores such as the elephant and giraffe is important from the tourism point of view. The scenery, including the extensive *Acacia xanthophloea* forests on Lewa, is equally important from the point of view of attracting tourists. A delicate balance exists in managing for both an abundance of large herbivores and maintaining the density and scenic beauty of the vegetation. Results from the present study indicate an immediate need to reduce the numbers of the main browsers on Lewa. These are the elephant, giraffe, eland and impala. The extent of the browsing pressure and damage to the vegetation, exerted by these browsers is clearly evident in the deteriorating and declining state of all the woody vegetation on Lewa but especially so in the *Acacia xanthophloea* forests. Lewa is not wholly fenced off and most of the wildlife can migrate out of, or onto the area. However, because Lewa affords ample protection, food, water and shelter to the resident wildlife, its habitats attract wildlife to the area and limit movement out of it. The potential for an overabundance of wildlife on Lewa is therefore real. The calculation of a realistic browsing capacity and stocking rates for the browsers on Lewa is therefore paramount. The maintenance of balanced stocking rates for the various browsers will ensure the survival, regeneration and recruitment of the vegetation, particularly the *Acacia xanthophloea* forests. It will also limit possible competition for resources between the browsers, especially during the dry season. Ultimately, the primary goals of Lewa will only be achieved if the recommended stocking rates are applied and continuous monitoring is done.

The purpose of this section is to present some broad management recommendations for Lewa, with specific guidelines for the management of the browsers. These recommendations are based on the results of the present study, but they should also be considered in conjunction with the recommendations proposed by Botha (1999) because all recommendations on stocking rates, habitat manipulation and general management considerations should be made from a balanced holistic perspective.

MONITORING

Monitoring should be considered as the most important facet of any wildlife management programme. Therefore, it should be a standard procedure on any wildlife area. Through effective monitoring, data are gathered for use in decision making. Monitoring also allows for certain predictions that facilitate adaptive wildlife management. Long-term monitoring is the only way in which a wildlife manager can obtain a basis for measuring changes that take place on his area over time. The changes measured can be evaluated against a broad ecological database and the area's long-term objectives to indicate whether the management strategy needs to be altered. Future monitoring on Lewa should be based on the results obtained and the recommendations made in the present study. A situation where the research staff on Lewa undertake, analyse and interpret their own monitoring should be strived for. The various types of monitoring, which should form the basis of the management programme for Lewa, are discussed next, followed by recommendations for proper wildlife management on Lewa. The use of the plant species checklist (Appendix A) should furthermore assist in the identification of the important plant species in the relevant surveys that are suggested for Lewa.

Environmental monitoring

- Rainfall is the most basic aspect to be monitored. It is also the most important aspect to monitor, and this can be done accurately with inexpensive equipment. There are currently 10 rain gauges placed at strategic points on Lewa, for the monitoring of daily, monthly and annual rainfall. Rainfall data are useful for the estimation of the ecological capacity of a natural area (Coe, Cumming & Phillipson 1976). Annual rainfall trends are nevertheless a useful indication of the production potential of the vegetation. There is no need to increase the number of rain gauges on Lewa at present. It is, however, important that the rain gauges are accurately read and that the rainfall figures are reported on a regular basis to the wildlife manager on Lewa.
- The temperature on Lewa can be measured with a simple and inexpensive thermometer, and is an important data set over the long term. It is not paramount to monitor the temperature at various locations on Lewa; a single station should suffice. At present there is a thermometer at the office complex on Lewa. Minimum and maximum temperatures should ideally be measured on a daily basis during the week, at 07:00, 13:00 and 16:00, at a standard height and in the shade.
- The relative humidity of the air is another environmental parameter that generally contributes to environmental monitoring. Relative humidity and air temperature have a major effect on fire intensity. If thresholds to these two factors are considered, the negative impact of fire on the woody vegetation can be minimised. Relative humidity can be measured with electronic equipment such as hygrometers or wet and dry bulb thermometers. Wet and dry bulb thermometers are extremely accurate, but the formulae used to calculate the relative humidity are complicated and not user-friendly. A hygrometer is therefore recommended to measure relative humidity on Lewa.

Habitat monitoring

- Aerial photography : This is an easy and effective way of evaluating the overall impact of animals on the vegetation, especially the woody component. The photographs must be taken from the same altitude, at the same time of the year, under similar weather conditions (cloudless days), and with the same type of film and lens. Aerial photography on Lewa should be done in the middle of the rainy season, as this will give an indication of canopy cover or loss thereof. Aerial photographs need to be taken at a maximum of five-year intervals, but the more frequently the better.
- Fixed point photography : Although this is a subjective way of evaluation, it gives a good indication of trends in the woody vegetation density of an area. Fixed point photographs on Lewa are taken annually at permanent monitoring sites. The importance of this type of habitat monitoring on Lewa cannot be stressed enough. Valuable information on trends in the woody vegetation growth has been gleaned from these photographs. This is important as far as the management of the habitat for black rhinoceros is concerned, and the current system should be continued.
- Permanent vegetation monitoring plots : Botha (1999) identified 25 permanent vegetation monitoring plots that cover all the plant communities on Lewa. These plots are essentially a most important monitoring tool and yield the best quality data, but they require commitment and continuous monitoring. The species composition and standing biomass of the herbaceous vegetation, and the available leaf biomass of the woody vegetation should be surveyed annually at each permanent vegetation monitoring plot. An easy and effective way of surveying the species composition of the vegetation is to record all the plant species present in each monitoring plot. Each plot should be 20 X 20 m in size. A comparison with the records taken from other plots and previous surveys therefore allows the wildlife manager to detect any changes in the species composition of the vegetation. The standing biomass of the vegetation must also be surveyed with the use of a disc pasture meter (Bransby and Tainton 1977). An estimate of the available combustible grass biomass to support a fire, is therefore possible. It is recommended that 100 disc pasture meter readings per monitoring plot is adequate for estimating the standing biomass of the herbaceous vegetation on Lewa. Botha (1999) has described this survey method for Lewa in more detail. The woody vegetation on Lewa can be surveyed using the BECVOL method described in Chapter 3.
- Exclusion plots : These are an essential part of habitat monitoring on Lewa. Exclusion plots have been constructed in the riverine habitats on Lewa to measure the impact of browsing, or lack thereof, on the regeneration and recruitment of *Acacia xanthophloea* seedlings. It is recommended that 15 more exclusion plots be established in the riverine habitats on Lewa. This would give a total of 20 exclusion plots on Lewa, including the existing ones. The sample size of the trees within the exclusion plots should also be increased to 20 trees or seedlings per plot. Furthermore, all the total exclusion plots should be protected from use by any browsing game. The mesh fence surrounding the total exclusion plots should be at least 2 m high, with two electric

strands, one 0.3 m and another 1.5 m above the ground. The exclusion plots should also be monitored once a month by the same person for a period of at least two years. The existing elephant and giraffe exclusion fences that surround some of the riverine habitats on Lewa should be extended to include more of the riverine habitats.

Monitoring of game numbers

The determination of animal population trends together with the monitoring of their habitats, is a vital part of any wildlife management programme. Although it is important for a wildlife manager to know the numerical strength of any animal population which he intends to manipulate, it is a meaningless statistic unless he can relate this figure to the population trend (Thomson 1992). The monitoring of game numbers on Lewa is vital to the successful management of the ranch in terms of correct stocking rates. In addition to the fluctuation of game numbers because of culling, translocation and reproduction, the effects of migrating game should also be taken into consideration.

Game counts on Lewa should be conducted on a regular basis. Botha (1999) has recommended that two game counts be conducted in each of the seasons. The type of game count employed on Lewa should be repeatable. In other words, it should give the same estimate for the same number of game each time it is done. On Lewa, however, it is more important to consider the health of the habitat, than to determine the exact number of game that should be removed from the area each year. A useful method of estimating the numbers of migrating game on Lewa, is to monitor the gap in the northern boundary fence on a daily basis. Experienced game scouts may also be able to determine the number of migrating game by counting the tracks near the gap in the fence. A combination of sample drive counts, known group counts and aerial counts have been conducted on Lewa in the past. During the study period, road strip counts were also conducted during the determination of habitat preferences of the elephant, giraffe and black rhinoceros populations.

The current game counting techniques employed on Lewa should be maintained. The game counts should be done at the same time of the year. Preferably two counts should be done in the wet season (April and November) and two in the dry season (January and August). The sample drive counts should be done between 6:00 and 10:00 or between 15:00 and 18:00, although morning counts are better, as the animals are more active at this time of the day and the counters are also fresh. When performing the sample drive counts, the entire area should be counted in one day. Botha (1999) recommended that the area to be counted should be divided into sectors of 10 km² in the open woodland habitats and 6 km² in the thickets. Teams of at least two people should be assigned to each sector. The aerial counts done on Lewa should serve as a control and should be done at 3-year intervals. Two aerial counts should be done on Lewa; one in each of the two seasons. Bothma (1996) recommends that aerial counts should be done between 7:30 and 10:30 and again between 15:00 and 17:30. Morning counts are preferable to afternoon counts, because the morning light is optimal for game counts, the animals are more active in the morning and because the observers are still fresh and rested. The aerial counts should preferably be done just before the sample drive counts are done to back up the results of the drive count. Road strip counts can be done easily on Lewa and do not require a lot of manpower. The existing eight road transects can be used in the future and they cover all of the habitat types on Lewa. A maximum of four people is needed to do a road transect count. They include a driver, a data recorder and two observers. The road strip counts should be done in the mornings from 7:00 to 10:00 and again in the afternoons from 15:00 to 18:00. The results of the road strip counts also broadly indicate the habitat preferences of game. Road strip counts are regarded as adequate to calculate a safe estimate of the minimum population of game in an area (Bothma 1996). In conjunction with conducting the game counts, age and sex classification of wildlife should also be done. This will assist in determining population trends. To reduce the growth rate of an animal population, the removal of the most productive females and often the mature males is an option. However, this must be done in balance with existing social behavioural parameters. In conclusion, the extent of animal population and habitat monitoring input performed on Lewa, and the quality of the ecological analysis, will determine the extent to which their animal population management objectives will be optimised.

Monitoring of game movements

It is important to monitor those areas on Lewa which the various animals prefer and utilise most. The animals that move the furthest distance on and off Lewa are the elephants. A number of elephant cows, presumably the matriarch in each herd, have been radio-collared and the herds' movements are regularly monitored by the wildlife managers on Lewa. The 12 elephant bulls that were captured and removed from Lewa in the beginning of 1997 were also radio-collared and their movements are also being monitored. Elephants move over large distances and the possibility that some of these translocated bulls could return to Lewa should not be ignored. The present method of monitoring the elephant movements on and off Lewa should be maintained.

The black rhinoceros population is confined within the boundaries of Lewa. The movements of these animals within Lewa should be monitored so as to get a reliable estimate of the range size of each animal, and to get an idea of the various habitats selected and utilised by these browsers. Monitoring black rhinoceros movements on Lewa is not a difficult task because each individual's location is already being reported on a daily basis. With the aid of a mapping system, the range size of the individual black rhinoceroses on Lewa can be determined. Alternatively, a computer programme can also be used to determine the range size of these animals. Lewa is in possession of such a programme and important and accurate information can be gleaned if it is used efficiently.

Seasonal game movements, especially by large herbivores such as the elephant and giraffe, can have a considerable impact on the vegetation of Lewa. Knowledge of the seasonal movements of these animals will be beneficial when calculating stocking rates for Lewa. During the dry season the elephants migrate onto Lewa. Therefore the stocking rates of the other browsers on Lewa should be kept in check. During the wet season, on the other hand, when food resources are abundant and large herds of elephant migrate off Lewa, browser stocking rates can be allowed to increase. A sound knowledge of the movements of animals on Lewa is an essential facet of the management of its wildlife.

Genetics

The black rhinoceros population on Lewa is part of a highly fragmented black rhinoceros population in East Africa. Besides Lewa, a number of black rhinoceros sanctuaries exist in Kenya, not to mention those elsewhere in Africa. Climatic, environmental and catastrophic events, as well as a narrow genetic base alone or in combination, may increase the chances of these small populations dying out (Garaï 1998). The black rhinoceros population on Lewa should therefore be seen as part of a larger meta-population. A number of methods exist to increase the genetic viability of an animal population. These include acquiring new males or females, swopping males and females with other sanctuaries, and artificial insemination. These methods are discussed below with specific reference to the black rhinoceros population present on Lewa.

Supplementation and exchange of black rhinoceros bulls between the isolated populations in Kenya would be the ideal way of increasing the viability of all these populations. Some scientists believe that interbreeding between small, isolated animal populations is not advantageous, as it potentially weakens each subpopulation's selective adaptation to its local environment. This is a valuable aspect to consider for certain animal populations. It is believed, however, that the situation already exists on Lewa that supplementation of the genetic pool with black rhinoceroses attained from other sanctuaries will establish a broader genetic foundation for the species and therefore strengthen its chances of survival. The introduction of black rhinoceros bulls from other sanctuaries should, however, be carefully researched so as to determine how genetically different the new bull actually is from the existing population on Lewa. Detailed, careful research and planning should precede the introduction of any new genetic material onto Lewa, as translocations are time-consuming, expensive operations and also place stress on the animals involved.

Another factor to consider when introducing black rhinoceros bulls to an area, is the aspect of social behaviour. New bulls may fight with the resident bulls. Lewa has already lost a number of black rhinoceros cows due to fighting with bulls. Subsequently the culprit bulls have been removed from Lewa. Numerous cases are known from elsewhere in Africa where rhinoceros bulls have been introduced into an area, and have suffered the penalty of death as a result of fights with resident bulls. In this case, the artificial insemination of black rhinoceros cows may be the wiser option. However, the expenses involved in capturing, sedating and inseminating the animal are exorbitant, and the chances of the animal falling pregnant may not be 100 percent.

Another option to increase the genetic diversity of Lewa's black rhinoceros population without risking the potential loss from fighting, is to introduce more females onto the area. Females will not challenge the male hierarchy, they do not need breeding territories and they will not fight other females to secure a range of their own (Thomson 1992). An increase in the number of females in any animal population will necessarily increase that population's breeding rate (Bothma 1996). Because one of the primary objectives of Lewa is to increase the growth rate of both the black and white rhinoceros populations, the feasibility of this method to increase both the genetic viability and the growth rate of the rhinoceros populations seems obvious.

BROWSE AVAILABILITY

An estimate of the available browse biomass is important when determining the browsing capacity of an area, which in turn determines the stocking rate of the area. The available browse biomass on Lewa was determined for each of the major plant communities. Based on the similarities in soil composition, topography and vegetation, these plant communities were grouped into four basic management units, each with similar management requirements. The available browse in each of these units and its implications in browser management are as follows:

- *Forest Management Unit* : The available browse biomass is 748 805.6 kg. This is the highest biomass of all the management units. This management unit plays a vital role in sustaining browsers such as the elephant, eland and black rhinoceros, especially during the dry season. A number of black rhinoceros bulls have established territories within this management unit. The forest verges, especially, are an important feeding ground for these animals. When the black rhinoceros population on Lewa increases, a heavier utilisation of this management unit will be the result. Unfortunately the large giraffe population on Lewa can only utilise a part of this unit because the forest is topographically inaccessible to the giraffe. The browsing pressure which is therefore exerted on the other parts of this management unit is excessive. This has already led to the death of a large number of *Acacia drepanolobium* trees.
- *Plains Management Unit* : The available browse biomass is 317 128.9 kg. The nature of the solonetz soils that are characteristic of this management unit make them prone to erosion. It has therefore been recommended that they should be rested for rehabilitation (Botha 1999). This management unit forms an extensive part of Lewa and it is heavily utilised by herbivores during the wet season. Species- and area-selective grazing is the result. Botha (1999) recommended that a controlled burning programme be implemented so as to increase the palatability of some of the grass species during the dry season. Another reason for the burning programme is to prevent the animals from overutilising the sensitive hills. The implementation of this burning programme has already shown positive results on Lewa. A visible lack of seedlings in this management unit, however, still indicates overutilisation by the browsers. The only effective way to reduce the over-utilisation of this habitat is to reduce the number of browsers that utilise it.

- *Hills and Rocky Outcrops Management Unit* : The available browse biomass is 722 994.5 kg. The results attained in this study (Chapter 5) indicate that this management unit is important for herbivores in the dry season, but especially so for the black rhinoceros and elephant. Over-utilisation in many parts of this management unit indicates the need to reduce the browsing and grazing pressure there. This can be done in two ways. The burning programme implemented on the Plains Management Unit already plays an important role in attracting animals away from the Hills and Rocky Outcrops Management Unit. Since the implementation of the burning programme, a noticeable regeneration of large bare patches on the hillsides is evident. Moreover, the removal of browsers and selective grazers will further reduce the browsing and grazing pressure and the area-selective feeding that is evident there.
- *Rivers Management Unit* : The available browse biomass is 19 344 kg. It might be expected of the riverine vegetation to yield a higher biomass, but most of the browse there occurs above 5 m in height. It is therefore not available to the browsers. The excessive overutilisation of the vegetation in this management unit is reflected in the lack of seedlings and juvenile *Acacias*. No regeneration of *Acacia xanthophloea* seedlings is presently occurring, and this can be attributed to the large number of browsers and grazers present there. These herbivores utilise this management unit in both the wet and dry seasons. Management actions to try and prevent the overutilisation of this management unit have already been taken. Parts of the riverine habitat have been fenced off to prevent access to the elephant and giraffe. This has proved to be successful, but to have a greater effect, larger areas should be fenced off. Such a fence will also prevent elephant bulls from pushing over mature *Acacia xanthophloea* trees.

BROWSING CAPACITY AND STOCKING RATE

The current total browsing capacity of Lewa is 0.11 BU/ha (2 732.36 BU). Using the BECVOL method to estimate the available browse biomass, the woody vegetation of Lewa was estimated to be able to support 1 180.93 BU of browsing game This equates to a browsing capacity of 0.05 BU/ha. This implies that the current number of browsing game on Lewa must be reduced by 57 % to bring it into balance with the existing browse resource. This seemingly excessive reduction is necessary if the degradation of the woody vegetation of Lewa were to be stopped, and it were allowed to recover and regenerate. A proposed massive reduction in the numbers of the eland, impala and giraffe is suggested to compensate for the movement of elephants onto Lewa during the dry season. The official ban on the hunting or culling of elephants in Kenya places a restriction on the numbers of other browsers that can be accommodated on Lewa. Recommendations on the stocking rate of individual browsers are given in Chapter 4. These briefly include the following: 66 eland, 60 elephant, 50 gerenuk, 100 reticulated giraffe, 30 greater kudu, 200 impala and 25 black rhinoceros. Together with the recommendations on adjusting the stocking rate of grazers on Lewa (Botha 1999), a conservative but sustainable ecological capacity should be possible. The browsing capacity is not a fixed value, but fluctuates as a result of certain environmental factors which include rainfall, the phenology of the vegetation, animal movements and the incidence of fire. Rainfall is the most important factor, however, because a reduction in rainfall will reduce the capacity of the woody vegetation to support browsers. In turn this will necessitate an increased animal harvest to reduce the browsing pressure on the woody vegetation. Conversely, years of good rainfall will result in increased woody vegetation growth and a corresponding increase in the browsing capacity. It is therefore essential to conduct the necessary monitoring surveys annually, so that the stocking and harvesting rates can be adjusted correspondingly and timeously.

HABITAT MANIPULATION

It is clear that some form of ecological separation occurs between the elephant, giraffe and black rhinoceros on Lewa. Moreover, the current woody vegetation decline has now led to the increased potential for competition for food resources among the browsers. Bearing in mind that one of the primary objectives of Lewa is to maximise black rhinoceros population growth, such competition should at best be eliminated. This can be done by maintaining conservative stocking rates, by habitat manipulation, or by both. It is suggested that both these factors should be considered in tandem on Lewa. There is also a broad management need to expand the browsing habitats on Lewa where this is ecologically and economically viable. Habitat conversions are, however, expensive and time-consuming. The same is true for erosion control projects on Lewa. Sound habitat management should therefore in the future plan for and preclude the need for more erosion control work.

The following specific steps are recommended here to assist in the manipulation of certain habitats on Lewa so as to increase the browsing capacity of the area and to reduce the potential for competition between the browsers:

- The most immediate and important action is the control of total browser stocking rates. It is important to note that elephants may play an important role in maintaining the structure of the woody vegetation at an available height for other herbivores like the black rhinoceros. The feeding methods of elephants often allow trees and bushes to coppice, therefore providing food at heights that are within reach of the smaller browsers. At the stocking rate recommended here for elephants, these animals will therefore be beneficial to the black rhinoceros in terms of their feeding ecology. The implications of overstocking have already been discussed with respect to the present situation on Lewa, and specific recommendations have been given.
- Fire can be used as a habitat manipulation tool. The implementation of fire on Lewa has been discussed elsewhere, where the positive effects of such a programme have also been outlined.
- The control of herbivore access to areas under habitat improvement projects is a prerequisite for the ultimate success of such projects (Weaver 1995). Habitat improvements rapidly lose their value if herbivores utilise the emergent, succulent vegetation produced too soon (Trollope 1990).

Access control can be accomplished by deliberate culling of local populations, by control of water-points, or by fencing off areas with mobile electric fences (Weaver 1995). A number of scattered water troughs occur on Lewa, mainly for the use of cattle. It is, however, not recommended that these be closed down, as this could cause the wildlife to concentrate in the already overutilised riverine habitats.

- The use of electric fences to control the access of elephants and giraffes to the riverine habitats has already had a beneficial effect. However, a greater beneficial effect will be achieved by expanding the size of the areas that are fenced off electrically. The manipulation of the riverine habitats on Lewa to increase the number of young and regenerating *Acacia* seedlings will be important for increasing the browsing capacity of these areas, especially during the dry season.
- The erection of exclusion plots in the riverine habitats will be important in aiding the regeneration of the *Acacia xanthophloea* seedlings. Besides preventing access to the elephant and giraffe, other browsers such as the eland and impala should also be prevented from having continual access to the riverine habitats. Electrically fenced exclusion plots that are placed strategically throughout Lewa should also have a beneficial effect on the conservation of the riverine vegetation. Once a noticeable regeneration in the woody vegetation has been achieved, the exclusion plots should be moved to other areas in the riverine habitats.
- There is a real need to rehabilitate the large bare patches of ground which are found on Lewa. Botha (1999) has discussed the control of erosion on Lewa in detail, and it will not be dealt with again here.
- The monitoring of all habitat improvement or conversion projects must form an integral part of these projects. The monitoring surveys that should be employed on Lewa have been discussed above.
- The enlargement of the property could be another way of managing the present habitats on Lewa. This can be done by either acquiring adjacent land or by forming conservancies with neighbouring game areas. Lewa in itself already exists as a conservancy. However, the possibility exists that the inclusion of neighbouring land on the western boundary, and perhaps also on the northern boundary, will benefit the black rhinoceros population. The habitat on the western boundary comprises hillside thicket, which is favoured black rhinoceros habitat. This habitat could also play an important role in increasing the browsing capacity of the area for elephants. A knowledge of the vegetation composition of these areas as a basis for the calculation of its browsing capacity will be beneficial if the opportunity should arise to remove the fences between Lewa and these areas.
- Finally, there exists a possibility to re-establish a migration route for the elephants through Lewa, on its southern boundary, to the forests on Mount Kenya. This would be a major alternative to the culling and translocation of much of the game on Lewa, especially the elephants. This option should be explored in detail.

FUTURE RESEARCH PERSPECTIVES

The following section deals with future research needs relevant to the present study. Brief suggestions for future areas of research are given below:

- Lewa is primarily a rhinoceros sanctuary, where one of its primary aims is to conserve both the black and the white rhinoceros species. The vegetation of Lewa cannot be described as prime black rhinoceros habitat because of the existence of vast open plains and also the lack of dense thicket vegetation. Therefore the suitability of neighbouring wildlife areas should be explored as a further alternative to increase the browsing capacity of the entire area for the black rhinoceros. This should be seen as a step towards the creation of a biosphere reserve through the amalgamation of Lewa with adjacent wildlife areas. The Mount Kenya National Park has been declared an International Biosphere Reserve by UNESCO, and the inclusion of Lewa and its neighbouring wildlife areas should be the focus of future research in the area.
- The lack of *Acacia xanthophloea* seedlings and the decline of the mature *Acacia xanthophloea* forests are of major concern to the wildlife managers on Lewa. The results of the present study indicate that the erection of exclusion plots in the riverine habitats on Lewa will play an important role in assisting the regeneration of the *Acacia xanthophloea* seedlings and hence increase the browsing capacity of the riverine habitats. The establishment of a seedling bank should be considered, where a nursery is formed and *Acacia xanthophloea* seeds are germinated and then planted in specially protected exclusion plots. The young trees should then be protected from any browsing until they are approximately 1 m in height. This recommendation warrants further research.
- Browsers that are present on Lewa in low numbers are the gerenuk and the lesser kudu *Tragelaphus imberbis*. Future research into the habitat requirements of these browsers should be conducted so as to attract them onto Lewa. One of Lewa's primary sources of income is from tourism. Therefore a greater diversity of animals should benefit the tourism. Lesser kudu are shy animals and are associated with thickets. Therefore habitat manipulation by planting *Acacia*'s will also benefit this species.

ECOLOGICAL SEPARATION BY BROWSERS ON THE LEWA WILDLIFE CONSERVANCY, KENYA

by

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SUMMARY

This study was conducted on the Lewa Wildlife Conservancy in the northern foothills of Mount Kenya. The conservancy covers an area of approximately 24 600 ha, and is located on an altitudinal gradient varying from 1 450 to 2 300 m above sea level. The vegetation of the area is transitional between a semi-arid highland and an arid lowland, and can be physiognomically described as wooded grassland.

The woody vegetation was surveyed by using the BECVOL method to assess and predict the productivity of the available browse. The BECVOL method quantitatively describes woody plant communities based upon the relationship between the spatial volume of a tree and it's true leaf mass. Estimates of canopy volume and dry leaf mass were used to estimate the browsing capacity of the woody vegetation. The current stocking rate of browsers on Lewa is 2 732.36 browser units (BU). The recommended stocking rate of browsers is 1 180.93 BU or 799.54 large stock units (LSU) and is based on the browsing capacity estimated with the BECVOL technique for assessing the condition of woody vegetation. Lewa is at present heavily overstocked with browsers such as the eland, impala, elephant and giraffe. Recommendations on balanced stocking rates of these browsers are given.

The dynamics of herbivore-habitat relationships were investigated, with the emphasis on the ecological separation of some of the major browsers. The target browsers studied were the black

rhinoceros, elephant and reticulated giraffe. Habitat selection by the major browsers was recorded in identified habitats to ascertain preferences and selection for various environmental parameters that may contribute to the ecological separation of these browsers. Road transects were used to quantify animal numbers. The habitat selection data were subjected to the unique, but time-consuming CATMOD procedure. Detailed analysis of the data was performed, and reliable, meaningful results were obtained. Ecological separation between the browsers was found in their seasonal choice of different habitats, although exceptions occurred in the *Acacia drepanolobium* – *Acacia seyal* woodland and in the mixed woodland hills. The highest degree of ecological separation between the elephant, black rhinoceros and giraffe occurred during the dry season. Preference for different habitat types, seasonal variations in these preferences, and the selection for specific environmental parameters contributed to the ecological separation of these browsers on Lewa. However, the current overstocking of Lewa clearly has a potential for increased competition between all the browsers. A reduction in the present stocking rate of all the browsers on Lewa, with the exception of the black rhinoceros, gerenuk and greater kudu, is therefore recommended.

The seasonal feeding ecology of the black rhinoceros, elephant and giraffe on Lewa was studied, with specific reference to plant species selection, plant part selection, browsing height and other factors which might influence food plant selection. Specific individual browsers were selected and tracked in order to observe their feeding habits. Qualitative vegetation and habitat data were collected to determine the various elements indicative of plant species and plant part selection. The feeding ecology data were also subjected to the CATMOD procedure. There was much overlap in terms of food plants used, plant parts selected for and other factors that influence the feeding ecology of these browsers on Lewa. It was consequently concluded that the ecological separation of these browsers is only partly achieved through food plant selection. Seasonal variations in the browsing height had the effect of reducing overlap in browse use between the various browsers. Apart from the general competition for food plants, facilitation of food by one species for another was also evident. Seasonal movement by the elephants out of Lewa in particular, alleviated competition for food plants between the browsers to a certain degree in the wet season. Although there is some ecological separation between the black rhinoceros, elephant and giraffe on Lewa, the large numbers of elephant and giraffe present create an excessive demand for browsable food resources, especially during the dry season. The continued survival of browsers on Lewa, but particularly of the black rhinoceros, depends primarily on the restoration and maintenance of a healthy woody vegetation component on Lewa.

A noticeable reduction in *Acacia xanthophloea* seedling regeneration and recruitment led to an investigation to determine the impact that browsing by the elephant, giraffe and impala populations on Lewa has on the regeneration of *Acacia xanthophloea* seedlings, specifically in the riverine habitats. Exclusion plots were established and subjected to varying degrees of protection from the browser species concerned. The rate of browse production of identified, tagged shoots of *Acacia xanthophloea* seedlings was determined on a monthly basis. It was found that the monthly growth increment of the shoots in the exclusion plots indicated overall growth. The stem diameter and tree height measurements were not considered to be indicative of the browsing impact and pressure by the elephant, giraffe and impala on the regeneration and recruitment of *Acacia xanthophloea* seedlings. The primary cause for the lack of regeneration and recruitment of *Acacia xanthophloea* seedlings was the present excessive browser stocking rate on Lewa. A reduction in the stocking rate is paramount if regeneration were to occur. Factors other than the high browser stocking rate were also presumed to have an effect on the regeneration and recruitment of *Acacia xanthophloea* seedlings. It is recommended that monitoring of the seedling regeneration and shoot production of the above trees in the exclusion plots be continued to establish a data bank on which a viable management plan that will benefit both the regeneration of the vegetation and the browsers on Lewa can be based.

Recommendations on the importance and necessity for monitoring the fauna, flora and climate on the Lewa Wildlife Conservancy were made. This was recommended to provide the scientific basis for applying adaptive management based on data obtained from the monitoring program.

EKOLOGIESE SKEIDING VAN DIE BLAARVRETERS OP DIE LEWA BEWAREA, KENIA

deur

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OPSOMMING

Hierdie studie is uitgevoer op die Lewa Bewarea van ongeveer 24 600 ha aan die voetheuwels van Mount Kenya. Die bewarea is tussen 1 450 en 2 300 m bo seespieël geleë in 'n oorgangsone tussen die halfdorre hooglande en die dorre laaglande van Kenia. Die plantegroei van die gebied kan fisionomies as houtagtige grasveld beskryf word.

Die houtagtige plantegroei is met behulp van die BECVOL - metode gekwantifiseer om die produktiwiteit van die beskikbare houtagtige materiaal te bepaal. Volgens hierdie metode word die verhouding tussen die houtagtige plante se ruimtelike kroonverspreiding en die ware blaarmassa gebruik om die houtagtige plantgemeenskappe kwantitatief te beskryf. Die blaarvreterkapasiteit van die houtagtige plantgemeenskappe is ook bepaal met behulp van dieselfde tegniek. Die huidige veebelading van blaarvreters op Lewa is 2 732.36 blaarvreeteenhede (BE). Die aanbevole veebelading van blaarvreters is egter 1 180.93 BE of 799.54 grootvee-eendhede (GVE). Die gesamentlike effek van blaarvreters soos die eland, rooibok, olifant en kameelperd veroorsaak dat Lewa se blaarvreterkapasiteit tans oorskry word.

Die dinamiese verhouding tussen herbivore en hulle habitat is ondersoek met spesiale verwysing na die ekologiese skeiding van die groter blaarvreters soos die swartrenoster, olifant en kameelperd. Die

habitatbenutting van die groter blaarvreters is bestudeer in 'n poging om voorkeurgebiede te identifiseer wat kan dui op die ekologiese skeiding van die blaarvreters. Verskeie omgewingsfaktore wat habitatbenutting kon beïnvloed is terselfdertyd bestudeer. Die habitatbenuttingsdata is ontleed met behulp van die CATMOD - prosedure. Ekologiese skeiding van die blaarvreters is gevind op 'n seisoenale basis, met uitsonderings in die *Acacia drepanolobium – Acacia seyal* savanna en die gemengde savannas op die heuwels. Die ekologiese skeiding van die olifant, swartrenoster en kameelperd is veral opvallend tydens die droë seisoen. Hierdie ekologiese skeiding is aangehelp deur verskillende voorkeurhabitatte, seisoenale verandering in die voorkeurhabitatte en die heersende omgewingstoestande. Die huidige oorbelading van Lewa in terme van blaarvreters kan moontlik lei tot 'n toename in kompetisie tussen die blaarvreters in die gebied. Gevolglik word daar aanbeveel dat die aantal blaarvreters op Lewa verminder word, met die uitsondering van die swartrenosters, gerenuks en koedoes.

Die voedingsekologie van die swartrenoster, olifant en kameelperd is bestudeer, met spesifieke verwysing na die plantspesie benutting. Daar is onder meer ook gekyk na die plantdele wat benut word, en die hoogte waarop die verskillende blaarvreters gevoed het. Hierdie data is ook onderwerp aan die CATMOD - prosedure. Daar is baie oorvleueling in terme van die voedselplante, die plantdele benut en ander faktore wat die voedingsekologie van die blaarvreters op Lewa beïnvloed. Gevolglik kan die ekologiese skeiding van die blaarvreters op Lewa net deels toegeskryf word aan voedselplantbenutting. Seisoenale variasie in die benuttingshoogte van blaarvreet het die oorvleueling in blaarvreetbenutting tussen die blaarvreters verminder. Die kompetisie vir voedsel word gedurende die reënseisoen ook verminder deurdat die olifante Lewa tydelik verlaat gedurende hierdie seisoen. Alhoewel ekologiese skeiding tussen die olifante, swartrenosters en kameelperde waargeneem is op Lewa, plaas die hoë olifant- en kameelperdgetalle in die gebied onnodige hoë druk op die plantegroei, veral gedurende die droë seisoen. Die herstel en volgehoue instandhouding van die houtagtige plantegroei op Lewa is noodsaaklik vir die langtermyn oorlewing van veral die swartrenosters in die bewarea.

'n Merkbare afname in die regenerasie van *Acacia xanthophloea* - saailinge het gelei tot 'n ondersoek om die impak van die olifant-, kameelperd- en rooibokbevolkings op die saailinge in veral die rivieroewerbos te bepaal. Verskeie uitsluitpersele is vir hierdie doel opgerig. Die plantegroei in die persele is blootgestel aan verskillende grade van benutting deur die blaarvreters. Die tempo van blaarvreetproduksie van *Acacia xanthophloea* - saailinge is bepaal deur die toename in lengte van gemerkte lote maandeliks te meet. Die hoë lading van blaarvreters op Lewa is die hoofoorsaak vir die stadige regenerasie en herstel van die *Acacia xanthophloea* - saailinge. Die tempo van die saailingregenerasie kan slegs toeneem as die getal blaarvreters op Lewa verminder word. Die invloed van ander faktore op die tempo van regenerasie kan egter nie misken word nie. Volgehoue monitering van die regenerasie en lootproduksie van *Acacia xanthophloea* - saailinge word dus aanbeveel in die uitsluitpersele. Sodoende kan 'n databasis opgebou word wat kan help met die daarstelling van 'n bestuursplan tot voordeel van beide die blaarvreters en die regenerasie van die *Acacia xanthophloea* - saailinge.

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APPENDIX A

The following plant species checklist is a complete checklist of trees, shrubs, forbs, ferns and wild flowers identified on the Lewa Wildlife Conservancy, Kenya, in the present study. It also includes the plant species checklist of Botha (1998). The studies of Agnew and Agnew (1994), Blundell (1987) and Arnold and De Wet (1993) were consulted. Plant families and genera are arranged alphabetically, according to Van Wyk (pers. comm)[6]. The use of "genspec" numbers was not considered here, as these are outdated and not used in the classification system any more.

ACANTHACEAE

Asystasia Blum
A. riparia Lindau
Barleria L.
B. spinisepala E.A. Bruce
B. sp. Z
Blepharis Juss.
B. integrifolia (L.f.) E. Mey. var. *setosa* (Nees) Oberm.
B. linariifolia
Crabbea Harvey
C. velutina S. Moore
Dyschoriste Nees
D. hildebrandtii (S. Moore) Lindau
D. radicans Nees
D. sp. A
D. thunbergiiflora (S. Moore) Lindau
Hypoestes Soland ex R. Br.
H. aristata (Vahl) Roem. & Schult.
H. hildebrandtii Lindau
Justicia L.
J. anagelloides (Nees) T. Anders.
J. calyculata (Deflens) T. Anders.
J. diclipteroides Lindau
J. odora (Forssk.) Lam.
J. uncinulata
J. unyorensis S. Moore
Thunbergia Retz
T. alata Sims

ADIANTACEAE

Actiniopteris Link
A. semiflabellata Pichi. Serm.
Cheilanthes Swartz
C. farinosa (Forssk.) Kaulf
Pellaea Link
P. calomelanos (Swartz) Link

AMARANTHACEAE

Achyranthes L.
A. aspera L.

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A. lanuginosa Schinz
Amaranthus L.
A. hybridus L.
Cyathula Blume
C. cylindrica Moq.
Digera Forssk.
D. muricata (L.) Mart.
Pupalia A. Juss.
P. lappacea (L.) A. Juss. var. *lappacea*
Sericocomopsis Schinz
S. hildebrandtii Schinz
S. pallida (S. Moore) Schinz

AMARYLLIDACEAE

Ammocharis (Herb.)
A. tinneana (Kotschy & Peyr.) Milne-Redh. & Schweik.
Crinum
C. macowanii
Scadoxus Raf.
S. multiflorus (Martyn) Raf.

ANACARDIACEAE

Lannea A. Rich.
L. alata (Engl.) Engl.
L. rivae (Chiov.) Sacl.
L. triphylla (A. Rich.) Engl.
Ozoroa Delile
O. insignis Del. ssp. *reticulata* (Bak.f.) Gillet
Pistacia L
P. aethiopica Kokwaro
Rhus L.
R. natalensis Krauss
R. vulgaris Meikle
Schinus L.
S. molle L.

APIACEAE

Agrocharis (Hochst.)
Hydrocotyle L.
H. ranunculoides L.f.
Steganotaemia Hochst.
S. araliacea Hochst.

APOCYNACEAE

Acokanthera G. Don
A. schimperi (A.DC.) Schweinf.
Carissa L.
C. edulis (Forssk.) Vahl.

ARALIACEAE

Cussonia Thunb.

C. holstii Engl. var. *holstii*
C. spicata Thunb.

ASCLEPIADACEAE

Caralluma R.Br.
C. speciosa N.E.Br.
C. tubiformis
Gomphocarpus R.Br.
G. semilunatus A. Rich.
Pachycymbium Leach
P. dummeri (N.E.Br.) M. Gilbert

ASPARAGACEAE

Asparagus L.
A. africanus Lam.
A. falcatus L.
A. setaceus (Kunth) Jessop

ASPHODELACEAE

Aloe L.
A. turkarensis
Anthericum L.
A. cooperi Bak.
Bulbine Wild.
B. abyssinica A. Rich.
Chlorophytum Ker-Gawl.
C. silvaticum Dammer Poelln.
C. somaliense Bak.

ASPLENIACEAE

Asplenium L.
A. aethiopicum (Burm. f.) Becherer

ASTERACEAE

Acmella L.C. Rich.
A. calirhiza Del
Adenostemma Forst.
A. mauritianium DC.
Aspilia Thouars
A. mossambicensus (Olive.) Wild.
A. pluriseta Schweinf.
Bidens L.
B. hildebrandtii O. Hoffm
B. pilosa L.
Cineraria L.
C. deltoidea Sond.
Conyza Less.
C. pendunculata (Olive.) Wild.
C. structa Wild.
Crassocephalum Moench
C. picridifolium (DC.) S. Moore

C. vetellinum (Benth.) S. Moore
Dicoma Cass.
D. tomentosa Cass.
Felicia Cass.
F. muricata (Thunb.) Nees
Gutenbergia Sch.Bip.
G. cordifolia Oliv.
Helichrysum Mill.
H. foetidum (L.) Moench.
H. globosum Sch.Bip.
H. glumaceum DC.
H. odoratissimum (L.) Less.
Kleinia Mill.
K. abyssinica var. *abyssinica*
Pluchea Cass.
P. ovalis
Pseudognaphalium Kirp.
P. luteo-album (L.) Hilliard & Burtt
Psiadia Jacq.
P. punctulata (DC.) Vatke
Reichardia Roth
R. tingitana (L.) Roth
Senecio L.
S. schweinfurthii O. Hoffm.
Sonchus L.
S. asper (L.) Hill
Sphaeranthus L.
S. cyathuloides
S. napierae Ross-Criag
Tagetes L.
T. minuta L.
Vernonia Schreb.
V. brachycalyx O. Hoffm.
V. lasiopus O. Hoffm.

BALANITACEAE

Balanites Delile
B. aegyptiaca (L.) Del.
B. glabra Mildbr. & Schlecht.

BORAGINACEAE

Cordia L.
C. africana Lam.
C. monoica Roxb.
Heliotropium L.
H. steudneri Vatke

BRASSICACEAE

Lepidium L.
L. bongariense L.

BURSERACEAE

Commiphora (A. Rich.) Engl.

C. africana (A. Rich.) Engl.
C. holtziana Engl. spp. *holtziana*
C. schimperi (O. Berg) Engl.

CACTACEAE

Opuntia Mill.
O. vulgaris Mill.

CAPPARACEAE

Boscia Lam.
B. angustifolia A. Rich.
B. coriacea Pax
B. mossambicensis Klotzsch
Cadaba Forssk.
C. farinosa
Cleome L.
C. allamanii Chiov.
Maerua Forssk.
M. angolensis DC.
M. decumbens (Brongn.) De Wolf
M. triphylla A. Rich.

CARYOPHYLLACEAE

Pollichia Ait.
P. campestris Ait.

CELASTRACEAE

Catha Forssk. ex Scop.
C. edulis (Vahl) Endl.
Elaedendron Loes.
E. buchananii (Loes.) Loes.
Maytenus Molina
M. senegalensis (Lam.) Exell

CHENOPODIACEAE

Chenopodium L.
C. album L.

COMBRETACEAE

Combretum Loefl.
C. molle G. Don.
Terminalia L.
T. prunioides Laws
T. spinosa Engl.

COMMELINACEAE

Commelina L.

C. africana L.
C. diffusa Burm. f.
C. latifolia A. Rich.

CONVOLVULACEAE

Convolvulus L.
C. jefferyi
Ipomoea L.
Merremia Dennst.
M. ampelophylla Dennst.

CRASSULACEAE

Cotyledon L.
C. barbeyi Schweinf.
Kalanchoe Adams
K. citrina Schweinf.
K. densiflora Rolfe

CUCURBITACEAE

Cucumis L.
C. aculeatus

CUPPRESSACEAE

Juniperus L.
J. procera Endl.

CYPERACEAE

Cyperus L.
C. obtusiflorus Vahl. var *obtusiflorus*
C. papyrus L.
C. rupestris Kunth. var *rupestris*
Fuirena Rottb.
F. pubescens (Poir.) Kunth.
Mariscus L.
M. congestus (Vahl) C.B. Cl.
Phoenix L.
P. reclinata Jacq.
Schoenoplectus Palla
S. corymbosus (Roem. & Schult.) J. Raynal

DRACAENACEAE

Dracaena L.
D. ellenbeckiana Engl.
Sansevieria Thunb.
S. suffruticosa N.E.Br.

EBENACEAE

Euclea Murray
- *E. divinorum* Hiern
- *E. racemosa* Murr ssp. *schimperi* (A.DC.) F. White

EUPHORBIACEAE

Acalypha L.
- *A. crenata* A. Rich.
- *A. fruticosa* Forssk.
- *A. volkensii*

Croton L.
- *C. dichogamus* Pax

Drypetes Vahl
- *D. gerrardii* Hutch

Erythrococca Benth.
- *E. bongensis* Pax

Euphorbia L.
- *E. candelabrum* Kotschy
- *E. graciliramea* Pax
- *E. kibwezensis* Pax
- *E. nyikae* Pax
- *E. schimperiana* Scheele
- *E. unligiana* Pax

Polygala L.
- *P. suffrutescens* Pax

FABACEAE

Acacia Mill
- *A. brevispica* Harms ssp. *brevispica*
- *A. drepanolobium* Sjøstedt
- *A. gerrardii* Benth.
- *A. hockii* De Wild.
- *A. mellifera* (Vahl) Benth.
- *A. nilotica* (L.) Del
- *A. senegal* (L.) Wild.
- *A. seyal* Del.
- *A. tortilis* (Forssk.) Hayne
- *A.xanthophloea* Benth.

Bauhinia L.
- *B. tomentosa* L.

Crotalaria L.
- *C. brevidens* Benth.
- *C. chrysochlora* Harms
- *C. deflersii* Schweinf.
- *C. mauensis*
- *C. polysperma* Kotschy

Dalbergia L.f.
- *D. lactea* Vatke

Dolichos L.
- *D. oliveri* Schweinf.

Indigofera L.
- *I. brevicalyx* Bak.
- *I. volkensii*. Taub.

Parkinsonia L.
- *P. aculeata* L.

Pterolobium Wight & Arn.

P. stellatum (Forssk.) Brenan
Senna Miller
Sesbania Scop.
S. goetzei Harms
S. sesban (L.) Merr.
Tephrosia Pers
T. subtriflora Bak.
Vigna Savi
V. parkeri Bak.
V. vexillata (L.) A. Rich.

FLACOURTIACEAE

Scolopia Schreber
S. zeyheri (nees) Harv.

GERANIACEAE

Geranium L.
G. aculeolatum Oliv.
Monsonia L.
M. angustifolia A. Rich.
M. longipes R. Knuth

HAMAMELIDICEAE

Trichocladus Pers.
T. ellipticus Eckl. & Zeyh. ssp. *malosanus* (Bak.) Verdc.

HYACINTHACEAE

Scilla L. (Ledebouria Roth.)
S. kirkii Bak.

HYPOXIDACEAE

Hypoxis L.

IRIDACEAE

Gladiolus L.
G. ukambanensis (Bak.) Marais

LAMIACEAE

Ajuga L.
A. remota
Becium Lindl.
B. hildebrandtii
B. obovatum (E.Mey.) N.E. Br.
Leonotis (Pers.) R. Br.
L. nepetifolia (L.) Ait.f.
Leucas R. Br.
L. deflexa Hook.f.

L. urticifolia (Vahl) R. Br.
Ocimum L.
O. suave Wild.
Orthosiphon Benth.
O. pallidus Benth.
O. rubicundus Benth.
Plectranthus L.'Herit.
P. hadiensis (Forssk.) Schweinf.
P. lactiflorus (Vatke) Agnew
P. lanuginosis (Benth.) Agnew
P. longipes Bak.
Tinnea Kotschy ex Hook. f.
T. aethiopica

LINACEAE

Linum L.
L. volkensii Engl.

LOGANIACEAE

Strychnos L.

LORANTHACEAE

Emelianthe Danser
E. panganensis (Engl.) Danser
Englerina V. Tieghem
E. woodfordioides (Schweinf.) Balle
Phragmanthera V. Tieghem
P. regularis (Sprague) Balle
P. usuiensis (Oliv.) M. Gilbert
Plicosepalus V. Tieghem
P. curviflorus (Benth.) V. Tieghem

LYTHRACEAE

Ammania L.
A. baccifera L.

MALVACEAE

Abutilon Mill.
A. mauritianum (Jacq.) Medic.
Hibiscus L.
H. aponeurus Sprague & Hutch
H. calyphyllus Cav.
H. cannabinus L.
H. flavifolius Ulbr.
H. palmatus Forssk.
H. pycnostemon
H. vitifolius L.
Pavonia Cav.
P. gallaensis Andr.
P. patens (Andr.) Chiov.
P. urens Cav. var. *urens*

Sida L.
- *S. cordifolia* L.
- *S. cuneifolia*
- *S. schimperiana* A. Rich.

MELASTOMATACEAE

Dissotis Bent.
- *D. senegambiensis* (Guill. & Perr.) Triana

MELIACEAE

Trichilia P. Browne
- *T. emetica* Vahl

Turraea L.
- *T. holstii* Gürke

MORACEAE

Ficus L.
- *F. craterostoma* Mildbr. & Burret
- *F. natalensis* Hochst.
- *F. sycomorus* L.

MYRSINACEAE

Myrsine L.
- *M. africana* L.

MYRTACEAE

Syzygium Gaertn.
- *S. guineense* (Wild.) DC.

NYCTAGINACEAE

Commicarpus Standl.
- *C. pedunculosus* (A. Rich.) Cuf.

OCHNACEAE

Ochna L.
- *O. ovata* F. Hoffm.

OLEACEAE

Jasminum L.
- *J. floribundum* Fresen.

Olea L.
- *O. europaea* L. ssp. *africana* (Mill.) P. Green

OXALIDACEAE

Oxalis L.
O. corniculata L.

PEDALIACEAE

Pterodiscus Hook.
P. ruspolii
Sesamum L.

PLUMBAGINACEAE

Plumbago L.
P. zeylanica L.

PODOCARPACAEA

Podocarpus L'Hérit. ex Pers.
P. falcatus Mirb. (P. gracilior Pilger)
P. latifolius (Thunb.) Mirb.

POLIGALACEAE

Polygala L.
P. sadebeckiana Guerke
P. sphenoptera Fresen.

POLYGONACEAE

Oxygonum Burch.
O. sinuatum (Meisn.) Dammer
Polygonum L.
P. setosulum A. Rich.

PORTULACACEAE

Portulaca L.
P. quadrifida L.
Talinum Adams.
T. portulacifolium (Forssk.) Schweinf.

RENUNCULACEAE

Clematis L.
C. brachiata Thunb.

RESEDACEAE

Caylusea A. St.-Hill
C. abyssinica (Fresen.) Fisch. & Mey.

RHAMNACEAE

Helinus E. Mey. ex Endl.
H. integrifolius (Lam.) Kuntze
Scutia Commerson ex Brongn.
S. myrtina (Burm. f.) Kurz
Ziziphus Miller
Z. mucronata Wild. ssp.*mucronata*

ROSACEAE

Prunus L.
P. africanus (Hook. f.) Kalkm.

RUBIACEAE

Canthium Lam.
Conostomium Cuf.
C. kenyense Brem.
Pentanisia Harvey
P. ouranogyne S. Moore
Pentas Benth.
P. parvifolia Hiern
Rubia L.
R. cordifolia L.
Vangueria Juss.
V. madagascariensis Gmel.

RUTACEAE

Teclea Delile
T. simplicifolia (Engl.) Verdoorn
Zanthoxylum L.
Z. chalybeum Engl. var. *chalybeum*
Z. usambarense (Engl.) Kokwaro

SAPINDACEAE

Dodonaea Miller
D. angustifolia L.f.
Pappea Eckl. & Zeyh.
P. capensis Eckl. & Zeyh.

SCROPHULARIACEAE

Craterostigma Hochst.
C. plantagineum Hochst.
C. pumilum Hochst.
C. sp. A

Verbascum L.
V. sinaiticum Benth.

SIMAROUBACEAE

Kirkia Oliver
K. tenuifolia Engl.

SOLANACEAE

Datura L.
D. stramonium L.
Lycium L.
L. shawii Roem. & Schult. = *L. europaem*
Solanum L.
S. aculeastrum Dunal
S. hastifolium Dunal
S. incanum L.
S. sessilistellatum Bitter
S. sp. A

STERCULIACEAE

Hermannnia L.
H. exappendiculata (Mast.) K. Schum.
Melhania Forssk.
M. ovata Cav.Spreng.
M. velutina Forssk.
Sterculia L.
S. africana (Lour.) Fiori

THYMELAEACEAE

Gnidia L.
G. involucrata A. Rich.

TILIACEAE

Corchorus L.
Grewia L.
G. bicolor Juss.
G. similis K. Schum.
G. tembensis Fresen.
G. villosa Wild.
Triumfetta L.
T. flavescens A. Rich.

ULMACEAE

Celtis L.
C. africana Burm. f.

VERBENACEAE

Chascanum E. Mey.
C. hildebrandtii (Vatke) Gillet
Clerodendrum L.
C. myricoides (Hochst.) Vatke

Lantana L.
- *L. trifolia* L.

Lippia L.
- *L. carviodora* Meikle
- *L. javanica* (Burm.f) Spreng
- *L. kituiensis* Vatke

Priva Adans
- *P. curtisiae* Kobuski

Verbena L.
- *V. officinalis* L.

VITACEAE

Cissus L.
- *C. cactiformis* Gilg
- *C. quadrangularis* L.
- C. *rotundifolia*

Cyphostemma (Planch.) Alston
- *C. adenocaule* (A. Rich.) Wild & Drum
- *C. cyphopetalum* (Fresen.) Wild & Drum
- *C. orondo*

ZYGOPHYLACEAE

Tribulus L.
- *T. terrestris* L.
- *T. parvispinus* Presl.

APPENDIX B

HABITAT SELECTION FIELD DATA SHEET

	1	2	3	4	5	6	7	8	9	10
Transect name										
Date										
Time										
Grid reference										
Browser species										
Group composition										
males										
females										
juveniles										
Total										
Activity										
browsing										
grazing										
drinking										
walking										
resting										
Habitat type										
Aspect										
Landscape position										
plains										
gentle slopes										
steep slopes										
valleys										
plateau										
riverbed										
Distance from water										
0 - 50 m										
51 - 250 m										
251 - 500 m										
501 - 1 000 m										
1 001 - 2 000 m										
> 2 000 m										
Tree canopy cover										
0 - 10 %										
11 - 20 %										
21 - 30 %										
> 30 %										
Bush canopy cover										
0 - 10 %										
11 - 20 %										
> 20 %										
Woody veg. density										
sparse										
open										
medium										
dense										
Grass cover										
sparse										
medium										
dense										

APPENDIX C

Data set variable definition as used for analysis with the CATMOD procedure for habitat selection by the black rhinoceros, elephant and giraffe on the Lewa Wildlife Conservancy, Kenya, from May 1996 to May 1997.

VARIABLE	DESCRIPTION	GROUP NUMBER	NUMBER OF CATEGORIES IN GROUP	CATEGORY AND ABBREVIATIONS USED
V1	Observation number	*	*	Observation 1 - 1 076 (n = 1 076)
V2	Habitat type	A	10	1. *Acacia drepanolobium* woodland (Acac dre) 2. *Acacia nilotica* woodland (Acac nil) 3. *Acacia drepanolobium - Acacia seyal* woodland (Drep sey) 4. Mixed *Acacia* hills (MAH) 5. Mixed *Acacia* plains (MAP) 6. Mixed woodland hills (MWH) 7. Mixed woodland plains (MWP) 8. Open grassland plains (OGP) 9. Riverine woodland (Riverine) 10. Shrub forest (Shru for)
V2	Habitat type	B	7	1. *Acacia nilotica* woodland (Acac nil) 2. *Acacia drepanolobium - Acacia seyal* woodland (Drep sey) 3. Mixed *Acacia* hills (MAH) 4. Mixed *Acacia* plains (MAP) 5. Mixed woodland hills (MWH) 6. Mixed woodland plains (MWP) 7. Riverine woodland (Riverine)
V2	Habitat type	C	5	1. *Acacia nilotica* woodland (Acac nil) 2. *Acacia drepanolobium - Acacia seyal* woodland (Drep sey) 3. Mixed woodland hills (MWH) 4. Mixed woodland plains (MWP) 5. Riverine woodland (Riverine)
V2	Habitat type	D	4	1. *Acacia drepanolobium - Acacia seyal* woodland (Drep sey) 2. Mixed woodland hills (MWH) 3. Mixed woodland plains (MWP) 4. Riverine woodland (Riverine)
V2	Habitat type	E	3	1. *Acacia drepanolobium - Acacia seyal* woodland (Drep sey) 2. Mixed woodland hills (MWH) 3. Mixed woodland plains (MWP)
V3	Time observed	A	9	1. 06:00 - 07:00 2. 07:00 - 08:00 3. 08:00 - 09:00 4. 09:00 - 10:00 5. 10:00 - 11:00

VARIABLE	DESCRIPTION	GROUP NUMBER	NUMBER OF CATEGORIES IN GROUP	CATEGORY AND ABBREVIATIONS USED
V3	Time observed	A	9	6. 11:00 - 12:00 7. 15:00 - 16:00 8. 16:00 - 17:00 9. 17:00 - 18:00
V3	Time observed	B	3	1. 06:00 - 09:00 2. 09:00 - 12:00 3. 15:00 - 18:00
V4	Browser species	A	3	1. Elephant 2. Giraffe 3. Black rhinoceros
V5	Herd size	*	*	Used as a weighting factor in CATMOD analysis
V6	Aspect	A	8	1. East (E) 2. North (N) 3. Northeast (NE) 4. Northwest (NW) 5. South (S) 6. Southeast (SE) 7. Southwest (SW) 8. West (W)
V6	Aspect	B	4	1. East (E) 2. North (N) 3. South (S) 4. West (W)
V6	Aspect	C	5	1. East (E) 2. North (N) 3. Northeast (NE) 4. West (W) 5. South (S)
V7	Activity	A	5	1. Browsing 2. Grazing 3. Walking 4. Resting 5. Drinking
V8	Distance from water	A	6	1. 0 - 50 m 2. 51 - 250 m 3. 251 - 500 m 4. 501 - 1 000 m 5. 1 001 - 2 000 m 6. > 2 000 m

VARIABLE	DESCRIPTION	GROUP NUMBER	NUMBER OF CATEGORIES IN GROUP	CATEGORY AND ABBREVIATIONS USED
V8	Distance from water	B	5	1. 0 - 50 m 2. 51 - 250 m 3. 251 - 500 m 4. 501 - 1 000 m 5. > 1 000 m
V8	Distance from water	C	3	1. 0 - 500 m 2. 501 - 1 000 m 3. > 1 000 m
V9	Landscape position	A	6	1. Gentle slope 2. Plain 3. Plato 4. Riverbed 5. Steep slope 6. Valley
V9	Landscape position	B	5	1. Gentle slope 2. Plain 3. Riverbed 4. Steep slope 5. Valley
V9	Landscape position	C	3	1. Slope 2. Plain 3. Valley
V9	Landscape position	D	2	1. Slope 2. Plain
V10	Tree canopy cover	A	4	1. 0 - 10 % 2. 11 - 20 % 3. 21 - 30 % 4. > 30 %
V10	Tree canopy cover	B	2	1. 0 - 10 % 2. > 10 %
V11	Bush canopy cover	A	3	1. 0 - 10 % 2. 11 - 20 % 3. > 20 %
V11	Bush canopy cover	B	2	1. 0 - 10 % 2. > 10 %

VARIABLE	DESCRIPTION	GROUP NUMBER	NUMBER OF CATEGORIES IN GROUP	CATEGORY AND ABBREVIATIONS USED
V12	Woody vegetation density	A	4	1. Dense 2. Medium 3. Open 4. Sparse
V12	Woody vegetation density	B	3	1. Medium 2. Open 3. Sparse
V12	Woody vegetation density	C	2	1. Medium 2. Open
			3	1. Dense 2. Medium 3. Sparse
			2	1. Dense 2. Medium
V14	Season of observation	A	2	1. Wet season 2. Dry season

APPENDIX D

FEEDING ECOLOGY FIELD DATA SHEET

	1	2	3	4	5	6	7	8	9	10
Date										
Habitat										
Aspect										
Slope										
Animal										
Sex										
Plant species utilised										
Plant portion utilised										
leaves										
flowers										
fruit										
shoots										
branches										
bark										
Height of utilisation										
maximum										
minimum										
Struct.of feeding station										
height										
canopy diameter										
lowest available leaves										
Time at feeding station										
begin										
end										
Total										
Distance from water										
0 - 50 m										
51 - 250 m										
251 - 500 m										
501 - 1 000 m										
> 1 000 m										
Windspeed										
Cloud cover										

APPENDIX E

Data set variable definition as used for analysis with the CATMOD procedure for the feeding ecology of the black rhinoceros, elephant and giraffe on the Lewa Wildlife Conservancy, Kenya, from May 1996 to May 1997.

VARIABLE	DESCRIPTION	GROUP NUMBER	NUMBER OF CATEGORIES IN GROUP	CATEGORY AND ABBREVIATIONS USED
V1	Observation number	*	*	Observation 1 - 2 829 (n = 2 829)
V2	Habitat type	A	11	1. *Acacia drepanolobium* woodland (Acac dre)
				2. *Acacia nilotica* woodland (Acac nil)
				3. *Acacia drepanolobium - Acacia seyal* woodland (Drep sey)
				4. Mixed *Acacia* hills (MAH)
				5. Mixed *Acacia* plains (MAP)
				6. Mixed *Acacia* woodland (MAW)
				7. Mixed woodland hills (MWH)
				8. Mixed woodland plains (MWP)
				9. Open grassland plains (OGP)
				10. Riverine woodland (Riverine)
				11. Shrub forest (Shru for)
V2	Habitat type	B	8	1. *Acacia nilotica* woodland (Acac nil)
				2. *Acacia drepanolobium - Acacia seyal* woodland (Drep sey)
				3. Mixed *Acacia* hills (MAH)
				4. Mixed *Acacia* plains (MAP)
				5. Mixed woodland hills (MWH)
				6. Mixed woodland plains (MWP)
				7. Riverine woodland (Riverine)
				8. Shrub forest (Shru for)
V2	Habitat type	C	6	1. *Acacia drepanolobium - Acacia seyal* woodland (Drep sey)
				2. Mixed *Acacia* hills (MAH)
				3. Mixed *Acacia* plains (MAP)
				4. Mixed woodland hills (MWH)
				5. Mixed woodland plains (MWP)
				6. Riverine woodland (Riverine)
V2	Habitat type	D	4	1. *Acacia drepanolobium - Acacia seyal* woodland (Drep sey)
				2. Mixed *Acacia* hills (MAH)
				3. Mixed *Acacia* plains (MAP)
				4. Mixed woodland hills (MWH)
V3	Browser	A	6	1. Elephant cow
				2. Elephant bull
				3. Giraffe cow
				4. Giraffe bull
				5. Black rhinoceros cow
				6. Black rhinoceros bull

VARIABLE	DESCRIPTION	GROUP NUMBER	NUMBER OF CATEGORIES IN GROUP	CATEGORY AND ABBREVIATIONS USED
V4	Plant species	A	29	1. *Acacia brevispica* (Acac bre)
				2. *Acacia drepanolobium* (Acac dre)
				3. *Acacia mellifera* (Acac mel)
				4. *Acacia nilotica* (Acac nil)
				5. *Acacia seyal* (Acac sey)
				6. *Acacia tortilis* (Acac tor)
				7. *Acacia xanthophloea* (Acac xan)
				8. *Achyranthes aspera* (Achy asp)
				9. *Asparagus* species (Aspa sp.)
				10. *Balanites aegyptiaca* (Bala aeg)
				11. *Boscia angustifolia* (Bosc ang)
				12. *Boscia coriacea* (Bosc cor)
				13. *Cadaba farinosa* (Cada far)
				14. *Carissa adulis* (Cari edu)
				15. *Commiphora africana* (Comm afr)
				16. *Cordia ovalis* (Cord ova)
				17. *Dyschoriste* species (Dysc sp.)
				18. *Euclea divinorum* (Eucl div)
				19. Forb
				20. Grass
				21. *Grewia bicolor* (Grew bic)
				22. *Grewia tembensis* (Grew tem)
				23. *Hibiscus* species (Hibi sp.)
				24. *Lycium shawii* (Lyci sha)
				25. *Maytenus senegalensis* (Mayt sen)
				26. *Rhus natalensis* (Rhus nat)
				27. *Solanum aculeastrum* (Sola acu)
				28. *Tinnea aethiopica* (Tinn eat)
				29. Other
V4	Plant species	B	12	1. *Acacia drepanolobium* (Acac dre)
				2. *Acacia mellifera* (Acac mel)
				3. *Acacia nilotica* (Acac nil)
				4. *Acacia seyal* (Acac sey)
				5. *Acacia tortilis* (Acac tor)
				6. *Acacia xanthophloea* (Acac xan)
				7. *Commiphora africana* (Comm afr)
				8. Forb
				9. Grass
				10. *Hibiscus* species (Hibi sp.)
				11. *Maytenus senegalensis* (Mayt sen)
				12. Other

VARIABLE	DESCRIPTION	GROUP NUMBER	NUMBER OF CATEGORIES IN GROUP	CATEGORY AND ABBREVIATIONS USED
V5	Plant part	A	8	1. Branches & bark (br, ba) 2. Branches, bark, leaves & shoots (br, ba, le, sh) 3. Branches (br) 4. Branches & leaves (br, le) 5. Branches, leaves & shoots (br, le, sh) 6. Leaves (le) 7. Leaves & shoots (le, sh) 8. Branches, bark, leaves, shoots, flowers & fruit (br, ba, le, sh, fl, fr)
V5	Plant part	B	7	1. Branches & bark (br, ba) 2. Branches, bark, leaves & shoots (br, ba, le, sh) 3. Branches & leaves (br, le) 4. Branches, leaves & shoots (br, le, sh) 5. Leaves (le) 6. Leaves & shoots (le, sh) 7. Branches, bark, leaves, shoots, flowers & fruit (br, ba, le, sh, fl, fr)
V6	Aspect	A	8	1. East (E) 2. North (N) 3. Northeast (NE) 4. Northwest (NW) 5. South (S) 6. Southeast (SE) 7. Southwest (SW) 8. West (W)
V6	Aspect	B	4	1. East (E) 2. North (N) 3. South (S) 4. West (W)
V7	Distance from water	A	5	1. 0 - 50 m 2. 51 - 250 m 3. 251 - 500 m 4. 501 - 1 000 m 5. > 1 000 m
			4	1. Average 2. Flat 3. Gradual 4. Steep
			3	1. Flat 2. Gradual 3. Average - steep

VARIABLE	DESCRIPTION	GROUP NUMBER	NUMBER OF CATEGORIES IN GROUP	CATEGORY AND ABBREVIATIONS USED
V9	Maximum height of utilisation	A	6	1. 0 - 1 m 2. > 1 - 2 m 3. > 2 - 3 m 4. > 3 - 4 m 5. > 4 - 5 m 6. > 5 m
V9	Maximum height of utilisation	B	5	1. 0 - 1 m 2. > 1 - 2 m 3. > 2 - 3 m 4. > 3 - 4 m 5. > 4 m
V9	Maximum height of utilisation	C	4	1. 0 - 1 m 2. > 1 - 2 m 3. > 2 - 3 m 4. > 3 m
V10	Minimum height of utilisation	A	6	1. 0 - 1 m 2. > 1 - 2 m 3. > 2 - 3 m 4. > 3 - 4 m 5. > 4 - 5 m 6. > 5 m
V10	Minimum height of utilisation	B	5	1. 0 - 1 m 2. > 1 - 2 m 3. > 2 - 3 m 4. > 3 - 4 m 5. > 4 m
V10	Minimum height of utilisation	C	4	1. 0 - 1 m 2. > 1 - 2 m 3. > 2 - 3 m 4. > 3 m
V11	Tree height	A	6	1. 0 - 1 m 2. > 1 - 2 m 3. > 2 - 3 m 4. > 3 - 4 m 5. > 4 - 5 m 6. > 5 m
V11	Tree height	B	5	1. 0 - 1 m 2. > 1 - 2 m 3. > 2 - 3 m

VARIABLE	DESCRIPTION	GROUP NUMBER	NUMBER OF CATEGORIES IN GROUP	CATEGORY AND ABBREVIATIONS USED
V11	Tree height	B	5	4. > 3 - 4 m 5. > 4 m
V12	Canopy diameter	A	6	1. 0 - 1 m 2. > 1 - 2 m 3. > 2 - 3 m 4. > 3 - 4 m 5. > 4 - 5 m 6. > 5 m
V12	Canopy diameter	B	5	1. 0 - 1 m 2. > 1 - 2 m 3. > 2 - 3 m 4. > 3 - 4 m 5. > 4 m
V13	Lowest available leaves	A	6	1. 0 - 1 m 2. > 1 - 2 m 3. > 2 - 3 m 4. > 3 - 4 m 5. > 4 - 5 m 6. > 5 m
V13	Lowest available leaves	B	5	1. 0 - 1 m 2. > 1 - 2 m 3. > 2 - 3 m 4. > 3 - 4 m 5. > 4 m
V13	Lowest available leaves	C	3	1. 0 - 1 m 2. > 1 - 2 m 3. > 2 m
V14	Time spent feeding	A	5	1. 0 - 30 seconds (0 - 30 sec) 2.> 30 seconds - 1 minute (> 30 sec - 1 min) 3. > 1 - 3 minutes (> 1 - 3 min) 4. > 3 - 10 minutes (> 3 - 10 min) 5. > 10 minutes (> 10 min)
V14	Time spent feeding	B	4	1. 0 - 30 seconds (0 - 30 sec) 2.> 30 seconds - 1 minute (> 30 sec - 1 min) 3. > 1 - 3 minutes (> 1 - 3 min) 4. > 3 minutes (> 3 min)
V15	Windspeed	A	5	1. 0 - 2 knots 2. > 2 - 5 knots

VARIABLE	DESCRIPTION	GROUP NUMBER	NUMBER OF CATEGORIES IN GROUP	CATEGORY AND ABBREVIATIONS USED
V15	Windspeed	A	5	3. > 5 - 9 knots
				4. > 9 - 13 knots
				5. > 13 - 24 knots
V16	Cloud cover	A	5	1. 0 - 1 %
				2. > 1 - 25 %
				3. > 25 - 50 %
				4. > 50 - 75 %
				5. > 75 - 100 %
V16	Cloud cover	B	4	1. 0 - 25 %
				2. > 25 - 50 %
				3. > 50 - 75 %
				4. > 75 - 100 %

APPENDIX F

ACACIA XANTHOPHLOEA **FIELD DATA SHEET**

CAMP NO.:
DATE:

No. of trees	Tree height	Stem diameter	No. of tagged shoots	Shoot length		
				1	2	3

APPENDIX G

GLOSSARY OF TERMS

The following terms are used in this study. An asterisk denotes terms that are defined in this glossary.

Available browse: This term refers to all the leaves, young twig material, bark, flowers and pods within an accessible height for a particular animal. It is determined on the basis of the maximum height above the ground to which an animal can potentially utilise browse, and usually refers to a more restricted quantity than the term browse*.

Bimodal: A frequency distribution having two peaks (Lincoln, Boxhall & Clark 1998). This term is used in the description of the rainfall of the study area, where two wet seasons and two dry seasons are prevalent.

Browse: The sum total of plant material on woody plants that is potentially edible to a specified set of browsing animals, and which is regarded as the current season's growth of leaves and twigs (Rutherford 1979).

Browse line: A line marking the height to which browsing animals have been feeding (Lincoln, *et al.* 1998).

Browse unit: An *Acacia karroo* tree with a height of 1.5 m. The difference between a tree equivalent* and a browse unit is that all leaf mass above the maximum browse height of 5 m is excluded in the calculation of the browse unit.

Browser unit: A kudu cow of 140 kg that browses exclusively (Snyman 1991).

Browsing capacity: The potential of an area to carry a certain number of animals in a good productive and reproductive condition, over a prolonged time, without the deterioration of the resources (Kruger 1994).

Canopy: The uppermost stratum of foliage formed by the crowns of trees and shrubs (Lincoln, *et al.* 1998).

Canopy cover: The percentage of the ground that is covered when a polygon drawn about the extremities of the undisturbed canopy* of each plant is projected upon the ground and the areas of all such projections within a given area are added (Allaby 1988).

Competition: The simultaneous demand by two or more species for an essential common resource that is actually or potentially in limited supply (exploitative competition), or the detrimental interaction between two or more species seeking a common resource that is not limiting (interference competition) (Lincoln, *et al.* 1998).

Coppice: Regrowth of trees and shrubs regenerating from cut stumps or the rootstocks of plants in which the above-ground component has been killed by fire, browsing or trampling (Cauldwell 1998).

Conservancy: The amalgamation of adjoining properties to form an extensive wildlife complex in order to enable better management and protection of some or all of the natural resources in that area. The legal provisions that conservancy members agree upon, in adopting their constitutions, vary greatly depending on the orientation and scale of each conservancy, as does the extent to which the members develop cooperative business enterprises based on their shared wildlife (Du Toit 1994).

Conspicuous: This term is used in the description of the plant communities of Lewa, specifically describing the forb species present. This is a function of the surrounding vegetation and does not necessarily imply that a plant species is dominant or abundant (Cauldwell 1998).

Contingency table: A table consisting of two or more rows and columns of data in which observations or individuals are classified according to two variables*. Tests of independence, such as the chi² test can be used to measure the relationship between the variables (Lincoln, *et al.* 1998).

Deciduous species: Applied to an organism that sheds certain parts readily or regularly, or to those parts themselves. Deciduous trees shed all their leaves at a particular season each year (Allaby 1988). Deciduous species are potentially dominant in subtropical areas, since they have a better competitive ability. They have high potential growth rates, rely on deep rooting and often have small and compound leaves (Danckwerts 1989).

Diagnostic: This term refers to a distinguishing plant species that serves to identify a plant community* (Cauldwell 1998). Lincoln, *et al.* (1998) refers to this term as any character or character state that unambiguously differentiates one taxon from others.

Diversity: This term is used as a measure of the number of plant species and their relative abundance in a plant community*. It is synonymous with species richness (Lincoln, *et al.* 1998).

Dominant: A term used in the description of the plant communities on Lewa. It refers to the characteristic, and often the tallest, species in a particular plant community*. The dominant species is the one that exerts the greatest influence on the character of the community and may give it its name (Allaby 1988).

Ecological capacity: In this study, the term refers to the potential of the area to support herbivores through grazing and/or browsing and/or fodder production over an extended number of years, without the deterioration of the ecosystem (Botha 1999). Bothma (1996) refers to ecological capacity as a characteristic of the entire habitat in which the vegetation, herbivores and predators are all a part. It is also referred to as carrying capacity in some literature, but this term is not used here because of the confusion surrounding it (Dhont 1988).

Ecological separation: The division of a resource between two or more species, so that each species has access to a different part of the resource (Chapman & Reiss 1995). Riney (1982) refers to mammals being ecologically separated when they share the same geographical area without interspecific competition. Scogings, Theron & Bothma (1990) refer to ecological separation as a study of the habitat preferences, resource utilisation and potential interspecific competition among animals of an area.

Endangered: In the proposed IUCN Criteria for threatened species, a taxon is endangered when it is known to be at a very high risk of extinction in the wild in the near future (Lincoln, *et al.* 1998). Allaby (1988) refers to endangered taxa, as those whose numbers have been reduced to a critical level or whose habitats have been so drastically reduced that they are deemed to be in immediate danger of extinction if the causal factors continue operating.

Evergreen species: A plant, typically a tree or shrub, that has leaves all year round and sheds them more or less regularly through all the seasons (Lincoln, *et al.* 1998). Evergreen species are more specialised to cope with dry conditions than deciduous species*. They rely on deep rooting and secondary thickening of their leaves to tolerate dessication. They have moderate growth rates and long-lived sclerophyllous leaves, making them lower in digestibility then deciduous species (Dankwerts 1989).

Exclusion plot: In this study the term refers to the five plots, 100 m X 60 m in size, used to determine the impact which browsing by the elephant, giraffe and impala populations of Lewa has on the regeneration of *Acacia xanthophloea* seedlings, specifically in the riverine and swamp areas. The plots were subjected to varying degrees of protection from the browser species concerned.

Forest: A mature woodland of closed canopied trees, usually composed of tall trees derived from seeds (Allaby 1988). A vegetation unit where the aerial cover of trees greater than 2 m exceeds 75 % (Edwards 1983).

Grassland: An area of vegetation that is dominated by grasses. Grasslands occur where there is sufficient moisture available for grass growth, but where the environmental conditions, both climatic and anthropogenic, prevent tree growth (Cauldwell 1998).

Grazing capacity: The productivity* of an area of vegetation, expressed in terms of the area of land (ha) required to maintain a specific number of animals in a good productive and reproductive condition over an extended period, without deterioration of the vegetation or soils while under a particular system of management (Cauldwell 1998).

Habitat: The locality, site and particular type of local environment occupied by an organism (Lincoln, *et al*. 1998). The organism is adapted to the particular physical conditions within the environment (Maartin 1983).

Habitat type: A group of plant communities that resemble one another because of similarities in the habitats they produce (Allaby 1988).

Large stock unit: An animal with a mass of 450 kg, with a growth rate of 500 g per day, on forage with a mean digestible energy concentration of 55 percent (Meissner 1982). When used in wildlife management, this term is based upon the nutrient requirements of domestic stock.

Legume: A pod that releases its seeds by splitting lengthways down both sides, often explosively. A legume is a fruit of a member of the Leguminosae (Allaby 1988).

Management unit: An area of land, plant community* or group of plant communities that is considered to be a single entity for the purpose of applying management actions such as controlled application of fire, protection from fire or vegetation monitoring (Cauldwell 1998).

Model: A simplified description of a system, used as an aid to understanding the system. Mathematical models are constructed from numerical values given to the components of the system and the relationships among components (Allaby 1988).

Odds ratio: The odds ratio represents the probability of a success compared to the probability of failure. For example, if an event is twice as likely to occur than not to occur, the odds are two to one that it will occur (Freund & Simon 1991).

Ordination: A method of summarising patterns in ecological community data onto a single graph (Lincoln, *et al*. 1998). In vegetation science, this is a widely used method to set out relevés in a sequence relative to one another in terms of the similarity of their species composition (Cauldwell 1998).

Phenology: The study of the timing of recurring natural phenomena with particular reference to climatological observations (Allaby 1988).

Plant community: An association of plants that has a definite floristic composition, a uniform physiognomy, and which is bound to uniform habitat conditions (Cauldwell 1998).

Population: Social aggregations of the same animal species occupying a particular space. A group of individuals sharing some feature in common and living in a particular defined area, that is considered without regard to interrelationships among them (Allaby 1988).

Probability: The likelihood or chance that a particular event will occur (Berenson & Levine 1996). The probability of the occurrence of any event ranges from .00 (no possibility of the event occurring) to 1.00 (the event is certain to happen) (Spatz & Johnston 1984).

Productivity: The total mass of organic food manufactured in an ecosystem in a certain period of time. It is the net yield of the producers and consumers and determines the amount of living matter in an ecosystem (Maartin 1983).

Range: The limits of the geographical distribution of a species or group (Lincoln, *et al.* 1998). The area within which they seek food (Allaby 1988).

Recruitment: The influx of new individuals into a population by reproduction or immigration (Lincoln, *et al.* 1998).

Regeneration: Renewal or restoration of structures or tissues after damage or loss (Lincoln, *et al.* 1998). It is common in plants, occurring from stem and leaf cuttings and by other means of vegetative propagation (Maartin 1983).

Shrub: A woody plant that does not have a main trunk and which branches from the base (Lawrence 1989).

Stocking rate: An operator's estimate of an allowable land to animal relationship that will provide the most beneficial returns in terms of a given management objective. It is an expression of the number of animals per unit area that the operator actually runs on his veld. Whereas the ecological capacity of a given area is a product of the quantity and quality of the natural resources present, the stocking rate is a personal preference of a given wildlife manager, which can vary with the stated aims of the area involved, but which should never exceed the ecological capacity*.

Sustainable utilisation: The maximum extent to which a renewable resource may be exploited without depletion (Allaby 1988). Sustainable utilisation can be consumptive or non-consumptive.

Transect: In the present study this term refers to the plots used for sampling the attributes of the woody vegetation.

Tree: A woody perennial plant which has a single main trunk at least 7.5 cm in diameter at 1.3 m height and a definitely formed crown of foliage (Lawrence 1989).

Tree equivalent: An *Acacia karroo* tree with a height of 1.5 m. All leaf mass is included in the calculation of the tree equivalent.

Variable: Any symbol or term to which a number of different numerical values may be assigned (Lincoln, *et al.* 1998).

Woodland: A plant formation that includes mature trees that are spaced more widely and are more spreading in form than forest trees (Cauldwell 1998). A vegetation unit where the tree cover is from 1 to 75 % (Edwards 1983).