AN ECOLOGICAL DESCRIPTION OF A SEMI-ARID EAST AFRICAN ECOSYSTEM

by

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Range Science Department Science Series No. 11
Colorado State University

January 1972

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PREFACE

This report represents a slight divergence from the work normally reported in this series. Field work was not supported by, nor directly related to, the Department of Range Science or the U.S. IBP Grassland Biome study. On the other hand, it represents the results of work of common interest conducted by a Grassland Biome participant. It is important to maintain broad perspectives regarding foreign settings, problems, approaches, and results; and herein lies the rationale for inclusion of this paper in the Range Science Series and typing and publication support by the Grassland Biome.

The Mkomazi ecosystem typifies much of Africa's grazing land resource. The area exhibits the acute bush encroachment, limited water supply, and tsetse fly problems so common to African rangelands. As such it provides insight into many of the developmental problems encountered by ecosystem managers in Africa today.

The results reported emanate from a study Dr. Harris, formerly of CSU's Natural Resource Ecology Laboratory, conducted during the mid-60's while serving as a U.S. Peace Corps volunteer to the Tanzania Game Division. The work was conducted on very meager support common to these areas while the investigator was developing boundaries, camps, and roads simultaneously. Subsequently the data sets were analyzed and submitted in a dissertation as a partial requirement for the Ph.D. degree at Michigan State University.

To date there has been little integrated ecosystems research reported from the African continent, and this study represents the rudiments of the ecosystem approach to ecological problems. The study was deficient in several regards, but the extensive nature of the investigations provides a valuable backdrop to the more intensive investigations commonly reported.

Thus, it is with pleasure that we are assisting the dissemination of results of this initial endeavor.

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Lawrence D. Harris

ABSTRACT

From late 1964 through mid-1967 climatological, soils, vegetation, and animal studies were conducted in the semi-arid Mkomazi Game Reserve of northeastern Tanzania. An elevational gradient from 230 m in the east to mountain tops of nearly 1600 m above sea level in the northwest underlaid similar rainfall and temperature gradients. Aridity coefficients, based on the different temperature and rainfall conditions alone, were about 50% greater in the central section of the reserve than in the higher elevation northwest.

The soils were classified by the American 7th Approximation to a Comprehensive Classification System and were found to consist of about 75% camborthids (aridisols), 20% pellusterts (vertisols), and 5% miscellaneous types. Soil texture, organic matter content, permeability, and profile depth all reflected a gradient of conditions from west to east.

The vegetation was categorized into four major types: (i) dry montane forest, (ii) bushed and wooded grassland, (iii) seasonally inundated grassland, and (iv) bushland. Grass-forb aboveground standing crop values ranged from approximately 600 g/m^2 in the 500 mm rainfall regions of the bushed and wooded grassland to about 200 g/m^2 in the 350 mm rainfall regimes of the central-section bushland. Minimal estimates of aboveground net primary production varied from about 400 g/m^2/year on previously unclipped plots in the northwest to about 170 g/m^2/year in the east central section, while denuded plot productivities were about 300 and 150 g/m^2/year, respectively. Differences in forage-density and ground-cover indices reflected generally poorer rangeland conditions in the central and eastern sections of the reserve.

While the mean annual large herbivore density ranged from 12 animals/km^2 (5,548 kg/km^2) in the northwest to about 0.5 km^2 (700 kg) in the central and eastern sections, the dry season densities ranged from 23.7 animals/km^2 (12,705 kg/km^2) to much less than 1 animal/km^2 in the eastern sections. Seasonal herbivore biomass distribution patterns reflected a large wet season ingress of elephants (*Loxodonta africana*), zebra (*Equus burchellii*), oryx (*Oryx beisa*), and Grant's gazelle (*Gazella granti*) from adjacent Kenya as well as an eastward movement of herbivores from the dry season water source in the northwest. The east-west herbivore density gradient was nearly extinguished during the wet seasons.

Both spatial and temporal patterning within the large herbivore array is a major attribute of the animal community structure. Although 22 species of large indigenous herbivores inhabit the reserve, these are partially segregated by their affinities for the different vegetation types. A maximum of 12 and a median number of four species ($\bar{x}$ = 4.26) were recorded in local areas at any one time. Rhinoceros (*Diceros bicornis*) were most equitably distributed among the four major vegetation types (niche breadth index = 3.42) with eland (*Taurotragus oryx*), warthog (*Phacochoerus aethiopicus*), giraffe (*Giraffa camelopardalis*), and elephant next in order. Bushbuck (*Tragelaphus scriptus*), duiker (*Sylvicapra grimmia*), and buffalo (*Syncerus caffer*) were the least equitably distributed. Eland, gerenuk (*Litocranius walleri*), reedbuck (*Redunca redunca*), and giraffe were most equitably distributed through time. Herbivore species diversity was greatest in the bushed and wooded grassland and lower in the open grassland, bushland, and dry montane communities.

The niche overlap (on the habitat dimension) of hartebeest (*Alcelaphus buselaphus*), impala (*Aepyceros melampus*), and ostrich (*Struthio camelus*) was great (>0.8, limit = 1.0) while that of bushbuck, klipspringer (*Oreotragus oreotragus*), and duiker with most other species was slight (as low as 0.04, limit = 0.00). Of the carnivores, jackals (*Canis adustus*) reflected the greatest time and space overlap with the herbivores, while hunting dogs (*Lycaon pictus*) reflected the least.

From an ecosystem point of view, three of four species were found to dominate the structure (numbers and biomass) as well as at least one measure of community function, i.e., energy exchange. About 17.5% of the aboveground primary production (in terms of biomass) was estimated to be channelled through the large herbivore-carnivore pathway. The independent effects of elephants, cattle (*Bos indicus*), and fire on the vegetation are illustrated as are the combined effects of elephants, cattle, herbivores, and fire.

INTRODUCTION

Classically, ecological studies have meticulously described the structure of various communities. Rarely, however, have these works considered the functional properties of the components and only lately have they involved quantitative analysis to any substantial degree. While plant ecologists have only recently moved from the area of phytosociology, animal ecologists have been largely occupied with population dynamics. Thus, only of late has theoretical emphasis been placed on the structural and functional interrelations of natural systems.

Studies in the applied fields such as game management, on the other hand, have too frequently combined the abiotic and biotic components not of immediate interest into a "description-of-the-study-area" with the subsequent autecological results and conclusions portending conflicts of interest (Slade and Anderson 1970). The ecosystem concept, although described nearly 100 years ago (Forbes 1887), has fairly to play an integral role in the development of ecological studies and philosophy.

As normally defined (Odum 1962), the structural properties of an ecosystem refer to the (i) composition of the biological community; the species, numbers (and thus diversity), biomass, spacial and temporal patterning, and life history phenomena of the component species; (ii) the quantity, quality, and distribution of abiotic elements such as water, nutrients, climatic properties, and fire; and, importantly, (iii) the gradients of conditions extant in the system.

Systems function, on the other hand, is process oriented and involves rate functions: the biomass, energy, or nutrient flow rates through the system; primary and higher level productivity and decomposition rates; and the regulatory effects of animals on their environment and vice versa.

This study presents an analysis of some of the above mentioned properties of an East African semi-arid ecosystem. In particular, an attempt is made to interrelate structure and function since systems structure seems at least partially dictated by its function (Weiss 1958). The field work was conducted over a 30-month period from late 1964 to mid-1967 in the Mkomazi Game Reserve of northern Tanzania.

The analysis of a semi-arid community seemed particularly needed in view of the great extent of this kind of habitat the world over. Also, because of their marginal agricultural status, these lands constitute a high proportion of the natural area remaining in Africa today. As such, they are economically important to the controlling states because of the great tourist attraction and potential for game utilization. Moreover, the East African systems are of scientific value insofar as they constitute one of the most highly evolved and integrated biological systems on earth. Relative to other communities (e.g., temperate forests) our knowledge of semi-arid areas is primitive; and therefore, investigation of this ecosystem is important for theoretical as well as pragmatic reasons.

LOCATION AND HISTORY OF THE AREA

The Mkomazi Game Reserve of northern Tanzania lies along the Kenya border approximately midway between the Indian Ocean and Mount Kilimanjaro (Fig. 1). The ocean and Kilimanjaro are about 43 and 98 km from the nearest reserve boundary points, respectively. Stretching from the North Pare Mountains in the west to the Umba River in the southeast, the reserve includes most of the area between the Usambara Mountains and the border. More precisely, it lies between 3° 47' 30" and 4° 33' south latitude; and 37° 45' and 92° 12' east longitude.

The Reserve comprises 3,276 km^2 with a maximal length of 130 km and a maximal width of 41 km. Administratively, it is included in the Pare and Lushoto districts of the Kilimanjaro and Tanga Regions.

Baron Karl von der Decken traversed what is now the reserve in 1861 and was one of the first to leave a written account of his experiences (von der Decken 1869). Along with very poor hunting success in the area, he very nearly perished for lack of water. The Pangani Caravan Route crossed the area (Willoughby 1889), and several early explorers wrote accounts of passing through and hunting in the area. In 1886 Count Teleki killed one leopard and wounded another near the present Ibaya camp (von Hahnel 1890). Monseigneur Le Roy travelled through the area two years later and mentioned "antelopes everywhere" (Le Roy 1893). During World War I, Colonel von Lettow Vorbeck used the area extensively in his campaign to destroy the British railway line in what is now Kenya. In addition to Lettow Vorbeck's supply routes, other access tracts were cut through the area in 1928 for a hunting safari by the Prince of Wales.

The Mkomazi Reserve was officially established in October 1951 (Anstey 1956). Although game rangers then explored and patrolled the area extensively to prevent illicit hunting, effort was also made to establish boundaries, tracks, camps, and water supplies. Unfortunately, their meager resources stifled success.

For over a decade it has been debated whether or not the wildlife and aesthetic values of the area warrant preservation as a game reserve. Other human interests in the area have been high, and it has been frequently suggested that the agricultural value may exceed that of a game reserve.

Observations in the area from 1880 to the early 1950's suggest that wildlife was then abundant. Willoughby (1889) referred to it as offering "excellent and varied sport." Game Department reports of the Thirties also praised it highly, and in the 1932 annual report (Tanganyika Game and Tsetse Division 1933), the Pare Reserve (immediately south of the present Mkomazi) was listed as "one of the four most valuable." In 1934 (Tanganyika Game and Tsetse Division 1935) it was stated that "with closer protection . . . the same District can become one of the most attractive game areas in the territory," and in 1950, before its establishment as a reserve, the area was described as carrying "large concentrations of game."

On the other hand, human pressures have been high and the animal populations have not responded to protection as many game officials felt they should. Indeed, the mere establishment of the Mkomazi Reserve is, in part, a reflection of human pressure since it was a *quid pro quo* negotiation for the former Pare Reserve which was "dereserved" in 1950 for agricultural development. Since its establishment, the boundaries were retracted in 1957 and again in 1966. Departmental files are full of denied applications to hunt, harvest wood, graze, mine, fish, and live in the area, yet offenders have had a high degree of success and the 3,000 cattle resident in the reserve in 1967 attest to their continued pressure.

With the establishment of the College of African Wildlife Management at Mweka in 1963, the Mkomazi was first chosen as a field study area. This decision was reversed however, since it was thought that the area did not contain animal populations large enough to be sufficiently valuable for instructional purposes. Despite the prevalent attitude among conservationists that as many areas as possible should be brought under National Park jurisdication and the recommendation of a UNESCO adviser (Huxley 1961) that the Mkomazi area should be included in the park system as a representative semi-arid area, the Tanzania Parks administration seems to have given the area low priority for inclusion in the system.

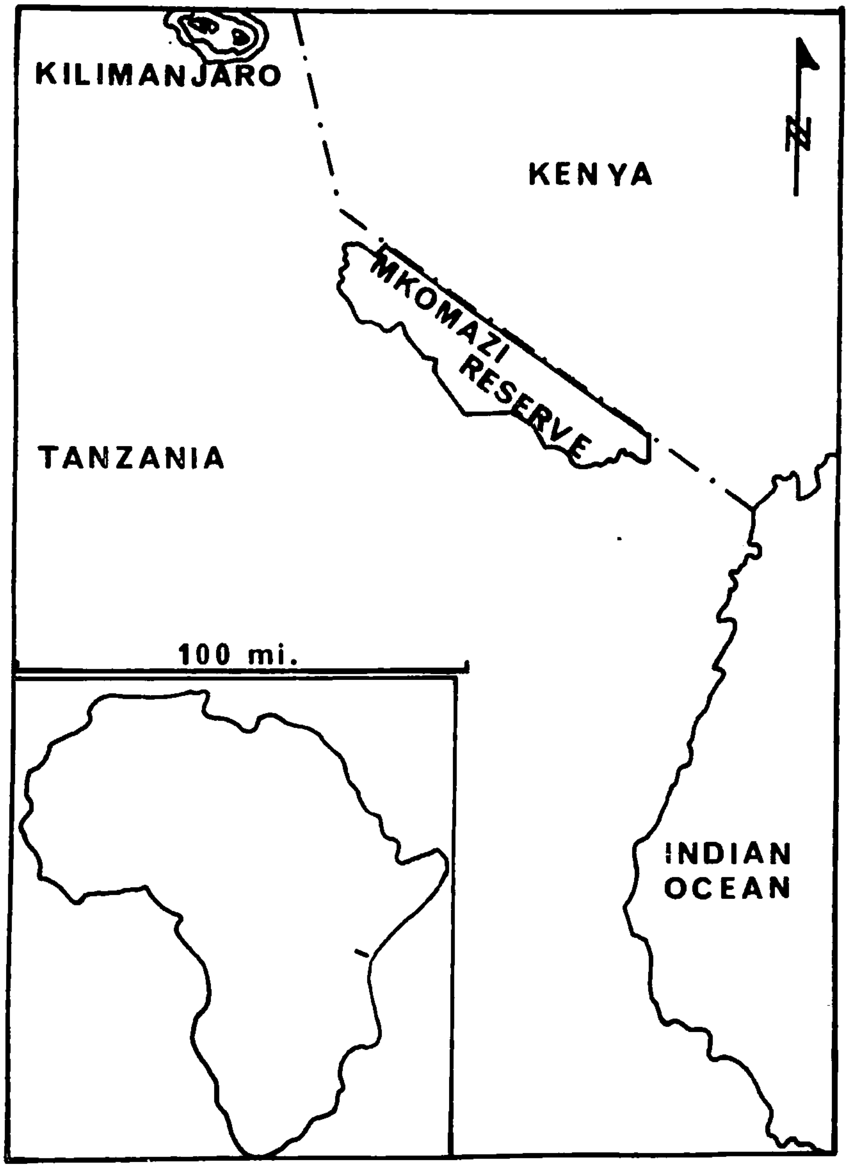


Fig. 1. The Mkomazi Game Reserve of northern Tanzania lies along the Kenya border between Mt. Kilimanjaro and the Indian Ocean.

PHYSIOGRAPHY AND GEOLOGY

The foothills of the North Pare Mountains and the extensive plain of the Umba Steppe are the two main physiographic features of the reserve.

The North Pare Mountains form the northwestern boundary of the reserve. Kinondu Hill, the westernmost and highest point of the reserve, reaches an elevation of 1,594 m above sea level and several other peaks exceed 1,225 m. The area covered by these mountains is approximately 130 km^2, or about 4% of the total. A geologic fault in the mountains formed the Pangaro-Dindira valley which is presently at 850 m elevation and only slightly above the level of the surrounding plain. With the exception of the Maji Kununua-Pangaro fault, there are no spectacular escarpments, and many large, open valleys and dip slopes on the eastern side of these mountains form the transition zone from mountain to plain.

The Umba Steppe, comprising the open plains area of the reserve, rises from an elevation of 230 m above sea level in the southeast to 760 m in the northwest, while residual hills and hill ranges rise to 600 m above the plain and approach mountain stature. These hill ranges, grouped in six general masses, occupy an area of approximately 200 km^2. Only 15 km south of the reserve, the massive Usambara Mountains rise more than 1800 m above the plain to attain heights of nearly 2500 m.

The slightly southeastward-sloping plain has a moderately rolling topography with shallow alluvial valleys cutting through the bush and grassland. These drainage "mbugas," as they are known in East Africa, are spaced approximately 10 km apart on the more gently rolling land surface, but may be at 5 km intervals where the slopes are greater. Although they are usually grassed and flat, occasionally steep-banked gullies cut and wind their way through the middle of these seasonally waterlogged drainageways. In general, the drainageways are directed southeastward, but along the Kenya border they tend to lie in an east-west direction.

Surface runoff is drained from the area by five rather ill-defined drainage systems. The extreme northwestern section of the reserve drains northward into Lake Jipe, while the rest of the watershed flows essentially southward into the Kisiwani and Umba Rivers. Since block faulting and tilting movements in the Pare Mountains have created barriers to easterly drainage (Tanganyika Ministry of Lands, Forests and Wildlife, Survey Division 1963), the only naturally-occurring permanent water in the reserve is the Umba River which forms the southeastern boundary. Artificial dams have been constructed (one in 1968 subsequent to this study) at two locations in the western half of the reserve and maintain permanent water sources by catching the seasonal runoff (see Fig. 2).

The North Pare Mountains are formed of metamorphic rock assigned to the Usagaran system of the Precambrian (Tanganyika Ministry of Lands, Forests and Wildlife, Survey Division 1963). The main rock types encountered are high-grade, metamorphic granulites and granulitic gneisses representing a very thick series of metamorphosed pelitic and psammitic sediments with intercalations of carbonaceous and calcareous strata. For the most part, the rocks are composed of four granulitic types: hornblende, pyroxene, quartz-feldspar, and calcsilicate. The pyroxene granulites dominate the mountainous areas, but the quartz-feldspar types are also common and frequently contain garnets.

The mountains have a complex structural history with high-grade metamorphism indicating that high pressures and temperatures were at work. Two main movements caused folding along a north-east axis with cross-folding along a northwesterly trend. The movements have so disturbed the original sedimentary layer that a pseudo-bedded series has been formed. Other faulting created the present tilted block-line form and the large Pangani valley to the west, while the Pangaro valley within the reserve was formed by subsequent faulting (Tanganyika Ministry of Lands, Forests and Wildlife, Survey Division 1963). Occasional minor earth tremors suggest continuing movement in the present time.

The open plains are underlain by Precambrian rocks covered with superficial alluvial Neogene deposits, including some calcareous tuffaceous material derived from the Kilimanjaro volcanicity and other deposits around Lake Jipe. Yet, where extensive erosion has occurred or where the sedimentary rocks have been thrust up, the ancient gneisses, schists, and crystalline limestones strike the surface.

The Ikongwe hills differ by being composed of a meta-anorthosite with drawn out diopsides forming prominent linear bands. The conspicuous whitish, high sodium-content soils in this area have developed from labradorite (Tanganyika Ministry of Lands, Forests and Wildlife, Survey Division 1963).

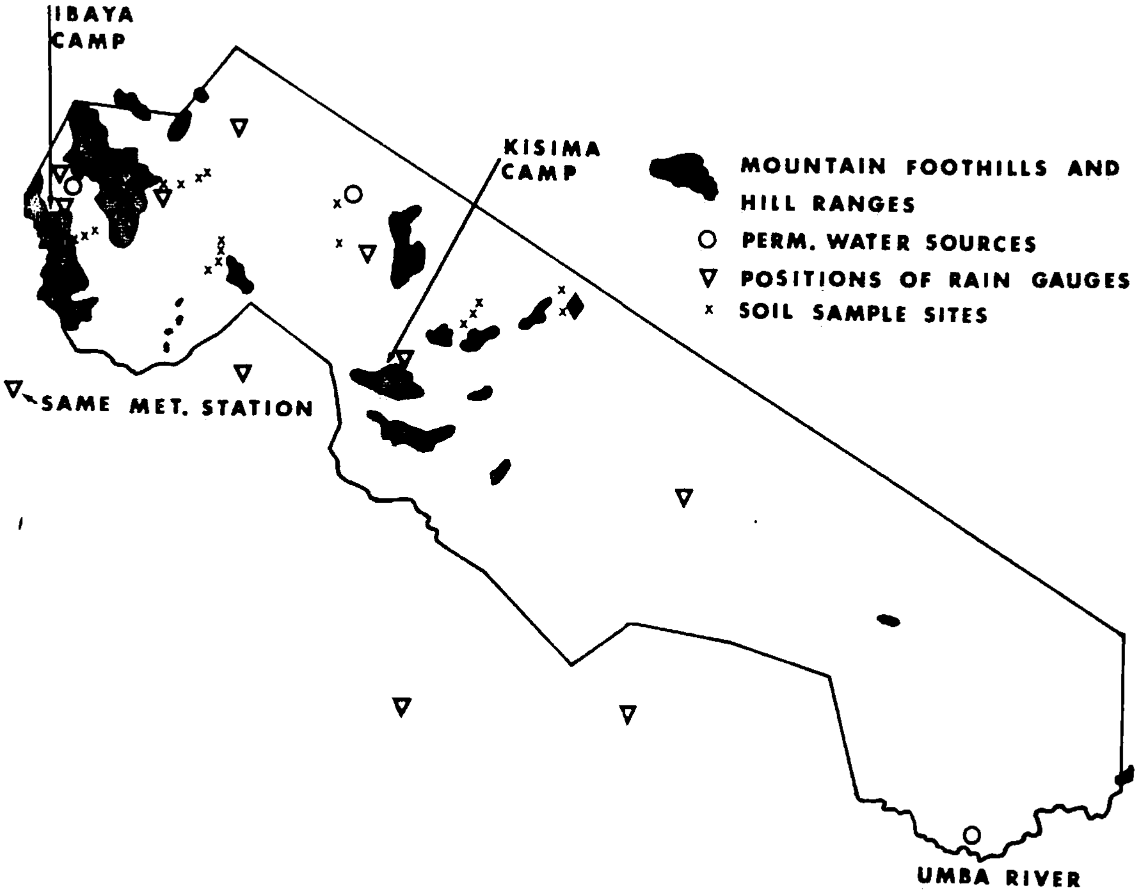


Fig. 2. The locations of hill ranges, permanent water sources, rain gauges, and soil sample sites in the Mkomazi Game Reserve.

CLIMATE

The factors controlling the overall weather patterns of East Africa are not yet fully known (Griffiths 1962). While some early observers tried to explain the conditions by continental weather fronts similar to those of temperate regions, others associated the phenomena with the Inter-tropical Convergence Zone (ITCZ), a zone of low pressure at the confluence of the NE and SE trade winds (Thompson 1965, Kimble 1960).

Although the seasonal variations in rainfall seem to correlate with the movement of this convergence zone back and forth across the equator, variations apparently due to topography and the great lakes of East Africa modify conditions to the extent that they cannot be said to follow the typical ITCZ pattern (Griffiths 1962). There is little or no evidence to suggest that rainfall in East Africa is associated with any moving air-mass systems, and storms are believed to be the result of local developments (Thompson 1965). Since equatorial temperatures characteristically show little variation, variations in rainfall are a dominant climatic factor, especially in a semi-arid area like the Mkomazi. Further, since the weather patterns are not associated with moving fronts, as is the case in temperate regions, the variance in rainfall is great and the deviations from the mean as well as the intensity of individual storms assumes a major role in ecosystem function.

As mapped by the East African Meteorological Service, most of the Mkomazi area lies between the 50 and 75 cm rainfall isohyets with the northwestern foothill area in the 75 to 100 cm isohyet zone. According to the Thornthwaite classification, the area falls within the megathermal climatic type (A') with a moisture index (D) of -40 and -20 and an annual water deficit of 80 to 100 cm (Carter 1954).

Techniques

During this study, climatic observations were made over a period of two and a half years. Eight standard, 5-inch (12.7 cm) diameter, storage type rain gauges were established in the western half of the reserve (Fig. 2). The gauges were buried in the ground with the upper rim extending 10.2 cm above the surface, and the surrounding vegetation which might intercept rain was consistently removed. Two gauges (at Ibaya and Kisima camps) were measured each day of rainfall except on a few occasions when no observer was on duty at the end of a month. Other stations were measured less frequently; and since the Kamakota gauge was over 100 km (by road) from the main camp, it was rarely measured more than once per month. Evaporation from the gauges did not appear to be significant since the funnel opening extended below the water surface.

Rainfall data were also obtained from four stations near the reserve, three of which are located on sisal plantations in the higher-rainfall foothills of the nearby mountains.

A meteorological station including wet and dry bulb and maximum and minimum thermometers, a cup-counter anemometer, and a calibrated Gunn-Bellani radiometer was established at Ibaya camp in the western end of the reserve (915 m elevation). The thermometers were housed in a standard Stevenson screen which, along with the rain gauge, anemometer, and radiometer were located in a barbed wire enclosure. The anemometer was positioned 3 m above the ground.

While the data from this station are important for defining local conditions and short-term variation, the long-term records of the East African Meteorological Station at Same, only 5 km from the reserve, have been used to estimate certain parameters.

Rainfall

Although 2 years is a minimal period to measure such a variable factor as rainfall, some meaningful results were obtained. The composite monthly rainfall data collected within the reserve along with the data of the Same Meteorological Station for the same period are given in Appendix I.1.

With the data of the Kisima station excluded because of its proximity to the Kisiwani mountains, a regression analysis of monthly rainfall on the east-west location of stations yielded an east-west rainfall gradient. From the west end of the reserve eastward, there was a mean reduction of approximately 1 cm of rainfall per year for each 5 km distance. From this it is predicted that the Kamakota station in the center of the reserve would receive 15 cm less rainfall annually than the western end of the reserve. This predicted decrease is slightly less than empirical results of the study indicate.

Rainfall statistics for the eight stations during the period of study indicated that the calendar year totals lie between 55 and 65 cm for the western end of the reserve, with the Kisima area in the west central section receiving about the same amount because of its proximity to the Kisiwani Mountains. The more open steppe area around Kisima received about 10 cm less, however, and the shortgrass prairie around Maori (20 km further east) received only 40 to 50 cm per year. Along with the rainfall statistics for the Kamakota gauge, the generally xeric conditions of the bush and the absence of drainage lines or erosion gullies suggest that this central section of the reserve must only rarely receive 40 cm of rainfall.

Although no rain gauges were positioned in the eastern half of the reserve, observations of storm patterns and vegetation conditions suggest a slight increase to 40 to 45 cm in the eastern end.

To evaluate the rainfall conditions during the period of study with respect to temporal trend it is necessary to refer to the long-term data of the four stations outside the reserve (Appendix I.2). Based on a composite of 52 years of observations, the 1964, 1965, and 1966 totals were all below the average for the respective stations. It is therefore concluded that the period of study was relatively dry with respect to the general conditions for the area.

Trend analysis of the data from the four stations outside the reserve revealed no significant monotonic or cyclical trend in any of the data (Cox and Stuart's test for monotonic trend and Noether's test of cyclicity as found in Bradley 1968).

The seasonal pattern of rainfall in the reserve is one of a clear bimodal distribution with peaks of occurrence in March and October (Table 1). The total, however, is not equally distributed. About 50% of the annual amount occurs during the "long" rainy season centered on the vernal equinox, while only about 25% occurs during the "short" rains associated with the autumnal equinox. A further 20% usually occurs in January and February as an extension of the autumnal rains or as an antecedent to the vernal rains. The remaining 5% occurs from June through September as scattered showers during the long dry season.

To substantiate this pattern, reference was made to the long-term data of the outside stations. But before such reference is valid it must be established that the pattern of rainfall for stations within and outside the reserve is similar. Concurrent observations at the Ibaya station (within the reserve) and the Same Meteorological Station were made for over two years and the 28 monthly totals for the two station are very highly correlated (P < .001). Correlations of data from other gauges in the western end of the reserve with the Same data are also highly significant (P < .01), and correlations of gauges in the central section of the reserve with other stations outside the reserve are also significant (P < .05). It appears, therefore, that the long-term Same meteorological data can be validly used to describe the seasonal pattern of rainfall in the western end of the reserve. The 30-year monthly totals corroborate the bimodality of the pattern.

Data for individual storms suggest that 5-cm rain storms are quite common, while only one or two 10-cm storms occur per year. The most intense storm observed was that of February 7, 1967, when over 27 cm fell at Dindira Dam in approximately 30 hours. Normally, the rains of the vernal equinox are more effective because of their mild nature, while less penetrating downpours occur more frequently during the autumnal equinox and often cause severe runoff and erosion.

Table 1. Seasonal rainfall and aridity coefficient patterns for the Ibaya station in the Mkomazi Reserve. The upper figure of each set refers to the seasonal rainfall in centimeters, while the lower figures give the mean aridity coefficient with standard error as calculated by the Thornthwaite method. The lower aridity coefficient limit is -1.0.

Season	1964-65	1965-66	1966-67
Short dry	--	0.0	0.0
(Dec.-Jan.)		-1.00 ± .0	-1.00 ± .0
Long rainy	45.2	90.7	162.8
(Feb.-May)	-0.62 ± .2	-0.45 ± .2	+0.32 ± .2
Long dry	4.1	0.0	--
(June-early Oct.)	-0.96 ± .2	-1.00 ± .0	
Short rainy	52.8	37.1	
(Oct.-Nov.)	-0.45 ± .2	-0.42 ± .1	

Temperature

Full time climatological observations were not possible, and even daily temperature observations at standard times could not be assured. The maximum and minimum temperature recordings are valid, however, since the mercury column remains in the most extreme position until reset by the observer. The maximum recorded temperature for Ibaya camp was 37.8°C, while the minimum was 9.4°C.

The temperature data from the Ibaya station are not sufficiently complete to warrant calculation of mean daily, monthly, or annual temperatures. The ambient temperatures were, however, highly correlated with those of the Same station and the afternoon (1600 hours) temperatures were not significantly different. Data from the Same station are therefore used as representative of conditions in the western end of the reserve.

The mean annual temperature for the two full calendar years of the study (1965 and 1966) was 23.1°C with a mean annual minimum of 17.5°C and maximum of 29.0°C (Appendix I.3). Mean monthly temperatures calculated from the daily recordings are most valuable for determining seasonal patterns; and the data show that July and August are usually the coolest months, while the highest daily temperatures occur from December through February. The difference between the mean monthly temperatures for these seasons, however, was only 5°C.

The maximum recorded temperature for the Same station during the study was 36.8°C and the minimum was 10.8°C (Appendix I.4). The greatest absolute range in temperature during any month was 20°C, while the mean monthly range was 17°C.

In accordance with Chapman's Rule (a change in the mean annual temperature of approximately 6°C for each 1000 m of elevational change, Allee et al. 1949), it is hypothesized that the central section of the reserve averages 2.5°C higher and that the eastern end has temperatures about 4°C higher than those reported above.

Solar Radiation

As for several of the meteorological instruments, data recordings from the radiometer were too infrequent to warrant quantitative analysis. All measurements fell within the isopleths given by Thompson (1965) however, and the following figures represent elevation and latitude corrected interpolations from his Nairobi and Dar Es Salaam values.

The mean solar radiation for the western, central, and eastern sections of the reserve are approximately 4.54×10^3, 4.47×10^3, and 4.40×10^3 kcal/m^2/day, respectively. The maximal values of about 5.7×10^3, 5.6×10^3, and 5.5×10^3 kcal/m^2/day occur in February, while the annual daily minima of about 3.4×10^3, 3.5×10^3, and 3.6×10^3 kcal/m^2/day occur during the cloudy periods of July.

Relative Humidity

The absolute amount of moisture in the air relative to the saturation density at any given ambient temperature is frequently used as a measure of the evaporative power of the atmosphere. This measure is refined considerably when air movement is included in the calculation, but patterns of relative humidity are also instructive as an index to evapotranspiration. Monthly maxima, minima, and mean relative humidity figures have been calculated from the 1600 hour wet and dry bulb thermometer readings at the Same station (Appendix I.5). The lowest mean monthly relative humidity values (40 to 50%) occur during the short dry season of January and February, and the highest values (50 to 60%) occur during the vernal rainy season of March to May. Although these mean values appear high for a semi-arid area, the afternoon relative humidity rarely falls below 20% during the most severe dry periods.

Wind

Daily and seasonal wind patterns are important as they greatly affect evapotranspiration rates. Along with the increase in the evaporative power of the air, there is a bending and flexing of leaves and stems which probably affects plant losses.

The greatest wind movement occurs during the long dry season when a daily run of the anemometer frequently exceeds 160 km. Although daily wind patterns are largely associated with differential rates of heating of the air column and the consequent convection currents, seasonal patterns are determined by the SE and NE trade winds from the Indian Ocean. The SE trades are more noticeable and normally blow over the area from May to October, whereas the NE trades have only a mild effect from November to May. Significant air movement is usually not initiated until around 1200 hours, but by 1600 hours the winds are considerable and gusts up to 15 km/hour frequently occur during the dry season. Air movement usually subsides shortly after dusk.

Aridity Coefficients

It is an oversimplification to describe the seasons of East Africa as simply rainy or dry (Howe 1953). Integration of the factors discussed above, along with the hours and intensity of solar radiation, soil water storage, and others, produces an overall effect which is greater than the sum of the parts (Jowett and Eriaku 1966). For instance, a week in June with no rainfall is climatologically very different than a similar period in October. Soil water is much more reduced during the latter period; and wind, solar radiation, temperature, relative humidity, and day length all effect a much greater severity of conditions on the biotic components of the system.

Evaluation of this whole array of factors is probably more important when dealing with natural animal populations than with geography or crop science since animals are dependent upon a host of environmental requirements over and above the water and nutrient balances which largely control vegetation growth. Furthermore, doing the simplest quantitative analysis of animal ecology requires the use of some quantitative measure of seasonal climatic conditions. The more of the above considerations that can be integrated into a single index of climatic severity, the more meaningful will be any analytic results.

The Thornthwaite (1948) classification of climate takes into account several factors other than rainfall while remaining calculable with a limited range of meteorological statistics. His potential evapotranspiration index contains expressions of temperature, day length, and radiation while using 4 inches (10.2 cm) as the mean available water storage capacity of different soil types. The overall index of aridity is calculated with the deficiency (evapotranspiration minus precipitation) as a percentage of need (potential evapotranspiration). Thus, in periods when precipitation exceeds potential evapotranspiration, there is a surplus of water and the index is positive; whereas if evapotranspiration exceeds precipitation, there is a negative balance.

The Thornthwaite measure and other equations based on mean temperature have been criticized on several grounds. The most important of these is that they do not account for the lag of temperature behind radiation. But since soil temperatures on or near the equator are characteristically isothermal (Weber 1959, Banage and Viser 1967) and since no short-term estimates are made here, any error involved would seem at least partially obviated by the conditions of the study. Use of the Penman equations (Penman 1948, McCulloch 1965), which are presently favored in East Africa (Dagg 1965), required meteorological statistics not commonly available. Furthermore, these equations have also been criticized as inadequate (Holdridge 1967).

In spite of its admitted defects (Thornthwaite and Hare 1965), the Thornthwaite measure of water balance is used here with the major purpose being to derive a comparative index of aridity for different seasons of the year and different areas within the reserve; any constant bias will be of negligible importance. Only rarely does the amount of precipitation exceed the need for any appreciable period of time (Table 1). As expected, however, the aridity coefficients are largest (negative) during the June to September dry season (-1.0 is the limit) when there is no appreciable rainfall and smallest (frequently positive) during the vernal rains.

From Chapman's relation of increasing temperature with decreasing elevation and Kenworthy's regression equation for mean annual temperature as a function of elevation in East Africa (Trapnell and Griffiths 1960), it can be predicted that the annual potential evapotranspiration in the center of the reserve is approximately 162 cm (Appendix I.6). This is over 10% greater than that of the western end (145 cm). When the lower amount of rainfall of the central section is also considered, the mean aridity coefficient for 1966-67 (-.71 ± .10) was nearly 50% greater than that of the Ibaya station (-.49 ± .14). From this I conclude that the general climatic conditions in the center of the reserve are at least 50% more severe than those of the western end.

The General Climatic Pattern

Beginning with the vernal, low-intensity rains of February and March, the ground is continually moist for a period of approximately 10 weeks. The humidity is sustained at a reasonably high level, and the vegetation quickly reaches its asymptotic standing crop. The temperature gradually decreases as the season progresses and the sun moves away from its apogeal position.

June is the month of transition into the dry season, and southeasterly trade winds begin to blow as the rains subside. The sky frequently remains overcast until late morning early in the month, but clear nights and days prevail later on. By July the weather turns cool and the year's minimal amounts of solar radiation and minimal temperatures occur. The grass dries out quickly as the winds increase and humidity drops. By August the countryside is usually heavily burned, leaving the blackened grass tussocks to absorb more heat.

A period of intense desiccation prevails throughout August and September as the ambient temperature rises, near highest daily sunshine hours and light intensities occur, and wind velocity reaches the maximum.

In mid-October the first thunder showers of the autumnal rains occur, and considerable erosion often takes place as a result of the heavy downpours and the lack of vegetation cover. As the vegetation regains its stature, humidity increases, and temperatures are moderated by the cloud cover and evaporation of the rainfall.

The sporadic rains of November and December are followed by a short dry season of six to eight weeks duration. The lack of rain during this period is accentuated by maximal annual temperatures and amounts of solar radiation (Thompson 1965).

Thus, in spite of the relatively isothermal conditions, sharp seasonal differences exist; and there seems little doubt that the long dry season from June through October is as severe an environmental stress on the organisms as the winter months of the north temperate regions are on mid-latitudinal species. These seasonal differences are likely to be manifested in various ways by the animals inhabiting the area.

Along with the seasonal patterns, the rainfall and temperature gradients within the reserve also must cause differing degrees of environmental stress. In addition to the generally 50% greater mean aridity coefficients of the central section, the soils get shallower toward the central and eastern sections (profile G was only 50 cm deep). Based on texture, structure, and organic matter considerations, these soils undoubtedly have lower water holding capacities than those of the west. If quantitatively evaluated, such edaphic factors would force yet a greater divergence of aridity coefficients between the east and west. Similarly, compared to the northwest, the central and eastern sections have greater air movements and less cloud cover which must accentuate the evapotranspiration and overall severity of conditions.

In total, climatological observations show appreciable differences between the different areas within the reserve. These conditions surely induce great differences in vegetation and animal productivities as well as in animal densities and movement patterns.

SOILS

To date there is no generally accepted classification of African soils or even overall agreement in naming the more important groups (Anderson 1963, Sys 1967). The soils of the region encompassing the Mkomazi Reserve have been variously described by soil researchers as: "skeletal-montmorillonoid with $CaCO_3$ (semi-arid phase)" (Calton 1954); "kaolinite soils" (Spurr 1954); "red soil to calcareous black soil sequence, with intermediate soils rarely containing murram concretions and undifferentiated lowlying grey soil dominant" (Tanganyika Atlas 1955); and "brown to yellow-red sandy clay loams with laterite horizon" (Scott 1962*a*).

In an attempt to unify the soils work being done in Africa and provide a single classification system for the continent, the Commission for Technical Cooperation in Africa (CCTA) sponsored the production of a continental pedological map and explanatory monograph (D'Hoore 1964). In this work, the soils of the Mkomazi region are classified as "non-differentiated, ferruginous tropical soils (jd)."

It seems clear that much of the confusion regarding these classifications results from over generalization and inadequate attention to the definition of terms. This, of course, is partially justified by the scale of mapping necessary.

More recently, workers have attempted to define specific parameters for "keying out" various soils (Makin 1969*b*, USDA 1960, 1967), and the American 7th Approximation to a Comprehensive Soil Classification System (USDA 1960, 1967) is gaining wide recognition and support (Makin 1969*a*; Sys 1967, 1968; Donahue 1970). I have classified the Mkomazi soils according to the 7th Approximation and, even if the more rigorous classification into families, orders, and groups provides little heuristic value, it makes available for comparison the considerable literature on similar, well-studied American soils.

Techniques

Seventy-eight samples were collected during early 1967 from 20 sites and 18 profile pits. The locations were chosen to represent the important vegetation and soil associations of the western half of the reserve. Twelve profile pits were dug in three catenary sequences from high on the slope to the valley below (see Fig. 2). All pits exceeded a .9 m depth and most were dug to 1.8 m or more.

Sampling was done according to instructions and procedures described in the USDA Soil Survey Manual (1951). Complete field descriptions including vegetation, surface and profile drainage, moisture, texture, structure, consistence, permeability, organic matter, roots, and fauna were recorded. Color was determined by comparison with a Munsell chart. When profile horizons were not obvious, sampling intervals of 30 cm were used for the surface downward. Samples were chipped from the profile wall, bagged in cloth, air dried, and sent to the Northern Agricultural Research Center, Tengeru, Tanzania, for chemical analysis.

Procedures of analysis followed those of Mehlich et al. (1962). Bases were extracted by leaching the soils with normal ammonium acetate at pH 7.0, and exchange capacity was determined by displacing absorbed ammonia with normal potassium sulphate and by subsequent distillation of the ammonia. Mechanical analysis was by the hydrometer method using a mixture of sodium silicate and sodium hexa-metaphosphate as a dispersing agent. Total and organic phosphorus were determined by the method of Walker and Adams (1958), and organic carbon by the Walkley and Black method, assuming 80% recovery of carbon (Anderson and Talbot 1965).

Based on the field descriptions and analytical reports, the soils were classified according to the keys in the supplement to the 7th Approximation (USDA 1967).

The Catena Concept and Typical Soil Sequences

Milne (1936) noted that where the topography of an area consisted of a repetition of similar crests and hollows, there was also a recurrence of the soil sequences from one slope to another. He then coined the term "catena" for this succession of soil types along topographic gradients and later adopted it as a mapping unit (Scott 1962*b*). A catena consists of three major complexes: the upper slopes termed eluvial; the lower, often concave, slopes termed colluvial; and the valley bottom or lowland termed illuvial or alluvial. This concept seems especially applicable to the Mkomazi as it lies in the region of Milne's work, and field observations confirm that where climate and parent material are similar these topographical soil sequences are also quite similar (Milne 1947; Burtt 1942; Morison, Hoyle, and Hope-Simpson 1948). The pattern is so predictable that Morison et al. (1948) stated that, "The monotony consists rather in the repetition of the same limited series of changes over huge tracts of country." In practical terms, the three zones can be recognized by their red to reddish brown, brown to gray brown, and gray to black soil colors, respectively. Although specific parameter values vary considerably in local areas where parent material, climate, or some other ecological factor has greatly influenced the development, the concept is empirically sound.

Fig. 3 illustrates a typical catenary sequence of soils from high on the slopes to the seasonally waterlogged drainageways below. The nomenclature follows that of the 7th Approximation; and a complete listing of the names derived for the soils sampled, along with similar soil series described in the U.S. and its territories, is listed in Appendix II.

The Red and Reddish Brown Soils

The predominant soils of the Mkomazi are the medium-textured red earths (aridisols) which occupy most hills, ridges, and fan slopes and are characteristic of the freely drained areas (Milne 1936, Dames 1959). Ranging from rather heavy sandy clays to lighter-textured sandy and silty loams, they are all low in organic matter (usually <1%) and

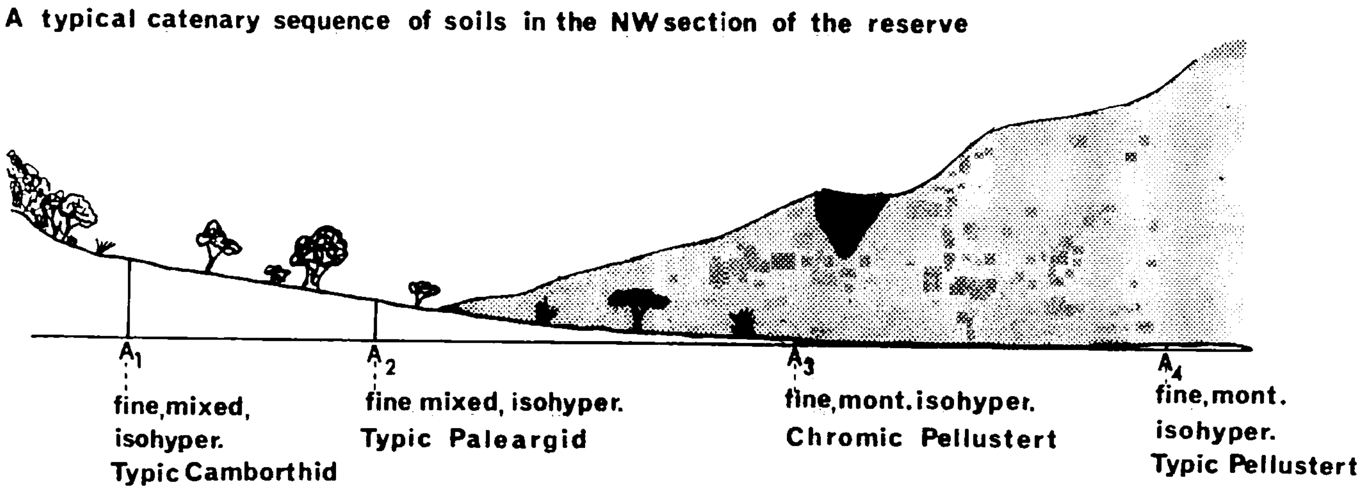


Fig. 3. The catenary sequence of soils along a topographic gradient in the northwestern section of the Mkomazi Reserve near the Dindira study area. The abbreviated adjective "mont." refers to a montmorillonitic clay structure, while "isohyper." means isohyperthermic.

erosive. Although surface runoff is often excessive, there is usually rapid water infiltration and profile drainage.

Although predominantly yellowish red (5YR4/8), local variations in organic matter and chemical makeup cause slight variations. Red coloring results from unhydrated iron oxide which is unstable under moist conditions and therefore lost in the less freely drained areas. This coloring is accentuated in the central and eastern sections by more severe dehydration of the hydroxides, and it is more prominent due to the lower percentage of grass cover and the absence of a humic layer (Milne 1947).

These soils tend to be shallow and coarse textured high on the slopes, becoming deeper and finer textured with more organic matter lower down. In the northwestern area of the reserve these soils are very deep (4 m or more), but farther east on the Umba Steppe they tend to be shallow with frequent rock outcrops.

Typically, the red soils high on the slopes are Camborthids and manifest eluviation by the absence of significant clay accumulations. But as the slope decreases, there is an accumulation of silicon clays in an argillic horizon which puts the soils in the suborder of argids as opposed to orthids. If this accumulation of clay particles exceeds 35%, as is the case in the B catena near the Mbula study area, the classification becomes Paleargid. The G profiles toward the center of the reserve manifest erosion; and in the case of G_2, even though an argillic horizon exists, the percent of clay is sufficiently low to change its classification to Haplargid. In the case of G_1, erosion has so truncated the profile that the classification is changed at the ordinal level (to an Entisol); and the shallow, skeletal soil is described as a Lithic Torripsamment.

In a few local areas the soils have a greater percentage of organic matter (from 1 to 2%) without a change of texture or structure. This tends to increase the color and chroma values, and the soils are classified as Mollic Paleargids. Although a number of factors may influence the amount of organic matter present, it is likely that the combination of lighter grazing pressure, less frequent burning, and somewhat less erosion explains this increase, at least in the area of the B catena.

Brown and Gray Brown Colluvial Soils

Normally, a narrow zone of colluvial soils lies between the red eluvials of the upper slopes and the heavy black clays of the valley bottoms. This band of transitional soil may be of negligible width and only perceptible by textural and structural characteristics, or it may be of considerable extent. This texture may vary considerably because of the differential deposition from above, but most are fairly heavy textured loams and clay loams with a somewhat sandy surface. They have high conductivities (200 to 300 mmhos/cm) relative to the more freely drained profiles above, and the cation exchange capacities also increase because of the increased clay and organic matter fractions. By being low in the catenary sequence they have escaped leaching; the profile drainage is slow, and yet they are sufficiently above the lower drainageways to escape waterlogging. Regardless of their relative unimportance due to the small area covered, these soils are valuable because of the "edge-effect" of high mineral reserves and favorable structural and textural characteristics.

Though commonly occurring in the intermediate catenary sequence, these soils at times occupy the whole surface of ridges and slopes and may blend with red soils at arbitrary but well-defined points in an otherwise uniform topography (Milne 1936, 1947). The upland gray and gray brown soils are frequently firmly packed clays, but also blend to lighter textured soils with poorly developed structure. Soils of the "C" profile sequence exemplify the characteristics of the elevated clays of the Mkomazi. Because profile drainage is poor and the expansibility coefficient is low, little dry season cracking occurs. The soils of this series tend to be lighter colored (5YR/1) than the lowland vertisols, and the whole group (particularly C_1) is underlaid by an extremely deep (over 7 m) light gray alluvium. The extreme erosibility of these soils is at least partially due to the high amounts of sodium salts causing floculation and a low structural stability.

Heavy Black Clays of the Valley Bottoms

Commonly known as "black cotton" soils in Africa, these clays are usually limited to drainageways and poorly drained bottomlands. They are products of considerable base accumulation and the formation of montmorillonitic clay particles which have high expansion coefficients. Characteristically containing more than 35% of these 2:1 lattice clay particles, they are plastic and sticky when wet and wide-cracking (up to 10 cm) and rock-like when dry. Because the lower horizons are subject to pressure when the soils swell, they are compact and nearly impermeable to water (Smith 1965); and since they occupy the drainageways and depressions, they receive considerable runoff water becoming seasonally inundated and waterlogged. Despite the fact that their water retention capacity is high, the absolute amount of moisture available for plant utilization is very low (Smith 1965).

Profiles A_3, A_4, B_5, and D_3 are representative of this soil type. All are classified as Pellusterts because of climatic conditions and their color chromas, but each is put in a separate subgroup for various reasons. Although these soils are very rich in the mineral elements of fertility as well as organic matter, salinity and alkalinity are often too great for preferred rangeland vegetation species; and vegetation productivity may even be suppressed by induced elemental deficiencies. Moreover, their utility is greatly limited by their physical characteristics and the gilgai microrelief may well affect ungulate locomotion.

Fertility Considerations

Approximately 80% of the total reserve area is constituted by the freely-drained red soils (aridisols). All have greater than 50% base saturation in all horizons, and only one (profile E) of the 12 profiles analyzed has less than 85%, while seven have 100% base saturation in all horizons. The pH values were approximately neutral for all the samples analyzed with the exception of those in the same profile which was also acidic (pH = 5 to 6). This was a freely drained profile under shortgrass prairie, and the pH is not unlike that of temperate prairie soils.

The mean total milliequivalents of exchangeable bases per 100 g (cation exchange capacity--C.E.C.) in all horizons is 14.2 ± 1.9. There is a significant increase ($P < .05$) in the C.E.C. between the upper and lower horizons of the profiles and a significant increase ($P < .01$) from the top of the catenary sequence to the bottom. In general, then, progression down in profile depth or down the catenary sequence results in an increase in exchange capacity and the percent base saturation.

A similar pattern holds for organic matter. The mean percentage of organic carbon (× 1.72 = organic matter) for all horizons and all profiles of the red soils was 0.45 ± .05. There is a significant reduction from the upper horizons (0.74 ± .1) to the lower horizons (0.21 ± .03), while there is a significant increase from soils high in the catenary sequence to the bottomland soils.

The same pattern also holds for nitrogen in which the mean percentage for all profiles and horizons analyzed is 0.098 ± .000, while the top 10 cm samples have a mean of 0.14 ± .05 and the 30 to 40 cm horizon has a mean of 0.06 ± .00. Although there is not an appreciable change in the percentage nitrogen from red soils high on the slopes to those lower down, the vertisols of the valley bottoms have significantly more (0.102 ± .00) than the aridisols in the upper catenary positions. The carbon/nitrogen ratio of the red aridisols (7.5 ± .52) is also significantly lower than that of the clay vertisols (12.2 ± .50) of the valley bottoms.

It is more difficult to describe the levels and gradients of specific ions in general terms as there is considerable local variation. Furthermore, the levels of any one cation may be misleading unless viewed in relation to the levels of other available cations since the ratio is frequently of great importance. Calcium and magnesium sharply increase in amount in the lower horizons of the profile near the bottom of the slope (profile B_4, Fig. 4), and the amounts in the heavy clay of the valley bottom far exceed those of the profiles above. This pattern also applies to sodium and occasionally to phosphorus.

No appreciable increase of potassium or manganese occurs while progressing down the catenary sequence, causing a considerable shift in ratios of these to other minerals like calcium. As a consequence, the wide K/Ca ratios of the bottomland soils may possibly result in potassium deficiency. Manganese, however, being a divalent ion is less affected by the change in ratio. Although it is generally not available in the lower horizons of any profile, it seems that its distribution reflects an accumulation in the surface layers by plant extraction from the deeper zones and a subsequent recycling.

The vertisols of the bottomlands are very rich in total base elements; but as the exchange capacities, base saturations, and percentages of organic matter and clay particles increase, so does the concentration of sodium salts. Consequently, many less freely drained soils have soluble salts at or near the surface. The elevated clays of the C series reflect concentrations of sodium salts; and whereas the accumulation in profile C_2 is restricted to the lower horizon, profile C_1 is a saline/alkali soil.

The C/N ratio widens considerably in the heavy clays and reflects less availability of nitrogen than might be suspected from the absolute amounts present. Empirical results indicate that some nutrient deficiency or toxicity inhibits plant growth on several of these clays; and since manganese is generally low (or not detectable as in D_3), it seems reasonable to suspect microelement deficiencies at least in the more alkaline heavy clays.

Discussion

Inasmuch as the nutrient content of vegetation reflects the mineral status of the soil on which it was grown, the soil-wildlife relationship is important. Furthermore, the vegetation communities of East Africa seem extraordinarily closely associated with the underlying soil associations (Shantz and Marbut 1923, Burtt 1942, Morison et al. 1948, Phillips 1929, Gillman 1949); and soil considerations play important roles in ecological studies of the region (Swynnerton 1936, Jackson 1954, Boaler 1966, Lang-Brown and Harrop 1962). More specifically, recent studies indicate that East African game distribution patterns are at least partially dictated by soil types, probably mediated through vegetation species composition and/or nutrient status (Petrides 1956, Anderson and Talbot 1965, Bredon 1963).

My results suggest no generally deficient element; and in accordance with other experimental work conducted in East Africa, it is unlikely that the grasslands would show large responses to common N-P-K fertilizers (Evans and Mitchell 1962, Mills 1954). Even though increased grassland productivities have been obtained in East Africa by applying sulphate of ammonia (Evans and Mitchell 1962), it is frequently only the interaction and residual effects of treatment combinations which are significant (Evans 1963*a*,*b*).

As a general condition for East African livestock, Naik (1965) gives minimal levels of calcium and phosphorus as 5 me% and 10 ppm, respectively. Based on these levels only two profiles analyzed are deficient in calcium, although several are marginal. Both of these are paleargids, but in contrast most vertisols of the valley bottoms appear to be only marginal or deficient in phosphorous according to the above level.

Excesses of manganese (causing toxicities) and other minor elements have posed problems in East African soils (Chenery 1954), but this is not likely to be the case in the Mkomazi. In fact, excesses of sodium and other salts in local areas are more likely to induce microelement deficiencies.

Although the quantitative analyses of extractable elements are believed to be representative of the predominant associations in the reserve, it is important to view the nitrogen figures with some reservation. Senb and Robinson (1969) and others have illustrated that the seasonal flush of mineral nitrogen is particularly important in seasonally wet and dry soils. Since the soil sampling for this study was conducted shortly after the onset of the vernal rains, it is possible that the nitrogen levels are not representative of the full calendar year.

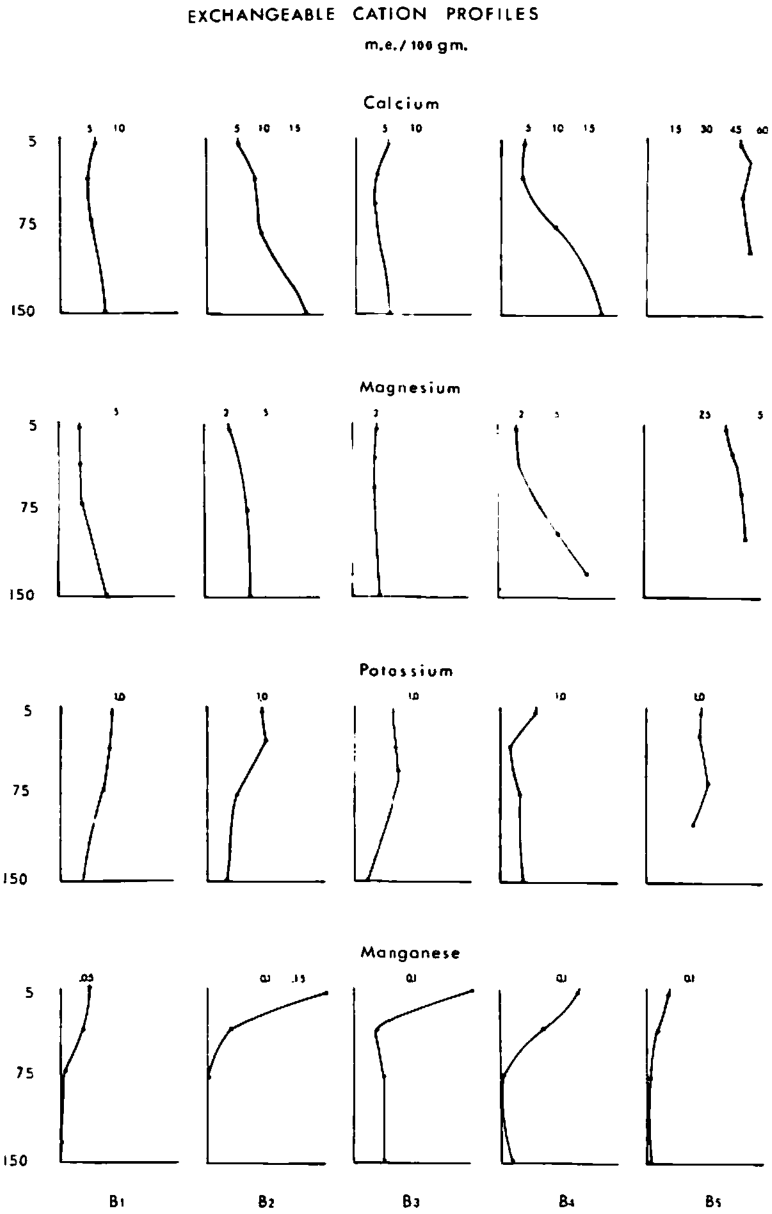


Fig. 4. A typical array of exchangeable cation profiles with respect to profile depth and topographic location. The vertical axis of each tier represents profile depth in centimeters, while the horizontal axis represents the exchangeable cation level measured as milliequivalents per 100 g of soil. The five graphs of each tier correspond to the five profiles sampled in the B catena near the Mbula study area. B_1 was a typical aridisol highest on the slope, while B_5 represents the vertisolic clay of the valley bottom.

Scott (1962*b*) demonstrated a clear relationship of decreasing exchangeable bases with increasing rainfall in semi-arid areas and a reversal of this trend in areas receiving greater than 75 cm of rainfall. Subsequent to my study, Dr. G. D. Anderson, Soil Chemist of the Northern Region Research Center (Tengeru), extended my sampling work so that the combined observations are representative of the entire reserve (Anderson 1968). These added samples corroborate the above conclusions, but more importantly, they permit interpretation for the full 130 km length of the reserve. Based on these observations, there is no significant correlation of percent base saturation with east-west location in the reserve or with the rainfall gradient as Scott (1962*b*) demonstrated for East Africa in general.

Other gradients are more clear:

i. The profile depths of the northwestern foothill area greatly exceed those of the east.

ii. The surface harness and impermeability also increase markedly from west to east.

iii. In spite of no consistent gradient in organic matter content, the bushland soils of the east and central sections generally contain less than those of the west.

iv. Neither root penetration nor the effects of microfauna are as great in the eastern areas, and soil arthropod populations are substantially lower in these soils.

v. Finally, because of their shallow and compact nature, their water retention capacity is substantially lower than the deep profiles of the west.

Collectively, these results suggest that there might be large-scale east-west effects of soils on the biotic components of the ecosystem over and above the differences due to local associations.

VEGETATION

Several lucid descriptive studies of East African vegetation communities (Shantz and Marbut 1923, Phillips 1929, Burtt 1942, Morison et al. 1948, Gillman 1949) provide considerable insight toward understanding and describing those communities. When supplemented by more recent classification works (Keay and Aubréville 1959; Trapnell and Langdale-Brown 1962; Pratt, Greenway, and Gwynne 1966; and Aubréville 1965), it would seem that terminology, at least, would be well established. This is not the case, however, and because of a reliance on local vernacular such as "nyika," "machaka," "miombo," and "mbuga," much of the terminology offers little to those not conversant in Swahili. The descriptive terminology used here largely follows that of the East African Range Classification Committee (Pratt et al. 1966).

The Mkomazi Reserve is encompassed by an extensive association of semi-arid bushland which occupies large parts of the Sudan and extends southward through Kenya into Tanzania where it meets the "miombo" woodland of the more southern countries (Fig. 5). It is usually an assemblage of woody plants mostly of a shrubby or bushy habit (i.e., branching or forking from the base), and in the semi-arid and arid regions, these plants possess thorns and spines. Larger, clear-boled trees are dispersed throughout, while the grass cover is generally short and widely spaced providing only basal cover.

Because of climatic and soil gradients, as well as the physiographic variation, the vegetation of the reserve is quite diverse. The higher mountain areas of the northwest support dry montane forest, while the plains of the western area are covered with bushed and wooded grassland. Riparian woodland and dense thicket are interspersed throughout the reserve, whereas the heavy clay drainageways support open, seasonally inundated grasslands.

Community Descriptions

Approximately 275 common species were collected and forwarded to the East African Herbarium for identification (Appendix III), while duplicate specimens were retained and catalogued for a reference and teaching collection.

Toward the end of the study community type locations and boundaries were plotted on 1:50,000 maps. These were then reduced to 1:250,000 and modified during aerial surveys of the area to provide more accurate delineation.

For the purposes of this presentation only four basic communities are mapped (Fig. 6), since division of these into more specific types is largely a subjective evaluation of the effects of animals and man. It was not feasible to depict small areas of riparian woodland, bush thickets, or other local variations.

Bushland

The most extensive and typical vegetation was bushland which covered nearly all the freely-drained, light textured soils (aridisols) under rainfall conditions not exceeding 50 cm per year. The elevated gray and black vertisolic soils under similar rainfall conditions also supported this community; in total, bushland approximated 70% of the reserve.

The bushland woody plants are mostly of shrubby habit, having a height of 7 m or less, depending on location. In the central and eastern sections, the canopy is frequently so low that medium sized ungulates (e.g., impala) cannot stand beneath it. Ground cover exceeds 20%, but is usually less than 40% unless approaching thickets (see Fig. 7a).

In the western areas where trees (i.e., one stem from the base) are the dominant form, *Commiphora schimperi*, *Acacia bussei*, *A. etbaica*, and *Albizia anthelmintica* are the most frequently encountered species. Other species of *Acacia*, *Sterculia*, *Lannea*, and *Terminalia* are also common and locally abundant. The most frequently observed emergent clear-boled trees are *Delonex elata*, *Adansonia digitata*, *Erythrina burtii*, and *Melia volkensii*. Bushes, shrubs, and herbs abound in the understory while the grasses are short to medium height. Common grasses are perennials of the genera *Chloris*, *Digitaria*, *Sporobolus*, *Heteropogon*, *Bothriochloa*, and *Themeda*.

The bushland of the lower-rainfall areas of the reserve is dominated by bushes and dwarfed tree species. This is also usually the case where reasonably well-drained gray and black clay soils occur. The *Commiphora schimperii* gives way to *C. campestris*, *Cordia rothii* and *C. ovalis*, *Cassia abbreviata*, and *C. longiracemosa* and *Grewia* spp., while *Capparis* spp., *Lannea* spp., *Maerua* spp., and *Platycelyphium voense* also commonly occur. The associated shrubs and herbs are again quite varied with the genera *Tephrosia*, *Sericocomopsis*, *Indigofera*, and *Hermannia* most frequently seen.

The grass cover and productivity are usually poor in the drier areas, with *Chloris roxburghiana*, *Cenchrus ciliaris*, *Sporobolus festivus*, *S. consimilis*, *Heteropogon contortus*, and *Aristida* spp. dominating.

Bushed and Wooded Grassland

In the higher rainfall (>50 cm) areas of the reserve the bushland is replaced by bushed and wooded grassland, and this community covers the more freely-drained eluvial soils on the hill and mountain foothill fan slopes. The widely spaced but always conspicuous trees and bushes have canopy covers of much less than 20%, but they usually stand 10 to 12 m high (Fig. 7b). The more common tree species are *Acacia tortilis* var. *spirocarpa*, *A. etbaica*, *A. senegal*, *Platycelyphium voense*, *Boscia salicifolia*, and *Melia volkensii*. Other species such as *Ziziphus mucronata*, *Sterculia africana*, and *Capparis tomentosa* occur infrequently.

The grassland in these areas reflects high vigor and productivity because of the added runoff water from above and usually exceeds a meter in height. *Themeda triandra*, *Heteropogon contortus*, *Digitaria* spp., and *Bothriochloa radicans* dominate. The more common bushes and shrubs are *Combretum molle* (second growth), *C. aculeatum*, *Acacia brevispica*, *Solanum incanum*, and *Thylachium africanum*.

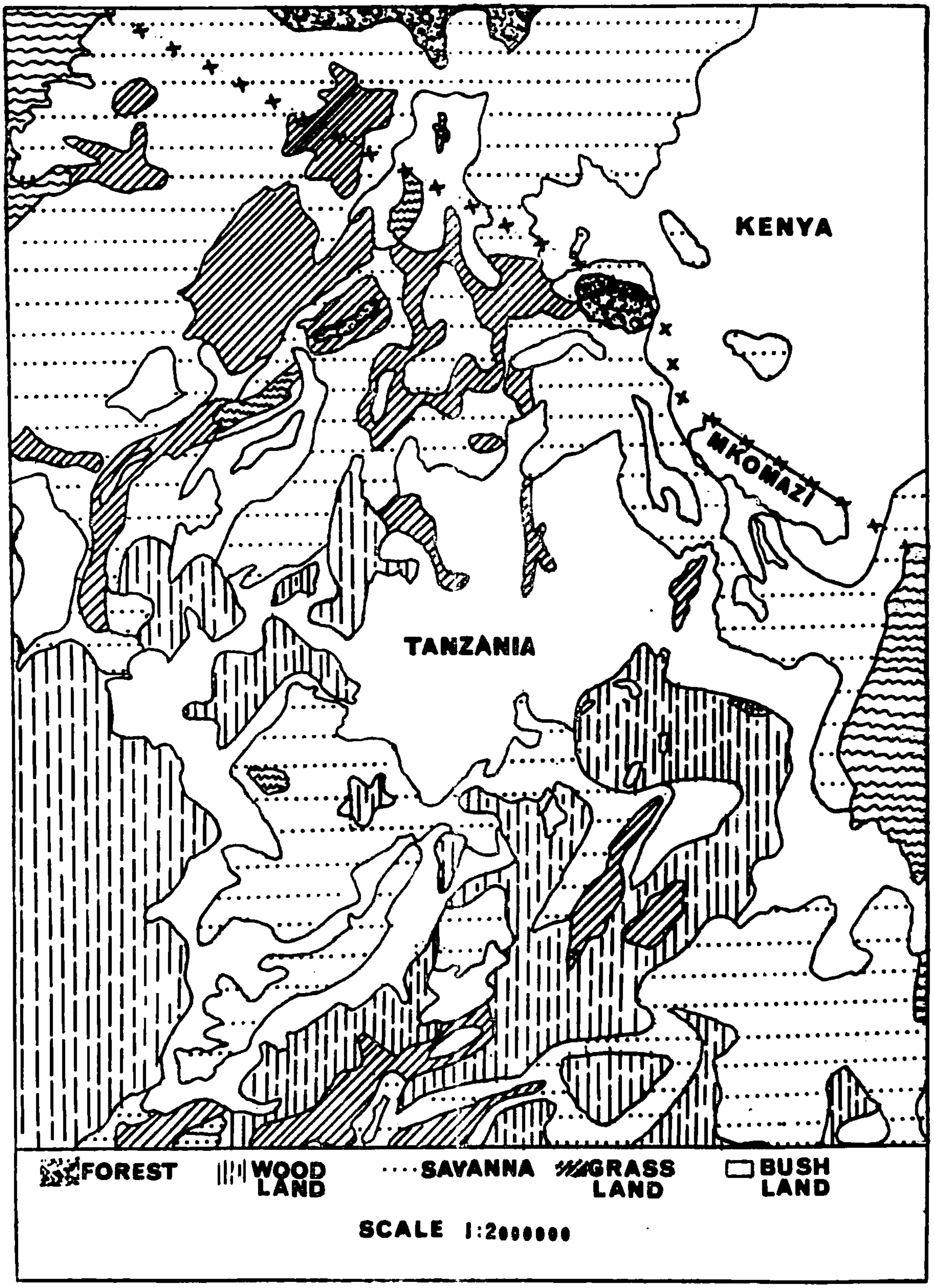


Fig. 5. The major vegetation types of northern Tanzania and southern Kenya. The Mkomazi Reserve is contained in the type known as bush, bushland, or "nyika." Redrawn from the Division of Overseas Survey D.O.S. 299E.

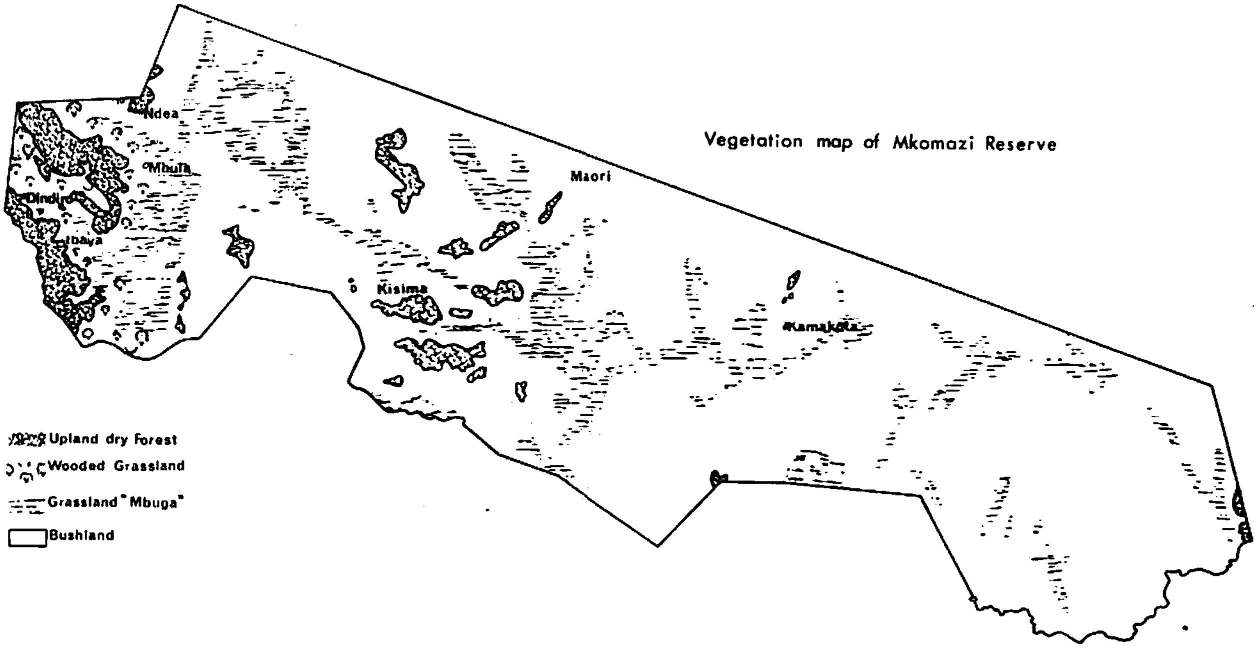


Fig. 6. A vegetation-types map illustrating the location and extent of the major vegetation associations within the Mkomazi Reserve. As depicted, the upland dry forest represents approximately 5% of the total area and occurs on most of the higher mountain peaks. In reality, closed canopy forest only occurs on the mountains above about 1000 m elevation, although the dominant species occur lower down. Similarly, included in the area depicted as bushland are localized areas of nearly open grassland (e.g., Maori) resulting from bush suppression. In general, the seasonally waterlogged grassland follows the distribution of the vertisolic clay drainageways.

Fig. 7a.

Fig. 7b.

Fig. 7c.

Fig. 7. a. Typical *Commiphora schimperi* and *C. campestris* bushland with *Cassia* spp., *Cordia* spp., and *Grewia* spp. subdominants in the central section of the reserve.

b. A typical association of bushed and wooded grassland (near the Dindira study area) in the western end of the Mkomazi Reserve.

c. Open *Pennesitum mezianum* grassland occurring on a heavy montmorillonoid clay drainageway in the northwestern section of the reserve. Adjacent, higher elevation bushland communities appear on either side of the corridor.

Grassland

Open grassland areas usually occur on the lowland heavy clay drainageways ("mbugas"). Because of water catchment from adjacent sloping terrain and the high water retention characteristics of these soils, they are usually seasonally waterlogged and free of tree growth. These grassland drainageways typically form long, narrow corridors bordered by the bushland of the adjacent well-drained soils (Fig. 7c). The dominant grass of these areas is *Pennisetum mezianum*, while other species such as *Dichanthium pappilosum*, *Dactyloctenium aegyptium*, *Schoenefeldia transiens*, *Ischaemum afrum*, *Sorghum verticilliflorum* and *S. versicolor*, *Panicum* spp., and *Brachiaria* spp. also occur widely.

Open grasslands also appear on the higher, more freely drained fersialitic soils, but usually only as fire disclimaxes. These grasslands are very different from the seasonally waterlogged ones; and since they occur locally (e.g., around Maori) among the bushland or wooded grasslands and consist of the same species, they are not differentiated on the map.

Upland Dry Forest

Almost all mountainous areas above 1000 m elevation are characterized by a closed canopy forest of 15 to 20 m height with a substantial growth of epiphytes. Although frequently termed "cloud forest" because of frequent envelopment in clouds, the rainfall is apparently too low to warrant this name. *Calodendrum capense*, *Brachylaena hutchinsii*, *Clerodendrum hildebrandtii*, *Albizia harveyi*, and *A. petersiana* dominate the canopy; while *Croton dichogamus*, *Hoslundia opposita*, *Maerua kirkii*, *Haplocoelum foliolosum*, *Lonchocarpus* sp., and *Strychnos* sp. compose the understory bush layer. The common shrubs are *Aspilia mossambicensis*, *Thylachium africanum*, and *Solanum incanum*. Although usually closed, occasionally open glades and less densely crowned areas support growths of tall rank grasses such as *Chloris roxberghiana*, *Panicum deustum*, *P. maximum*, and *Cynodon dactylon*. The same species of bushes and shrubs usually grow down the mountain slopes to lower levels and frequently form dense thickets, especially in ravines and gullies.

While it appears (see Fig. 6) that this forest type is of considerable extent, all the closed forests have, in fact, an extensive peripheral zone of more open canopy. This is most probably a manifestation of fire encroachment, and if fire were prevented the younger age classes would soon fill in the canopy. Therefore, a designation such as "fire-induced wooded grasslands" as suggested by Anderson (1968) might be justified on a more detailed vegetation map.

Riparian and Miscellaneous Types

Smaller areas of riparian woods and groundwater forest are important as game sanctuaries and frequently occur along the seasonal watercourses or in areas supporting a high water table. These forest remnants are dominated by *Tamarindux indica*, *Afzelia cuanzensis*, *Newtonia hildebrandtii*, *Terminalia kilimandscaharica*, *T. prunioides*, and *Zizyphus mucronata*, while the understory species are commonly *Vitex strickeri*, *Hoslundia opposita*, *Grewia bicolor*, *G. villosa*, *Ehretia taitensis*, and *Haplocoelum foliolosum*. These species provide a valuable dry season forage for elephants and other browsers.

The smaller rock outcrops and rocky slopes of the mountains are frequently covered by a highly xerophytic shrub, *Vellozia aequatorialis* (or *V. spekei*) of the Velloziaceae. It apparently needs very little water and is a common species in the driest areas of the reserve.

The various areas of saline/alkali soil support interesting vegetation communities. One local area of considerable extent (soil profile D_3) supports no vegetation at all, whereas several other areas support salt tolerant species. The "miswaki" or "tooth brush bushes" (*Salvadora persica* and *Dobera loranthifolia*) are found only on these soils and may be used as indicator species. Another highly unique plant of these areas is *Adenia globosa* of the Passifloriaceae. Occurring as a giant aboveground potato-like sphere up to 2.5 m in diameter, it has no leaves and is usually covered by chlorophyllous spines and stems. This is one of the many dry season water sources utilized by game, particularly eland, but only after it has been "dethorned" by rhino or elephants. A similar but smaller plant possessing at least some leaves is *Pyrenacantha malvifolia*.

Net Primary Production

Grassland productivity studies were initiated in late 1965 and continued for 18 months until termination of the study in mid-1967.

Four barbed-wire 16 × 18 m exclosures were established in the northwestern half of the reserve with the locations representing different grassland and soil types and rainfall regimes. Two plots (A and B) were centered in each of the exclosures so that a margin of 2 to 3 m separated the plots from the exclosure wire. Each of the plots was then divided into 12, 6 × 1 m subplots with iron stakes demarcating the corners of each.

During the long dry season, plot A of each exclosure was clipped bare with hedge shears, and the aboveground standing crop was removed and weighed. Aboveground vegetation was then clipped from one of the 12 subplots of both the denuded and unclipped plots at approximately monthly intervals throughout the following year. The vegetation was bagged, returned to headquarters, and placed in an elevated, open-air, wire mesh drying structure completely covered with corregated roofing. Since the drying structure contained 16 wire mesh bins, the samples could be air-dried for two months before being removed and weighed on a single-beam scales.

After clipping and measuring the aboveground standing crop of the 24 subplots in each exclosure over a 12-month period, the exclosures were re-established in nearby areas and the studies continued during 1966-67.

A marked gradient in standing crop and cumulative net production from the western to the central section of the reserve was established. In the northwestern section the grass-forb aboveground standing crop on unclipped plots varied between 200 and 600 g/m^2 (× 10 = kg/ha) depending on the month

c. measurement, but with a growing-season asymptote of slightly less than 600 g/m^2 (Fig. 8). This figure fell to approximately 250 g/m^2 in the shortgrass prairie area in the west central section and to approximately 200 g/m^2 in the central section.

The cumulative (seasonal) net production on denuded and unclipped plots also follows the same trend. Net aboveground production on the denuded plots reached an asymptotic level of about 300 g/m^2 in the northwest, approximately 200 g/m^2 in the west central, and only 150 g/m^2 in the central section.

Mean daily productivities (monthly accrual/number days) for the different areas, seasons, and plots have also been calculated (Table 2). Although short duration daily rates exceeded 6 g/m^2/day in certain plots, the overall rainy season mean is 1.93 ± .30 g/m^2/day. There is no significant difference between the rainy season daily productivities for the different exclosures or for the denuded vs. unclipped plots.

On the other hand, there is a marked difference between the cumulative seasonal net production between the denuded and unclipped plots. Whereas the 1966 denuded-plot productivities were about 310, 165, and 140 g/m^2 in the three areas from west to east, the respective values for the unclipped plots were approximately 400, 240, and 170 g/m^2.

These values are corroborated by the general trend depicted in Table 2. Even though the denuded plots show higher mean daily productivities early in the season, the unclipped plot values generally surpass them within a couple months. The time lag affecting the unclipped plots is especially important later in the season when production continues later on and frequently buoys the long dry season mean above the zero point (sustained production early in the dry season exceeded late season attrition).

Two of the exclosures were located on water shedding sites, while the third (Kamakota) was on a level vertisolic soil. Not illustrated are the data for the fourth exclosure which was located on a receiving site near the bottom of a slope (near Kisima) in the west central section.

Table 2. Mean daily net aboveground primary production for different seasonal periods, rainfall regimes, and clipping treatments. The first area receives about 500 mm of rainfall annually, while the second and third receive about 400 and 350 mm, respectively. All values are reported as g/m^2.

Treatment Combination	Seasonal Period			
	Nov.-Jan.	Feb.-Apr.	May-June	July-Oct.
Mbula excl.				
Denuded	+1.11	+1.64	+1.85	-0.38
Unclipped	-0.22	+0.97	+3.08	+0.38
Maori excl.				
Denuded	+0.45	+0.71	+1.90	-0.04
Unclipped	+1.08	+0.82	+1.12	+0.22
Kamakota				
Denuded	+0.74	+0.90	+1.24	-0.16
Unclipped	+0.55	+1.00	+2.38	-0.05

The asymptotic standing crop of unclipped plots in this area during the growing season was 780 g/m^2 (±89.8), while the seasonal productivity reached an asymptote at 415 ± 26.5 g/m^2. There is little doubt that these figures are surpassed by the local areas of *Panicum* and *Chloris* on similar receiving sites in the northwestern area of the reserve.

Appreciably more precipitation occurred in the first half of 1967 than in 1966. The productivities reflect this, as no plot sampled in 1967 appears to have reached its asymptote by June, while all plots had already surpassed their 1966 productivities.

Range Analysis

In attempting to quantify the differences in range conditions for various regions of the reserve, range evaluation techniques developed by the U.S. Forest Service (1968) were utilized. The technique involves using a .75-inch (1.9 cm) diameter iron loop to measure the frequency of "hits" on various grassland components while walking along compass bearing transects. A "hit" is that species or item occupying more than 50% of the loop area when the loop is lowered to the ground every second step along the transect. By always lowering the loop in a guide notch placed in the observer's shoe sole and by not looking at the ground as he walks along the transect, the human sampling bias becomes negligible.

A set of 100 such measurements constitutes a sample, and the mean number of times that the loop hits the base of a perennial grass or forb is termed the plant density index. A ground cover index is then derived by subtracting the number of hits on bare soil, erosion pavement (pebbles <2.5 cm diameter), or rock from 100. Although largely qualitative, an assessment of range trend is made by considering the different values of the plant density and ground cover indices along with the occurrence of litter, erosion pavement, species composition, and plant vigor.

Index values derived from the results of ten sets of 100 samples from each of three transects in the Dindira study area show a mean plant density index of 33.8 and a ground cover index of 92.1 (Table 3). Despite the closeness to the permanent water and the severe dry season trampling, the mean incidence of bare ground was only 7.7/100 points.

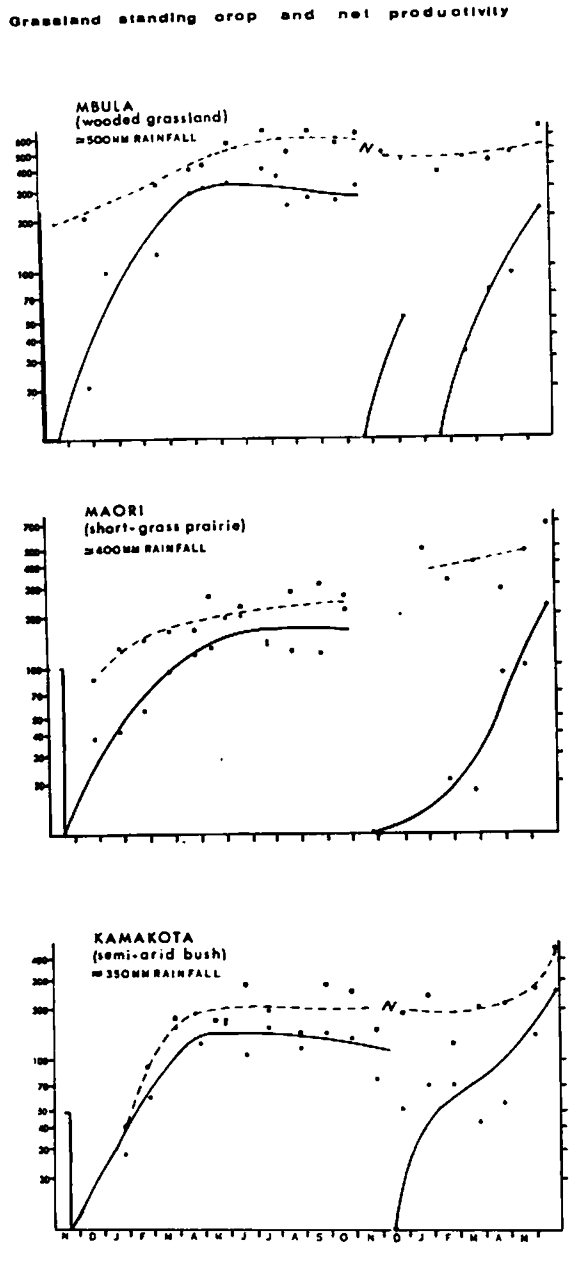


Fig. 8. Graphs representing the seasonal changes in the aboveground grass and forb standing crop (g/m^2) as well as seasonal net production values for three areas in the Mkomazi Reserve. The dashed lines refer to the standing crop on previously unclipped plots within barbed-wire exclosures. The solid lines represent the cumulative net production on sample plots which were clear-clipped before each growing season.

Table 3. Indices of vegetation condition and their standard errors in three areas of the Mkomazi Reserve. The plant density index refers to the mean number of "hits" on perennial grasses or forbs per 100 samples, while the ground cover index refers to all hits on live or dead vegetation. When similar soil types are considered, a gradient of conditions exists from west to east (i.e., Dindira to Kamakota).

Location and Soil Type	Plant Density Index	Ground Cover Index	Bare Ground or Erosion Pavement
Dindira study area Aridisolic soils	33.8 ± 1.2	92.1 ± 1.9	7.7 ± 1.7
Mbula study area Aridisolic soils	21.5 ± 1.7	74.5 ± 2.3	25.5 ± 2.0
Mbula study area Vertisolic soils	44.6 ± 2.2	91.2 ± 2.4	8.2 ± 1.6
Kamakota area Aridisolic soils	16.3 ± 1.6	41.3 ± 1.8	58.4 ± 2.1

Significant changes in the grassland structure occur from the western to the central section of the reserve. In the western area nearly 34% of the hits were on perennial grass bases, while the value for the grasslands around Mbula was 21.5 and only 16.3 for similar soils in the central section. Conversely, the bare-ground values increased from 7.7 in the west to 25.5 around Mbula to 58.4 in the central section (Table 3). The plant density (basal coverage) and ground cover indices for the seasonally waterlogged grasslands of the west are higher than the upland grasslands, but this is only infrequently the case in the central section.

Along with the higher incidence of bare ground in the central section, the frequency of erosion pavement also increases, while the frequency of hits on litter decreases. These index values certainly manifest overgrazing and consequent erosion as well as lower rainfall conditions.

Since few quantitative range evaluation standards have been developed for East African rangeland, it is not readily apparent what meaning the index values have other than for comparison of areas within the reserve. But as a crude approximation, the standards established for the foothill shrub community by the U.S. Forest Service (Range Analysis Handbook, Region 2) seem comparable (Hemingway, Cormack, and Robinette 1966). From these ratings (excellent, good, fair, poor, and very poor), the grassland of the western Mkomazi would be considered "good," while that of the central section is rated poor to very poor.

Discussion

Because of the methodology employed, the net production values reported here are minimal estimates. Asynchronous growth patterns of the different species, the inherent inadequacy of a monthly sampling interval, and consumption by arthropod consumers all mitigate against an accurate assessment by this method (Wiegart and Evans 1964, Golley 1965, Kelly et al. 1969). Nonetheless, these estimates are of value for comparison to many of the estimates presently in the literature.

Taking different rainfall regimes into account, the primary production estimates obtained from this study compare favorably to values obtained elsewhere in East and Central Africa (Brockington 1961; Harker 1961; Naveh 1968*a*,*b*; Anderson and Naveh 1968; McKay 1968). Nearly exact denuded plot predictions are obtainable from the Serengeti precipitation-productivity curve established by Braun (1969).

Of considerably greater interest, however, is the relationship between the denuded and unclipped plot productivities. The "clipping effect," or the subsequent realization of greater productivities by clipping, mowing, grazing, burning, or otherwise removing the aboveground standing crop, is a well established range management phenomenon (Stoddart and Smith 1955; Curtis and Partch 1950; Hopkins 1954; Hadley and Kieckhefer 1963; Penfound 1964; and Kucera, Dahlman, and Koelling 1967). The fact that this effect was not observed under these conditions is of both pragmatic and heuristic interest and is discussed later.

On the other hand, the idea that mowed and burned areas produce a "flush" of new growth quicker than unburned areas was seemingly substantiated. The quick response of the denuded plots is likely to be a consequence of the increased soil temperature resulting from exposure, as well as the greater growth rates generally exhibited by small or young organisms and populations (Voisin 1959). On the other hand, the terminal lag of production in the unclipped plots likely results from the greater moisture retention capacity of the more shaded and cooler substrate under unclipped conditions.

Although the relationships between the different plant communities and the large herbivores are discussed in the pinultimate chapter, it is important to stress here that primary production per se, or even the vegetation community structure, does not fully explain the interrelations with the large herbivores. Grazing and browsing successions do exist

(Vesey-Fitzgerald 1960. 1965; Talbot 1963*a*: Gwynne and Bell 1968), and therefore several community types are important to single animal species at different times of the year. In contrast to the ideas of Janzen (1967), I found that a highly asynchronous vegetation "leafing" and flowering pattern provided abundant opportunity for temporal patterns of utilization. The large animal species have adapted to and are very dependent upon these patterns.

Interestingly, the large herbivores have evolved anatomical and physiological mechanisms for most of the exigencies. The gamut runs from simple adaptations to thorns and spines and the successful utilization of myrmicophytic *Acacia* species which is generally not the case in the American tropics (Janzen 1966) to the more sophisticated physiological adaptations to strychnine (in the form of *Strychnos* spp., Burtt 1929, Lawton 1968) and the many alkaloids of the Solanaceae. Whereas species of *Solanum* are rarely browsed in the neotropics, (D. H. Janzen, personal communication) *Solanum incanum* and *Solanum* sp. (*taitense*?) appear to provide an important part of eland browse in the Mkomazi. Plant-animal relationships are therefore of obvious importance to an understanding of the community structure.

While the effects of fire on the environment are of major concern to range ecologists the world over, I can give but passing mention to the topic here. The interested reader should consult the excellent review articles and over 1000 literature citations included by Shantz (1947), Commonwealth Bureau of Pastures and Field Crops (1951), Ahlgren and Ahlgren (1960), West (1965), and Daubenmire (1968). Aside from its nearly undisputed effect upon bush encroachment there seems to be one other relation of overriding importance. In North America fire has distinctly different effects on primary productivity depending on the rainfall regime. In areas which receive greater than 50 to 60 cm of annual precipitation there are usually positive relationships between burning and productivity (Ehrenreich 1959, Hadley and Kieckhefer 1963, Kucera et al. 1967). Areas which receive much less than 50 cm precipitation per year almost always reflect a reduced production after burning (Aldous 1934, 1935; Elwell, Daniel, and Fenton 1941; Hopkins, Albertson, and Riegel 1948). It remains to be seen how long an enhanced productivity can be sustained by systematic burning in the high rainfall regime, but experimental work in Illinois has established a positive relationship for at least four years (Hadley and Kieckhefer 1963). Lay (1956) reported a fivefold increase in dry matter the first year after burning, but this had declined to a twofold increase by the third year.

The most reasonable explanation to account for such a relationship seems to be that as the higher rainfall areas are approached, there is a subtle shift from moisture to space limitation. Thus, available moisture may be a limiting factor in the low rainfall areas, and this is further accentuated by herbage removal. On the other hand, forage removal from the possibly space-limited stands of the higher rainfall areas would enhance productivity. This has relevance to the Mkomazi system insofar as the clipped plots consistently reflected lower net production values.

From this it is concluded that annual fires in the Mkomazi are likely to have a degratory effect on production, while a four to five year burning cycle may be necessary for bush control and the maintenance of highly diverse vegetation communities.

The overriding impression gained by most visitors to the Mkomazi is one of abundant giraffe (*Giraffa camelopardalis*), Coke's hartebeest (*Alcelaphus buselaphus*), and elephant (*Loxodonta africana*), with only slightly fewer numbers of impala (*Aepyceros melampus*), eland (*Tauratragus oryx*), and buffalo (*Syncerus caffer*).

Less ubiquitous but locally common species are zebra (*Equus burchellii*), oryx (*Oryx beisa*), steinbok (*Raphicerus campestris*), gerenuk (*Litocranius walleri*), and Grant's gazelle (*Gezella granti*). Rhinoceros (*Diceros bicornis*), lesser kudu (*Strepsiceros imbarbis*), waterbuck (*Kobus ellipsiprymnus*), and dik dik (*Rhynchotragus kirkii*) are not rare. Although lion (*Pantera leo*) is the most numerous large carnivore, leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), hunting dog (*Lycaon pictus*), and hyaenas (*Crocuta crocuta* and *Hyaena hyaena*) are all present.

The more common smaller mammals include mongooses (*Herpestes ichneumon*, *H. sanguineus*, *Helogale undulata*, *Mongos mungo*, and *Ichneumia albicauda*), gerbils (*Tatera robusta*, *Taterillus osgoodi*), the ground squirrel (*Xerus rutilus*), and the vervet monkey (*Cercopithecus aethiops*), while the monitor lizard (*Veranus exanthematicus*), puff adder (*Bitis arietans*), and black-necked cobra (*Naja nigracolis*) are dominant reptiles. Tsetse flies (*Glossina* spp.) and ground nesting termites (*Macrotermes bellicosus*, *Odontotermes* spp., and others) are conspicuous and ecologically important invertebrates.

The avian fauna of the reserve is varied and spectacular. The bushland community supports a great number of colorful and noisy species, possibly more than any other habitat type (Fuggles-Couchman 1948, Moreau 1935). In numbers of species and individuals, the doves (Columbidae), starlings (Sturnidae), hornbills (Bucerotidae), and weavers (Ploceidae) predominate.

The bird nomenclature used here is that of Mackworth-Praed and Grant (1957). The mammal nomenclature largely follows Swynnerton and Hayman (1951) with reference to Ellerman (1940) for rodents and Best, Edmund-Blanc, and Witting (1962) for big game animals.

Collection and Identification

Where species habits and habitats are known, important ecological insights can be gained by studying the relative abundance of various species present on an area. Throughout the course of the study, mammal and bird specimens were collected and identified. Common breakback traps and mist nets provided the bulk of small specimens, but a .410 gauge shotgun with dust shot, a .22 caliber rifle with scope, night-lighting techniques, and the analysis of owl pellets were also used. Specimens were sent to various specialists for identification (see Acknowledgements).

In total, 233 bird species were identified (Appendix IV.1), although the list is admittedly far from complete. Certain taxonomic groups (e.g., sunbirds), habitat-related species such as those of the montane forests, and activity-related species (e.g., nocturnal) are conspicuously absent or only poorly represented on the list.

Seventy-eight species of mammals were identified (Appendix IV.2) and six other known species are believed to be present, but not positively identified. The number identified is considerably below those of the more well studied areas of East Africa, but as further study is undertaken in the Mkomazi, the list should expand. The mammals so far recorded generally represent the lowland, more extensive areas of the reserve; and considerable effort should be directed toward the montane, riparian, and other less extensive habitats to establish the faunal composition of these communities.

The Standard North American trapline (Calhoun 1959) was frequently used to obtain comparative estimates of trapping success, and in general, the very low success rates suggest that small-mammal densities are very low compared to temperate areas where success rates 10 times greater frequently prevail.

Few quantitative data are available for the assessment of trends in the density of the various populations. It is certain however that at least three large species have been recently extirpated from the reserve. D. G. Anstey, Game Ranger, observed the greater kudu (*Strepsiceros strepsiceros*) in 1952 (Anstey, personal field notes); and the acting warden reported its occurrence in official letter no. 451/8/46 of 17 October 1955. I also found a greater kudu horn in the reserve in 1965. Both the colobus monkey (*Colobus angolensis*) and the crocodile (*Crocodylus niloticus*) were recorded by various game department personnel as late as 1957 (annual report, Game and Tsetse Division 1950, District Ranger's report 1957). Neither of these species has been recorded since 1957, and none presently exist in the area.

Evidence also suggests that at least two other ungulates formerly occurred in the reserve. Swynnerton and Hayman (1951) report records of sable antelope (*Hippotragus niger*) at Lake Jipe and Kisiwani which lie only a few kilometers to the north and south of the reserve, respectively, and are connected by the North Pare Mountains which extend through the western end of the reserve. Sable are still occasionally seen east of the reserve.

Eastern white-bearded wildebeest (*Gorgon taurinus*) were also common in Tanga Province and the area presently occupied by the reserve in the 1930's (Game and Tsetse Division annual report 1932; R. Bradstock, personal communication). No wildebeest occurred in the area during the Fifties and early Sixties. Twenty were restocked in 1966.

What little evidence exists regarding the cause of these extirpations suggests that heavy cultivation, overgrazing, and illicit hunting along the Umba River are responsible for the serious decline in the riparian woodland, permanent water, and thus the demise of the crocodile and colobus monkey. The hypothesis of general habitat degradation and hunting is frequently suggested for the loss of the kudu, wildebeest, and sable antelope; yet the introduced wildebeest population is growing after an initial decline, and hence the habitat of the western section now seems suitable for this species.

Techniques

Four techniques were utilized to estimate numbers and densities of the larger mammal species of the reserve. These were: (i) ground transects with associated visibility profiles, (ii) aerial transects, (iii) demarcated sample study areas, and (iv) sight-recording maps for the less abundant species.

Ground count transects. Especially because of the absence of roads or tracks, initial studies were limited to the northwestern section of the reserve. Ten ground transects patterned after Hahn's walking cruises (Hahn 1949) and similar to those used by Lamprey (1963) were established (Fig. 9a). Four of these, varying in length from 18.5 to 26.5 km, were located in mountainous areas; and animals were counted while walking along cleared and demarcated paths. Six other transects, from 15 to 68 km in length, traversed the open bush, and counts were conducted while driving at slow speed in a 4-wheel drive vehicle. Each of the 10 transects was subdivided into segments for more precise estimates of density patterns, variability, and movements.

An attempt was made to conduct each count at monthly intervals, but certain transects were counted more frequently, and others were sometimes missed because of the impassible soil conditions during rainy seasons and nonfunctional transport. In total, 377 counts were conducted along the 10 transect routes, representing over 2000 km walking and 5600 km driving distances. The counting technique was simple. More than one observer was always present; and when driving through the grassland or bush, one or more observers stood in the back of the open vehicle to facilitate animal sightings. After a sighting was made with the unaided eye, 7 × 42 binoculars were used to count and to classify the animals into sex and size categories. Records were tabulated on standard forms with a system of parentheses and superscripts denoting herd composition. The starting and finishing times were recorded along with the extant water, vegetation, temperature, and sunshine conditions for each count.

Visibility profiles. To convert the number of animals seen to density figures, an estimate of the area surveyed was necessary. Visibility profiles (Fig. 10) were established for several of the transects; and although it is not suggested that all animals in the area were counted, the numbers seen represent a minimal estimate of the number occurring in the respective areas. These profiles were constructed by sending khaki-clad game scouts with white handkerchiefs in their hip pockets in perpendicular directions from the transect line and subsequently pacing the distance at which they became obscurated by the vegetation. These distances changed with vegetation conditions, of course, and they also varied with the size of the animals involved. Therefore, two profiles were established with the inside distance applicable to small and medium sized animals and the outside profile representing the area in which elephant, giraffe, and herds of eland and buffalo greater than 10 individuals were visible. More or less circular visibility profiles were also established for hilltop observations; and after integrating with the linear profile, the sometimes weird-shaped areas were measured by a grid overlay of known scale.

Aerial surveys. A dual-seated Piper Supercub airplane was made available in January 1966, and monthly aerial surveys of the entire reserve were initiated at that time. A system of 18 permanent transects crossing the reserve transversely and spaced at 6 to 8 km intervals was established (Fig. 9b). The starting, turning, and terminal points of the transects were located at specific topographic features such as waterholes, drainage ditches, rock outcrops, or artificial markers along the reserve boundary. Similar features, as well as peculiar trees, vegetation community boundaries, and compass bearings, were also used as route markers.

Since the total linear distance of the transects was about 560 km and required a flying time of more than 4.5 hours, the combined transects were divided into three nearly equal segments. The three segments, totalling approximately 190 km each, were flown on consecutive days at monthly intervals. The counts were normally started about 1.5 hours after sunrise. Flying speed was held constant at 120 km/hour at a standard altitude of approximately 100 m.

All animals seen along the transect routes were tallied on standardized sheets, and locations of the larger species, as well as concentrations of game, were plotted on maps. A portable tape recorder was occasionally used to facilitate recording. Upon sighting large herds or concentrations of animals, the pilot would circle in a counterclockwise direction and climb to an altitude of 200 m or more, while the observer counted and rechecked the number of animals below. After counting such a group, the original position along the transect was regained and the normal census procedure resumed.

In addition to the systematic counts along the transect routes, high altitude "scavenger hunts" were performed later in the day to further assess the numbers and distributional patterns of the various species. Since these flights were not systematic, the data cannot be quantitatively analyzed and can only be used for subjective evaluations.

Sample plot study areas. To provide more accurate estimates of animal densities and seasonal changes, three sample plot areas from 10 to 15 km^2 each were established in mid-1966. The westernmost of these was located at the permanent water source of Dindira Dam, while one of the others was near a semi-permanent waterhole (Mbula), and the third (Mzara) represented an area with only seasonally available surface water (see Fig. 9a). These areas were demarcated by large drainage gullies, roads, distinct vegetation-soil type boundaries, or in the case of the Dindira area, the surrounding mountains (Fig. 11). Two of these areas contained hills elevated 50 m or more above the surrounding area. Prior surveillance from these vantage points made possible an accurate tabulation of those animals likely to be driven out of the area by subsequent counting activity.

Monthly counts (biweekly for Dindira) of these areas were carried out for over a year using a censusing technique similar to that of Petrides (1956). After initial surveillance, the landrover with observers was driven back and forth over the area at approximately 50 m intervals until it was certain that all animals of reedbuck size or larger had been enumerated. The location, movement, and

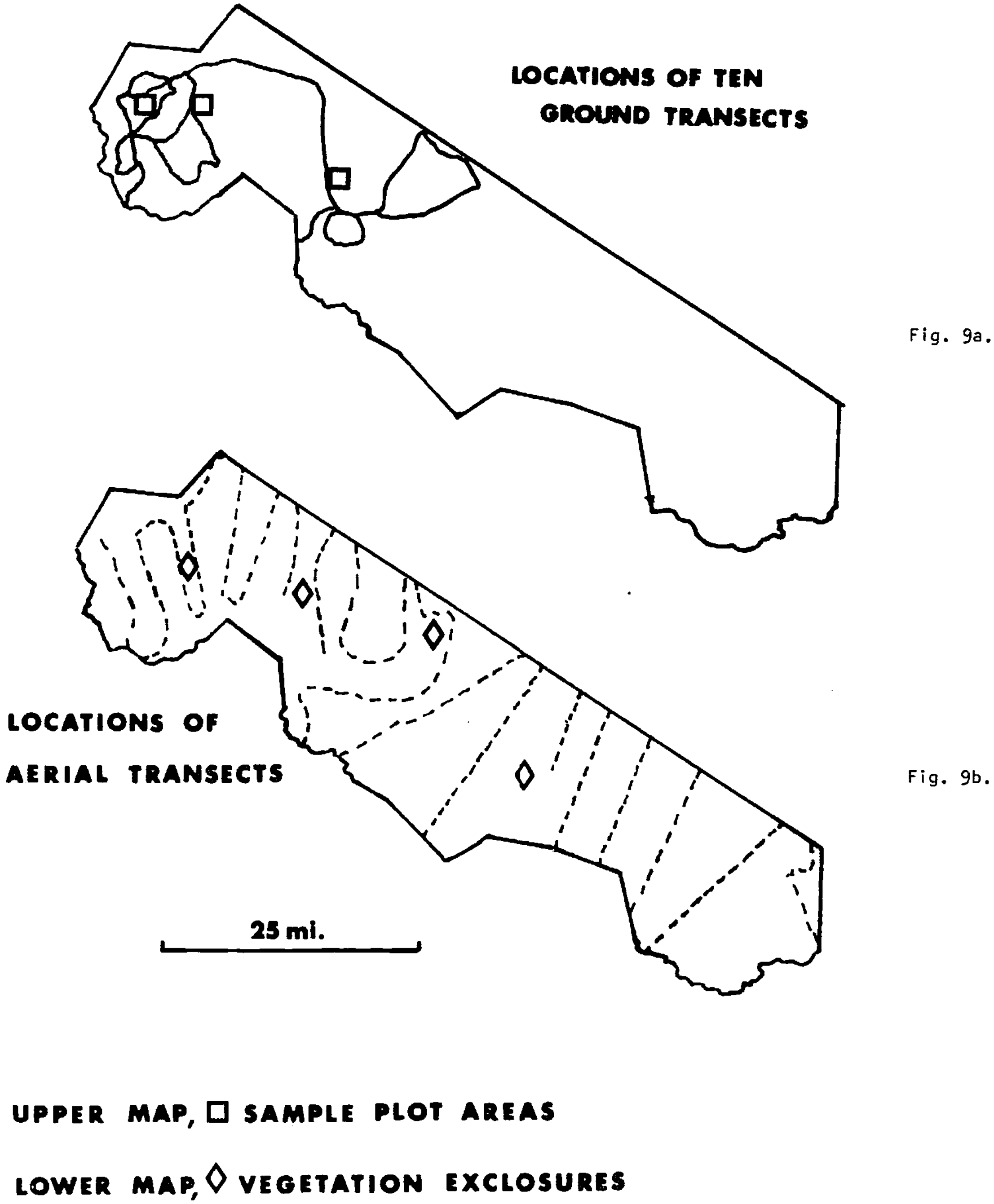
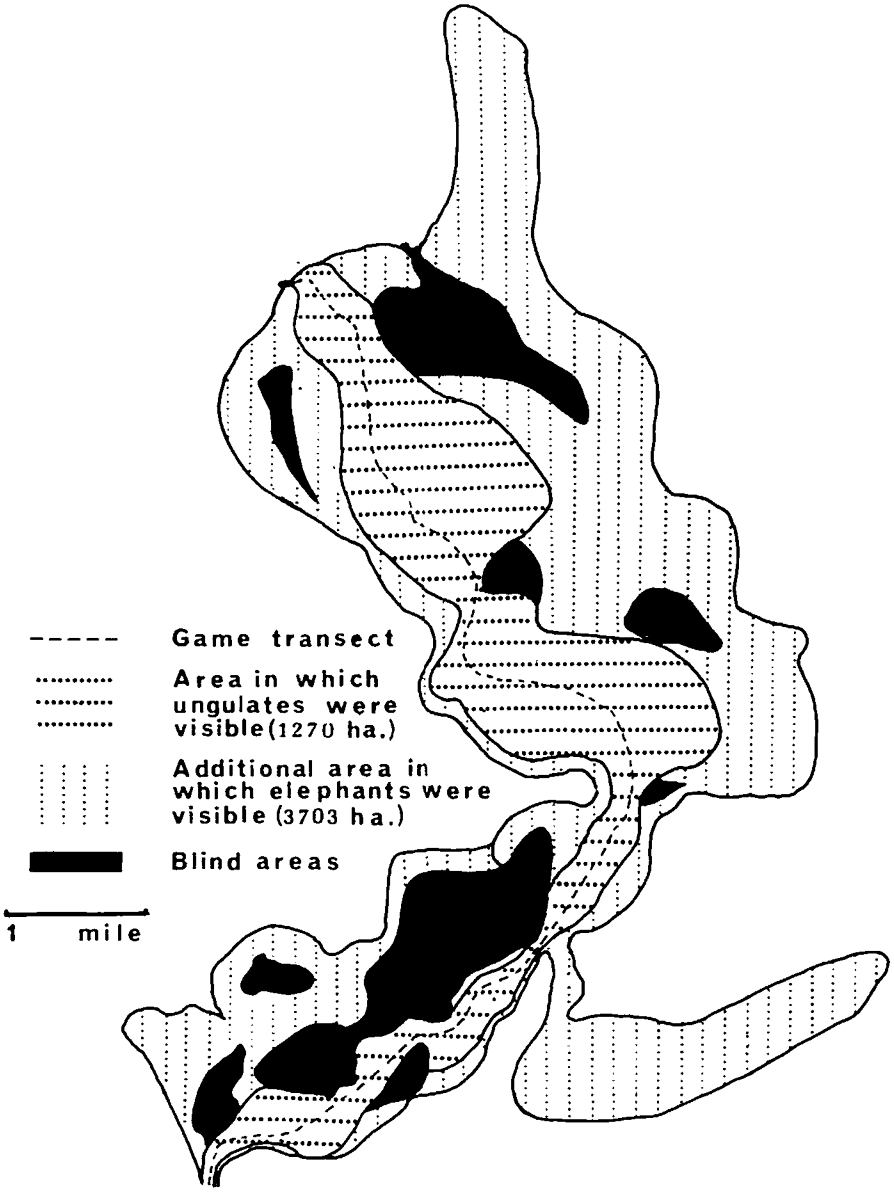


Fig. 9. a. Distribution of the 10 ground transects in the northwestern half of the Mkomazi Reserve. The transects were subdivided into a total of 30 segments for more precise enumeration of habitat preference, density, and movement patterns.

b. The aerial transect grid used for the monthly aerial surveys of the Mkomazi Reserve. The starting, turning, and terminal points were located at specific topographic features such as waterholes, drainage ditches, rock outcrops, and artificial markers. While the locations of the three sample plot study areas are depicted in the upper figure, the locations of the four vegetation exclosures for the study of net primary aboveground productivity and standing crop are included below.



VISIBILITY PROFILE FOR GATE TO IBAYA TRANSECT

Fig. 10. Visibility profile for the Gate-to-Ibaya ground transect. The inner profile was used to estimate the density of the small to medium sized herbivores, while the outer profile of considerably greater extent allowed the calculation of density for the larger species such as elephants and herds of eland and buffalo greater than 10 in number.

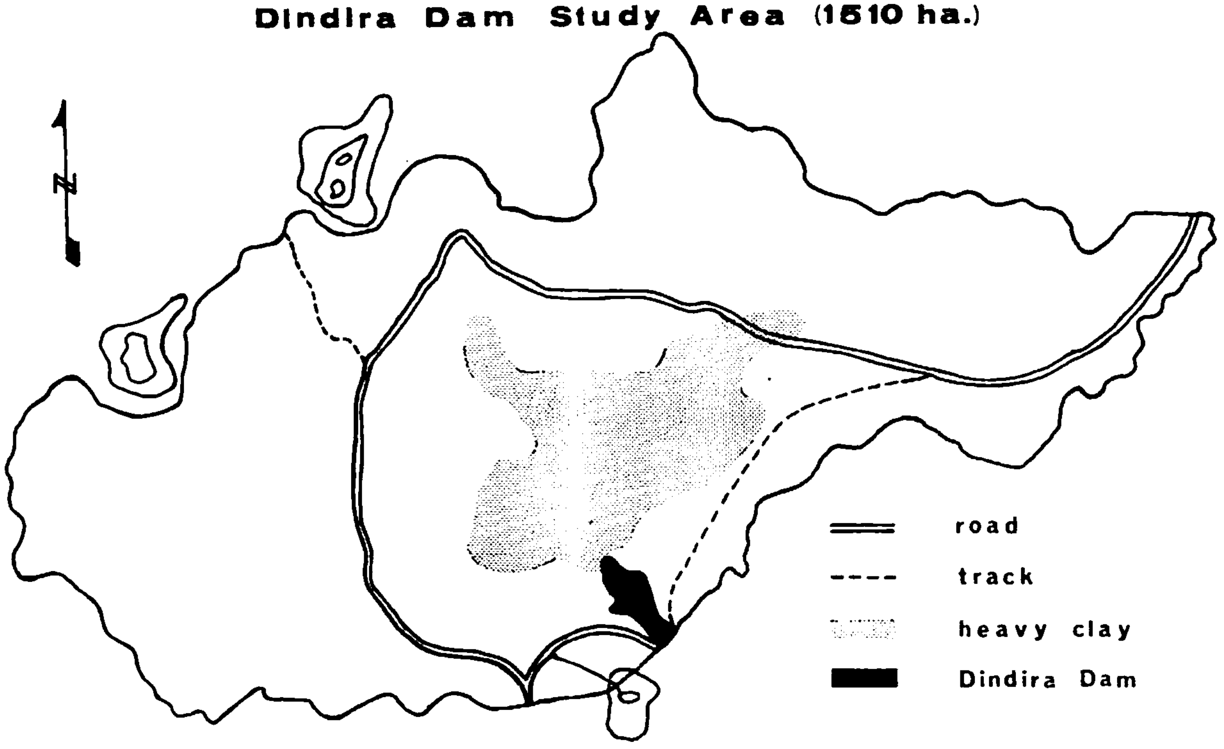


Fig. 11. The Dindira Dam study area consisted of a 15.1 km^2 plot completely surrounded by steep mountains of approximately 500 m elevation above plot level. Only three entrance and exit corridors existed, and animals likely to be driven from the area by the counting procedure could be enumerated from a small hilltop overlooking the area.

exact composition of all herds were plotted on maps to obviate recounting errors. It is firmly believed that these direct enumerations contained negligible bias or error.

With the assistance of several game scouts, simultaneous aerial surveys and ground counts of the same area were performed on numerous occasions. Thus, three censusing techniques could be compared for accuracy: (i) the initial hilltop estimate, (ii) the complete ground count, and (iii) the aerial survey.

Sight recording maps. Because of the very low density and the infrequency of observation of several species, sight recording maps were kept. When kept for long periods it was possible to deduce, within reasonable limits of confidence, the minimal number of certain species which was present. Peculiar markings and deformities of individuals were also noted, and in certain cases these animals served to indicate the minimal movements of the animal involved. The sight location records made during the monthly aerial surveys also provided data for describing migration patterns of the larger species.

Biomass calculations. Biomass is defined as the extant organic material present per unit area. In the following sections, however, the term refers only to animals, and more specifically, to the large herbivores.

In dealing with a system in which many large species occur, the total biomass may be closely approximated by summing only the large dominants. For example, one adult elephant weighs approximately the same as 10^5 rats; and therefore, the total contribution of small vertebrates and invertebrates is undoubtedly less than the sampling error involved with only the large herbivores. Further, since the half-life of dead animate tissue is probably less than a day in East African systems, the total animal biomass (alive and dead) is closely approximated by the standing crop (live only). The terms biomass and standing crop are used interchangeably therefore, although the figures quoted refer specifically to the latter.

Multiplication of size class abundance within species by the approximated weights of each size class is the best available estimate of total biomass per unit area (De Vos 1969). In cases where size-class recordings were not feasible, the total species number was simply multiplied by the adjusted mean weight for that species (Talbot 1964). This was the procedure followed for all aerial survey data reported here as well as for buffalo and the three small ungulates: dik dik, steinbok, and duiker.

Animal weights were taken from the literature, and even though great variation exists between the values reported for different areas and by different personnel, it is believed that modal values have yielded accurate estimates. When several values for different-aged animals were not available, the smaller size class values were derived by reverse extrapolation along a logistic growth curve. The mean species weights, derived for use when the animals were not classified by size, consist of the sum of the products of the size class weight estimates times the mean recorded class frequency of the population. Several compilations of weight estimates (Meinertzhagen 1938, Blancou 1962, Robinette 1963, Sachs 1967, Ledger 1968) along with numerous other sources of specific animal weights provided the basis of the weight estimations (Appendix IV.3).

Analysis. Subsequent to the collection of data on standard forms, a tabulated computer codification scheme was established. The systematic game count data were then transferred to approximately 35,000 computer cards for analysis. All computations were performed by Michigan State University's Control Data 6500 facility and an Olivetti programmable desk-top computer.

Results

Relative numbers. The western end of the reserve contained greater numbers of most species than did the central or eastern sections. As exceptions, however, zebra and oryx tended to utilize the west central and central portions of the reserve most, while elephants displayed a clumped but generally random distribution, with greater numbers in the east during the rainy season. Despite seasonal and species variation, the mean number of animals seen per unit distance (or area) over the entire course of the study clearly was greater in the western end. The mean number of animals seen on all ground and aerial transects in the western end was 9.6/km, while the central and eastern sections averaged 6.4 and 4.3/km, respectively.

This gradient of relative numbers is further confirmed by considering the number seen by the three counting techniques within precise zones along an east-west axis through the reserve (Table 4). The two exceptions to the smooth gradient (Table 4) represent the sampling of seasonally waterlogged grassland in otherwise bushland conditions. Both areas supported seasonal concentrations of zebra and oryx.

Table 4. The mean number of animals recorded (excluding elephants) by the various counting techniques over the entire course of the study in relation to distance from the western boundary of the reserve. The transect data represent the mean number per kilometer of transect, while the study plot data represent the mean density per square kilometer.

Counting Method	Distance from the Western Boundary (in km)					
	0 to 10	10 to 20	20 to 40	40 to 55	55 to 80	80 to 125
Ground transects	10.5 ± 2.2	7.4 ± 0.3	7.0 ± 1.9	11.4 ± 0.8		
Aerial transects	6.4 ± 0.3	5.5 ± 0.6	4.4 ± 0.7	3.0 ± 0.4	1.8 ± 0.2	1.9 ± 0.3
Sample plots	12.0	7.2	6.2			

Although the east-west gradient in relative numbers greatly overshadowed other distributional patterns, there was also a north-south trend. The areas along the Kenya border invariably supported greater numbers than comparable areas along the southern boundary. Thus when one gradient is superimposed upon the other, the overall gradient runs from northwest to southeast. Further evidence of these gradients is included in a discussion of biomass patterns.

Densities. The highest game densities of the reserve occurred in the northwestern corner around the permanent water of Dindira Dam. The mean annual density of large herbivores in this area was 12 animals/km^2 (Table 4). The density decreased rapidly, however, in all directions. Ten kilometers to the south and east the mean annual densities were 7.2 and 6.3 animals/km^2, respectively. The overall density dropped to less than 6 animals/km^2 in the west central section, and the bushland of the central and eastern sections supported an annual mean of less than 0.5 animals/km^2.

With the exception of buffalo, which reflected an extremely clumped distributional pattern and concentrated at the permanent water during the dry season, most species densities ranged from less than 1 to about 3.5 animals/km^2 (Table 5). The densities for all species combined ranged from dry season values of 23.7 animals/km^2 around the permanent water of the northwest to 3.4 animals/km^2 in the west central and much less than 1 animal/km^2 in the eastern sections (Table 5).

Table 5. Numbers and biomass per square kilometer for the major ungulates in three study areas of the Mkomazi Reserve during wet and dry seasons. The Dindira study area (Fig. 9a) is located in the northwestern corner of the reserve and represents an area of permanent water availability. The Mbula area is located near a semi-permanent water source, and the Mzara area in the west central section of the reserve had only seasonally available water.

	Dry Season			Wet Season		
	Dindira	Mbula	Mzara	Dindira	Mbula	Mzara
Buffalo	18.87	0	0	0	0	0
Eland	.05	0	0	0	0	.85
Elephant	1.81	.19	.02	.82	1.71	1.27
Giraffe	.34	.60	0	.08	.10	0
Gazelle	.18	1.06	1.26	.34	.31	0
Impala	.61	3.36	.56	3.35	3.58	1.99
Hartebeest	2.18	2.86	.93	.65	2.07	1.32
Rhino	.04	0	0	.07	0	0
Waterbuck	.29	0	0	.04	0	0
Zebra	1.22	0	0	0	.43	0
Other spp.	.48	.58	.58	.32	.48	1.10
Total no.	23.71	8.69	3.35	7.67	8.71	6.53
Total biomass kg/km^2	12,705.2	1,451.5	260.6	2,081.6	3,637.6	751.6

Absolute numbers. Estimates of the absolute numbers of large animals present in the reserve (Table 6) were deduced from a synthesis of: (i) the monthly totals observed from the aerial surveys and sight recording maps, (ii) extrapolations from seasonal mean densities for the different habitats and areas, (iii) long-term sight records of relatively short-ranging species such as rhino and waterbuck, and (iv) empirical knowledge resulting from approximately 5000 hours of field observations in the area. Even though approximate, a high degree of confidence is attached to these estimates.

Table 6. Minimal population estimates of the major animal species inhabiting the Mkomazi Reserve. The numbers of those species for which a range is given represent the dry and wet season values, with the highest number occurring in the wet season.

Buffalo	750	Oryx	100-400
Bushbuck	100	Ostrich	250
Eland	500	Reedbuck	50
Elephant	500-3000	Rhino	45
Gerenuk	250	Waterbuck	150
Giraffe	250	Zebra	100-400
Gazelle (Grant's)	150-600	Lion	80-100
Hartebeest	1000	Cheetah	35
Impala	600	Hunting dog	25
Kudu (lesser)	250	Hyaena	60

Elephants were the most numerous animals (Table 6), while hartebeest, buffalo, impala, and eland followed in that order. No other nonmigratory species numbered much over 250. Whereas Grant's gazelle, oryx, and zebra showed seasonally high numbers, the resident population of the reserve was much lower.

Relative biomass distribution. Since the body weights of the different species vary from a few kilograms for the smaller ungulates to several thousand for elephant, it is frequently more instructive to analyze biomass patterns rather than numbers. An area which contains only a few elephants may support an equal or greater biomass density than another with several hundred smaller ungulates. This tends to be the case in the Mkomazi.

Before developing the relative biomass patterns, a short description of the analytical technique is given. Mapping of continuous ecological variables offers considerable analytical advantage over attempts to discretize and then test or explain the variation between groupings. Several techniques such as the least-squares fitting of polynomial equations exist for such mapping endeavors. The technique used here is that of trend-surface-analysis for which computer programs are available (O'Leary, Lippert, and Spitz 1969). It is an application of multiple regression and has been used extensively in geology, systematics, and more recently, ecology (Sokal 1965, Vandermeer 1966, Marcus and Vandermeer 1966, Sneath 1967, Gittins 1968).

As used here, the north-south and east-west locations in the reserve are denoted by an X and Y value, and in turn, a Z value representing the mean biomass per square kilometer at that point is established. Thus for every datum, two independent variates (the X,Y coordinates) and one dependent variate (biomass density) exist.

To systematize the biomass data a grid of squares 10 km on a side (100 km^2) was drawn onto a profile of the reserve. In so doing, a system of 142 subplots was established. The biomass values for each datum represent the mean density in that area for three aerial counts. Since only the aerial transect data provided complete coverage of the reserve, the biomass densities used in this section are drawn exclusively from those data. Therefore the values given are only minimal estimates and are best viewed as index values.

Solutions to the regression of biomass density against location can be obtained for a number of different degree equations. Thus, if only a linear response is plotted, the general regression equation will be that of a plane suspended in three-dimensional space. It will take the form of:

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \varepsilon$$

where $\hat{Y}$ is the predicted value of the dependent variable (density), β_0 = the intercept of the plane with the vertical axis, $\beta_1 X_1$ = the partial regression coefficient of density on the X_1 coordinate times the X_1 distance from the origin, $\beta_2 X_2$ = the partial regression coefficient of density on the X_2 coordinate times the X_2 distance from the origin, and where ε = the residual error of prediction not explained by the two partial coefficients. All lines (responses) deriving from such an equation are linear since they are contained in a flat plane.

But generally, linear responses do not provide a very good fit to biological data. Consequently, the percent variation in Z (the dependent variable) explained by the X,Y coordinates (dependent variables) will be low and the percent attributed to residual error (ε) will be high.

From this it might be expected that the higher the order of equation becomes [e.g., quadratic (Fig. 12), cubic (Fig. 13), quartic (Fig. 14), etc.] the greater will be the percent variation explained by the equation (X and Y with their powers and products). The percent variation attributed to residual error will decrease correspondingly. From each equation, the regression coefficients, the coefficient of determination, and the multiple correlation coefficient are derivable.

Two analyses were required to evaluate the hypotheses that there were: (i) a dominant east-west biomass gradient, (ii) a subdominant north-south gradient, and (iii) a significant difference between the wet and dry season densities. That is, a wet season plot (lower pair of Fig. 12, 13, and 14), and a dry season plot (upper pair of Fig. 12, 13, and 14). But since elephants were known to play an important role in the overall biomass pattern, analyses including (left-hand pair of Fig. 12, 13, and 14) and excluding (right-hand pair of Fig. 12, 13, and 14) elephants were called for.

Consequently, four density maps had to be prepared to fully explain the relative biomass distribution pattern (dry with elephants = DWE; dry without elephants = D-E; wet with elephants = WWE; and wet without elephants = W-E).

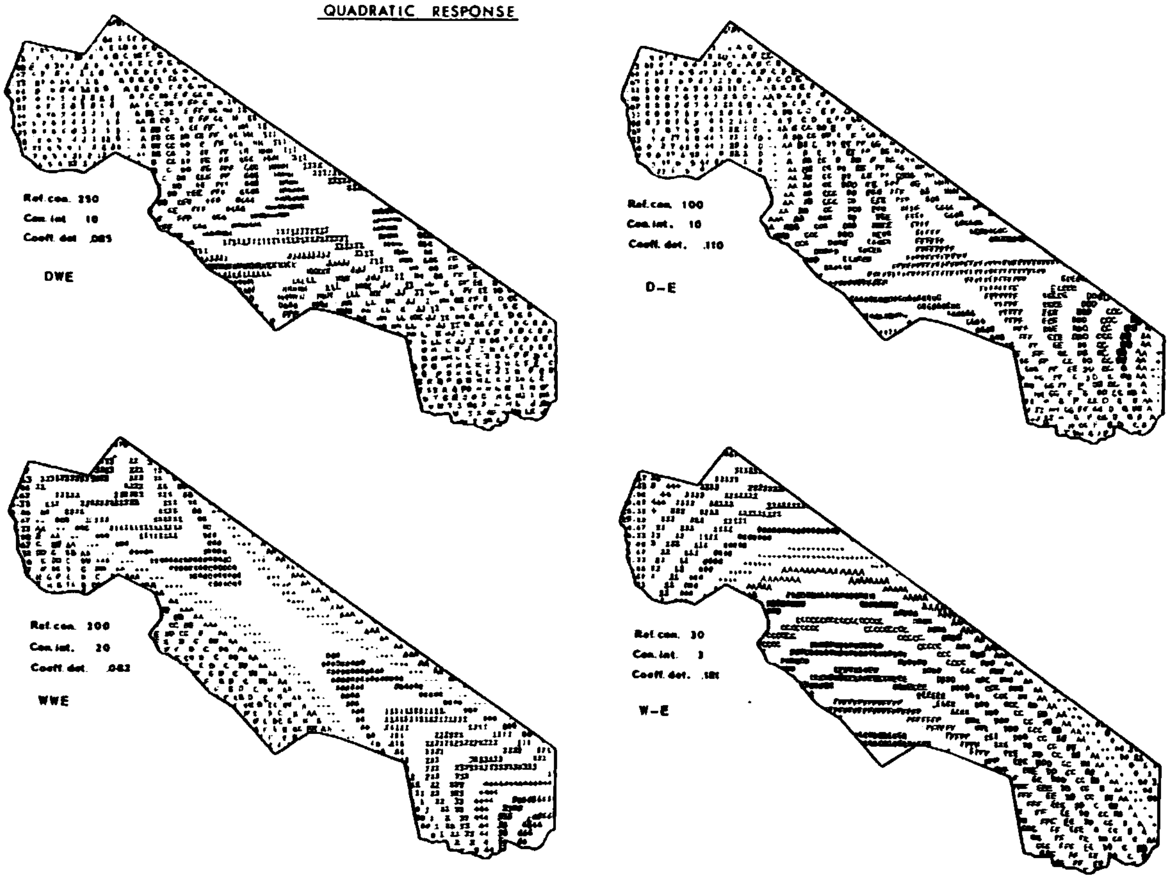


Fig. 12. Quadratic response plots of a trend-surface analysis of relative biomass density. The surfaces derive from a least-squares multiple regression procedure and may be interpreted as contour maps of biomass density for the respective areas of the reserve.

The upper pair of plots were derived from the mean biomass density (kg/km^2) of three dry season aerial counts, while the lower pair derives from the mean density of three wet season aerial counts. The left-hand pair of plots is based on total biomass, while the right-hand pair refers to large herbivore biomass exclusive of elephants.

Since the maps are based on aerial transect data, the values only represent the minimum biomass estimate (not absolute) and are therefore best considered as indices to relative biomass distribution. Interpreting the maps is the same as reading a contoured topographic map. That is, the reference contour (Ref. con."":..":) depicts an arbitrary density isopleth whose value in kilograms per square kilometer is given along with the plot. Density isopleths (contours) denoted by numerals (0 to 9) represent values higher than the reference contour; explicitly, an increase in density by the stated contour interval (con. int.) amount for each "edge" of the successively higher numbered bands.

As an example, consider the lower right-hand map which refers to the wet season without elephant biomass density (W-E). Note the reference contour of 30 kg/km^2 which crosses the reserve in two places in the west central and eastern ends. Each edge of a successively higher numbered band depicts an increase in density by the interval amount (in this case 3 kg/km^2). Therefore, the band or contour of 1's represents an isopleth of density between 33 and 36 kg/km^2, while in the northwestern section a short band of 4's represents a density between 51 and 54 kg/km^2. The density gradient runs perpendicular across the contours.

Contours denoted by letters represent decreasing density values for successive letters of the alphabet. Therefore, using the same sample, the band of A's depicts a density of between 24 and 27 kg/km^2, while the B contour denotes a narrow zone of between 18 and 21 kg/km^2. Again, the decreasing density gradient runs perpendicular to the contours.

The coefficient of determination (coeff. det.) derived from the least-squares analysis is given along with each plot. Along with the example plot (W-E) a value of 0.181 means that 18.1% of the variation in biomass density was explained by the second order regression equation of density on location. The square root of 0.181 yields the multiple correlation coefficient of 0.426 which is highly significant.

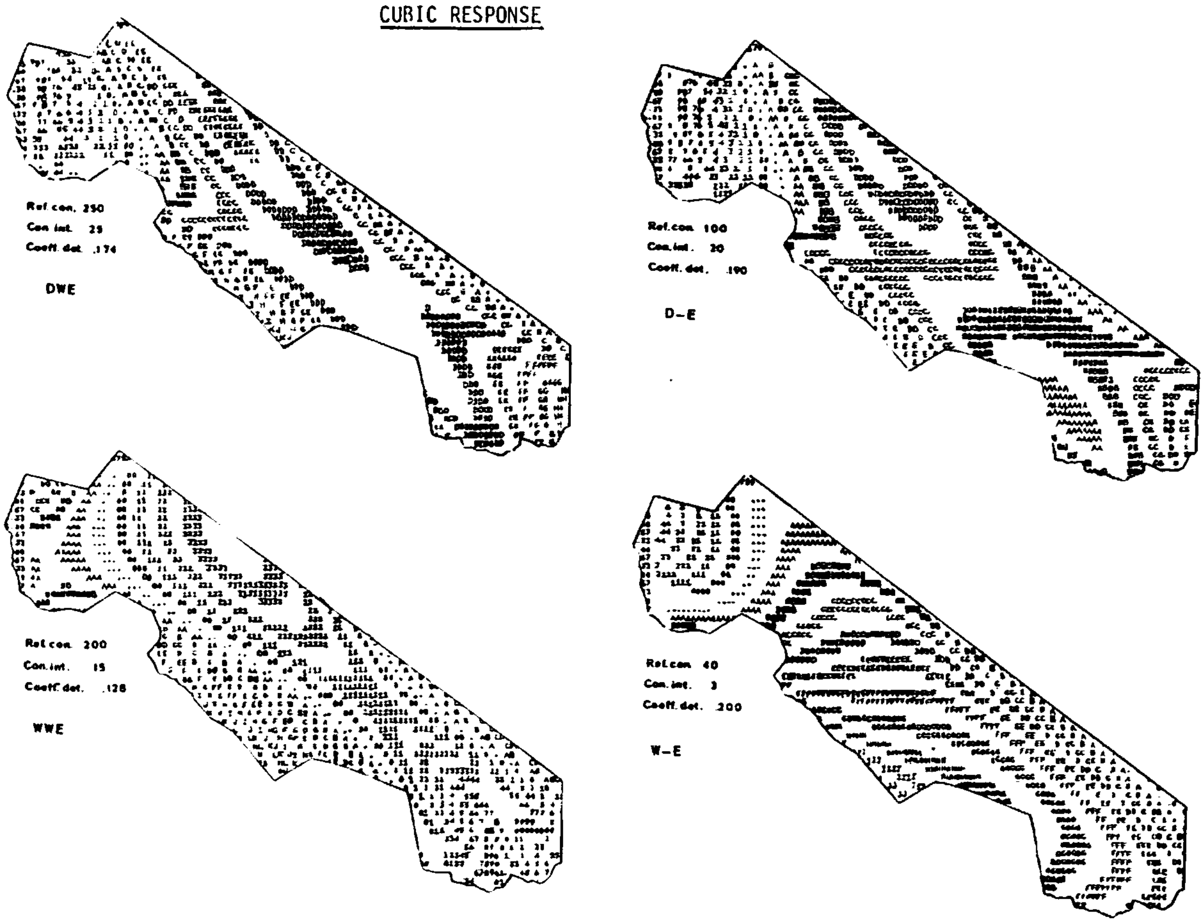


Fig. 13. Cubic response surfaces derived from the third order least-squares regression equation of biomass density on location. The data are the same as those used in Fig. 13, but the higher order equation allows a "better fit." Thus, here, 20% of the variation in wet season nonelephant biomass (W-E) is explainable by location.

QUARTIC RESPONSE

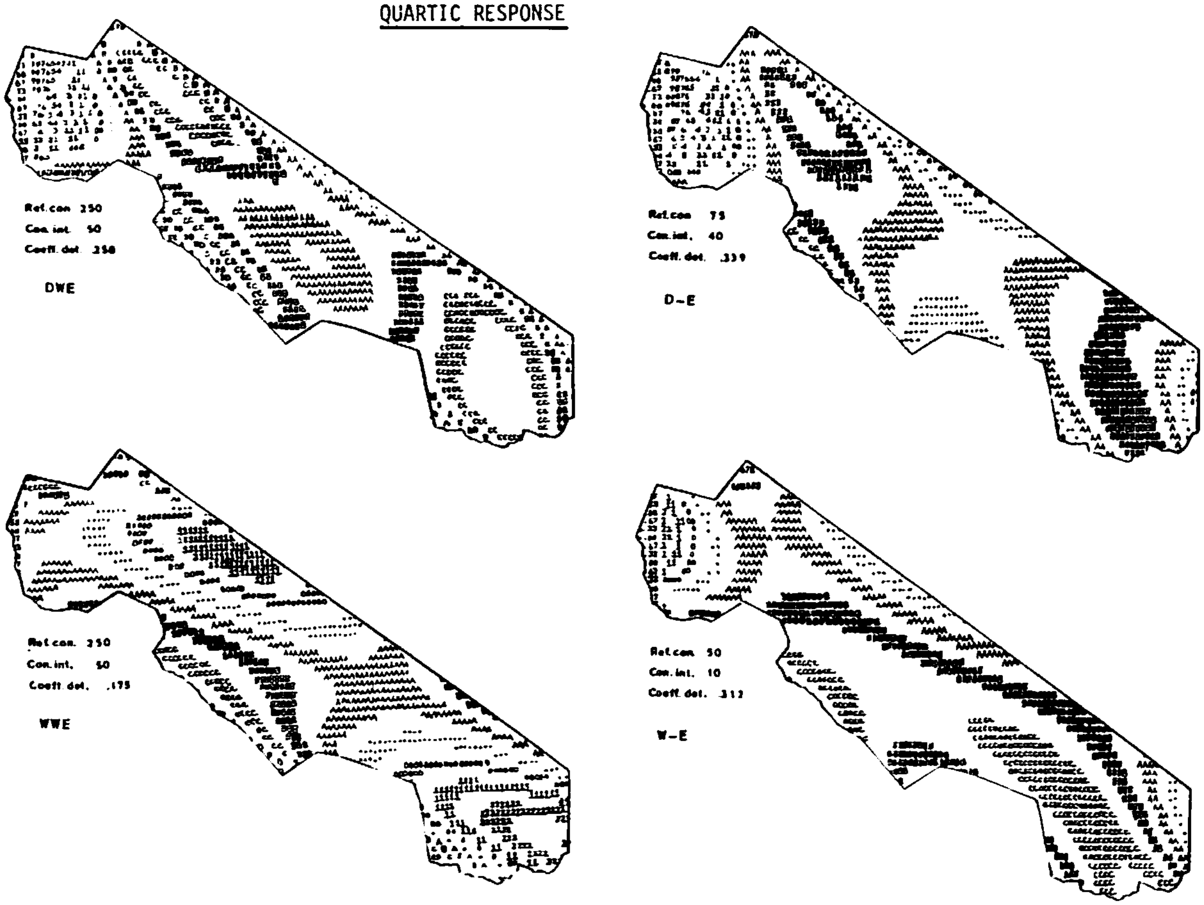


Fig. 14. Fourth degree response surface resulting from the multiple regression analysis of large herbivore biomass density on the X,Y location in the Mkomazi Reserve. The data are the same as those used for the quadratic and cubic responses. The least-squares regression equation from which these results were obtained is of the form: $\hat{Y} = \beta_0X_0 + \beta_1X_1 + \cdots + \beta_nX_n + \varepsilon$. With powers and products the equation contains 16 terms. The highest coefficient of determination of the analysis was obtained with this response (no higher order equations were fitted). Approximately 34% of the dry season biomass density exclusive of elephant can be explained by knowing the X,Y position in the reserve.

There is indeed an east-west biomass gradient within the reserve (Fig. 12, 13, and 14). The gradient is most pronounced during the dry season (upper pairs of maps) and exists regardless of whether or not elephant biomass is included in the calculations. During the rainy season (lower pairs of maps), on the other hand, the added elephant biomass completely changes the distributional pattern. When the elephants are included (WWE), there is a marked depression (low biomass density) in the center of the reserve with increasing densities in both directions. If elephants are excluded from the analysis (W-E), the east-west gradient is largely restricted to the northwestern section of the reserve.

As mentioned previously, the north-south gradient is subordinate to the east-west gradient. Therefore, during the dry season when the east-west gradient is strongest, the north-south gradient is barely perceptible (upper pairs of maps, Figs. 12, 13, and 14). During the rainy season, on the other hand, when the east-west gradient is less obvious, the north-south gradient appears most pronounced (lower pairs, Fig. 12, 13, and 14). In the treatment combination of wet season without elephants (W-E) the north-south gradient dominates the distributional pattern.

In only two of the combinations were the linear multiple correlations between density and location not significant. In all cases, the multiple correlation ($\sqrt{\text{coeff. det.}}$) became highly significant with the second (Fig. 12), third (Fig. 13), and fourth (Fig. 14) degree responses.

The percent variation in biomass density explainable by knowing the X,Y location in the reserve is given by the coefficients of determination (coeff. det.). Thus, with the second order equation (quadratic response, Fig. 12), only between 8.2 and 18.1% of the variation is explained by location. As the degree of the equation is increased, however, the more local variation can be explained. Thus with the third degree response (Fig. 13), between 12.8 and 20% of the variation is explainable by the X,Y location. The percent variation explained by the fourth degree response (Fig. 14) is generally greater than 25% and accounts for about 34% of the variation in the dry season biomass of herbivores other than elephants.

Absolute biomass densities. Although the relative biomass distribution maps reflect the overall pattern within the reserve, more precise estimates of the standing crop were obtained from ground transect and sample plot evaluation. Whereas the highest biomass densities approached 13,000 kg/km^2 for the Dindira study area during the dry season (Table 5), the mean annual biomass for the same area was 5,548 kg/km^2. The mean annual standing crops for the Mbula (semi-permanent water) and the Mzara (seasonal water) study areas were 1,934 and 707 kg/km^2, respectively. The density values derived from the ground transects and visibility profiles corroborate this trend and suggest that within the western end of the reserve, concentric density isopleths radiated from the Dindira area. At a radius of about 10 km, the mean annual biomass was only 2,000 kg/km^2; at 15 km from the permanent water the mean annual density fell to about 1,000 kg/km^2.

The mean annual biomass over the entire area of the reserve was about 1,200 kg/km^2. But since elephants constitute over 90% of the biomass in the eastern half of the reserve, all other herbivores combined sum to only about 100 kg/km^2.

Movement and Temporal Dynamics

Previous statements and data have alluded to strong seasonal fluctuations in the numbers of animals in the reserve. As the only system of counts covering the entire reserve, the monthly aerial transect data provide the best overall index to this pattern. Trend analysis of the longer-term ground transect data provides a more accurate assessment of local variation, while still further refinement has been achieved by plotting herd locations and game concentrations as they moved across the transect and study plot grid.

Seasonal movements in the Mkomazi were characterized by a major north-south movement of animals across the Kenya border and an almost equally strong east-west movement within the reserve. While only the north-south migrations accounted for overall changes in numbers of animals, the east-west movements greatly affected seasonal distribution patterns.

North-south International Migrations

When the total numbers of animals seen on the monthly aerial transects were plotted against time (Fig. 15), a significantly nonrandom ($P < .05$) time trend was evident. These monthly totals are also significantly correlated ($P = .02$) with the mean monthly aridity coefficient for all stations. The highest numbers of animals occurred during the months of highest rainfall. The pattern is, of course, seasonally cyclical.

Within the overall annual pattern, two distinct types of migrant populations were evident. The elephant numbers fluctuated with dramatic presence-absence pulses, while the numbers of zebra, oryx, and, to a lesser degree, Grant's gazelle showed more moderate sinusoidal fluctuations.

The north-south movements were characterized by aggregates of many herds moving as a unit. An eastern population of about 1,500 elephants migrates northward across the international boundary during the drier months (Harris 1968; Watson, Parker, and Allen 1969). Their occurrence within the Mkomazi is highly correlated ($P < .01$) with extant vegetation and water conditions as measured on an ordinal scale. The resident population of the eastern half of the reserve is very low during the dry season, and thus the presence or absence of the migratory animals causes dramatic fluctuations in total numbers and biomass.

A distinct western elephant population, approximately the same size as the eastern, inhabits the region west of the central hill mass. Of the total number in this population only some 600 migrate seasonally, while a considerable number remain in the reserve. These dry season residents tend to

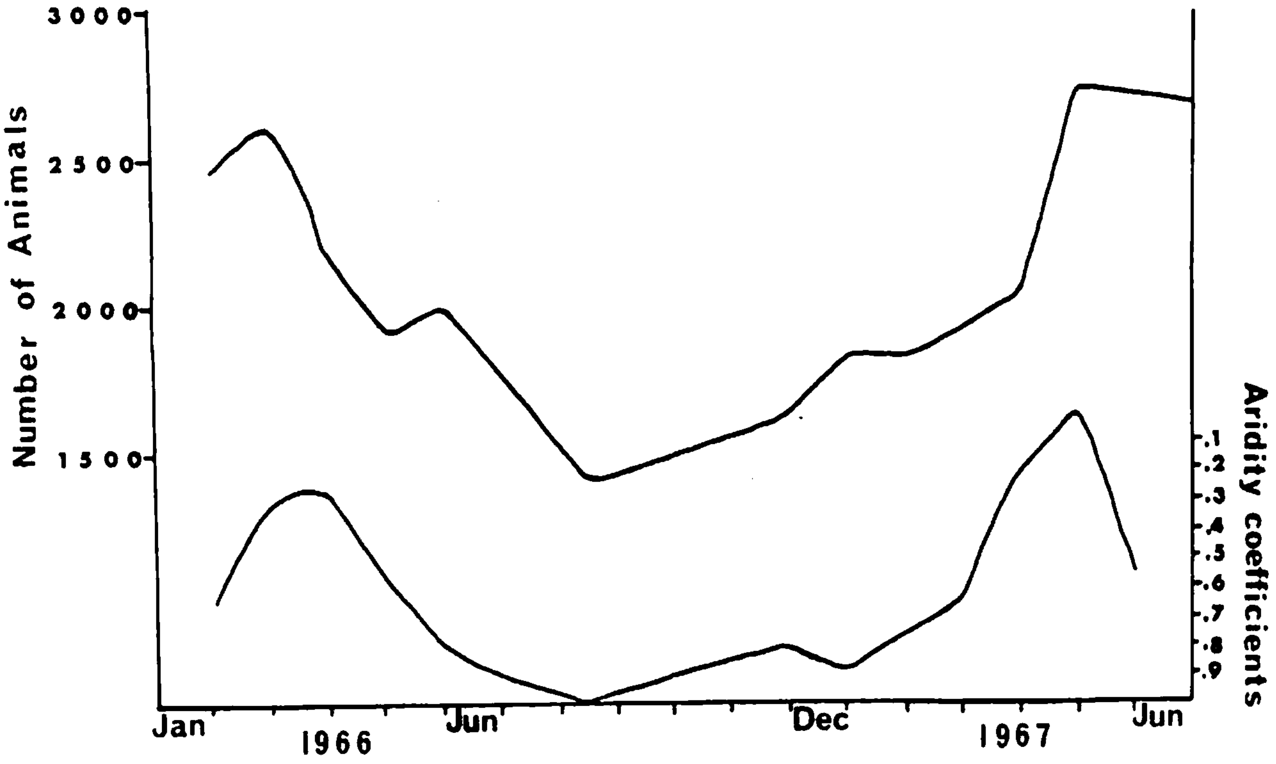


Fig. 15. The seasonal relationship of numbers of animals seen along the monthly aerial transects and the mean monthly aridity coefficients of all stations. The curve has been "smoothed" by plotting a 2-month running mean. The correlation between the "unsmoothed" numbers and the aridity coefficient was highly significant (P = .02), and the monthly nunbers of animals seen was significantly nonrandom (P < .05).

congregate in the mountain foothills within range of Dindira Dam. The migrants move into the Lake Jipe area of Tsavo National Park in Kenya. Since the difference between the wet and dry season totals of the western half of the reserve is only twofold, the fluctuations in total numbers are not nearly as great as those produced by the eightfold difference in the east.

The north-south movements of the zebra, oryx, and gazelle are as seasonally predictable as any, but for several reasons their changes in numbers are much less pulse-phasic. First, the distribution pattern of these animals is much less clumped than the aggregates of migrating elephants; they tend to move as small independent herds. They also appear to be much less dependent on surface water, and thus their arrival and departure times are less strict.

Whereas elephants seem to cross the Kenya border at all points with no specific movement routes, the ingress and egress routes of zebra, oryx, and gazelle are more or less restricted to the four areas where open grasslands extend over the Kenya boundary. Therefore, early in the rainy season the number of these species increases on the grasslands along the border (Mbuga ya punda milia, Maori, Kavuma, and below Kwamkala ridge in the very eastern end). As the season progresses, they gradually move southward until they reach the southern boundary of the reserve. They inhabit these southern reaches for 6 to 10 weeks during favorable periods, but as the grazing pressure increases they gradually retreat northward. Their numbers then increase in the northern areas again until they finally leave the reserve for lack of dry season water and forage.

Table 7. Two-way analysis of variance illustrating significant differences in the density of large animals on the three sample plot areas, as well as significant seasonal differences. Importantly, there is a highly significant interaction effect manifesting the change from the highest dry season density near the permanent water to the lowest density in this area during the wet season. (* = Significance at P = .05, *** = Significance at P = .001).

	Dindira Dam (Permanent Water)	Mbula (Semi-permanent Water)	Mzara (Seasonal Water)
Dry Season	$\bar{X}$ = 30.0 S^2 = 390.1 N = 6	$\bar{X}$ = 6.6 S^2 = 7.5 N = 6	$\bar{X}$ = 2.4 S^2 = 1.2 N = 6
Wet Season	$\bar{X}$ = 7.1 S^2 = 4.1 N = 7	$\bar{X}$ = 9.2 S^2 = 8.3 N = 7	$\bar{X}$ = 9.5 S^2 = 13.6 N = 7

Source	df	MS	F
Study area	2	553.4	10.8***
Seasons	1	223.2	4.4*
Interaction	2	921.0	18.1***
Error	33	51.0	

East-west Movements

Distinct from the north-south migrations are seasonal east-west movements. Of the animals remaining in the reserve during the dry season, the elephant, buffalo, giraffe, gazelle, and eland all tend to congregate around the permanent water of Dindira Dam. Therefore, when the mean monthly densities of the three sample study areas are analyzed with a two-way analysis of variance, (Table 7), there is a significant difference ($P < .05$) between pooled wet and dry season means as well a highly significant ($P < .001$) interaction effect. That is, during the dry season the mean density around the permanent water greatly exceeds that of the other two areas. But during the wet season, densities in the two areas away from the permanent water exceed that of the Dindira area.

Because of their highly-clumped distributional patterns and relatively large body size, buffalo movements deserve special mention. Over 90% of the total population occurred in three large herds from 175 to 300 animals each. Although the three large herds moved as independent entities, it was frequent that two and sometimes all three of the herds (totalling from 300 to 750) inhabited the Dindira area simultaneously for considerable periods during the dry season. These animals then moved eastward as separate herds during the periods of surface water and forage abundance. Although never recorded as far as the eastern boundary, their range extended at least 100 km to the Kandea area. They also frequently moved short distances into Kenya, but this was during the wet months, rather than the dry as is the case with other species.

There was also an east-west movement of elephants in the reserve which occurred during the wet season and was not associated with the permanent water of Dindira Dam. In January to February 1965, in January 1966, again in March 1966, and in April 1967, elephants concentrated around the northernmost hill mass in the central section of the reserve. These concentrations numbered from 1,200 to 1,600; and, judging from their temporary absence elsewhere, they consisted of animals from both the eastern and western sections of the reserve. After a week or two, the concentrations dispersed and the distribution throughout the reserve returned to normal. Although several other hypotheses might explain this phenomenon, it seems that the concentrations are associated with seasonal breeding patterns (Quick 1965, Laws 1968).

Seasonal Biomass Patterns

The temporal biomass pattern follows that of the numbers closely. Therefore, during the dry season when overall numbers are low, the east-west gradient is steepest (upper pairs of maps Fig. 12, 13, and 14). The mean dry season biomass for the entire reserve reaches a perigee of about 570 kg/km^2 during this period, while the densities in the western end are at a maximum of nearly 13,000 kg/km^2. During the rainy season, the east-west gradient is nearly extinguished (lower pairs of maps, Fig. 12, 13, and 14), and the mean biomass for the entire reserve rises to 1,925 kg/km^2.

Two salient factors are involved with this seasonal reversal of biomass distribution. During the rainy seasons, elephants constituted about 82% of the total game reserve biomass while only 46% of the dry season biomass was made up of elephants. Since there is a disproportionately high ingress of elephants into the eastern end, the overall pattern reflects a large depression in the center of the reserve with highs on either end (WWE, Fig. 12, 13, and 14).

But of equal importance is the liberation of the other herbivores from the constraints of the dry season water source in the western end. This fact was demonstrated by the highly significant interaction effect of areas × seasons (Table 7), but is even more substantiated by the almost complete lack of any wet season east-west gradient when elephants are excluded from the relative biomass calculations (W-E, Fig. 12, 13, and 14). From this it seems clear that utilization of the artificial permanent water source in the western end plays a major role in the ecology of the reserve.

Discussion

Based on the east-west gradients of climate, soils, and vegetation established in previous chapters, it is not surprising to find that animal density gradients also exist.

It is of interest, however, to note that the total number of animals and biomass in the reserve are greater during the wet season than during the dry. This seasonal pattern is opposite that reported for most African parks and reserves where animals move into the protected areas during stressful periods and move outside during periods of abundant forage and water. In this sense, most of the Mkomazi Reserve serves as a wet season liberation area for animals which take dry season refuge in the Tsavo National Park of Kenya.

The opposite pattern, that of moving into protected areas during the dry season periods of stress, applies to the relatively small area in the northwestern section of the reserve, however, where permanent water has been provided.

To me, this phenomenon reflects the inability of the semi-arid eastern sections to support the wet season densities throughout the year. Whereas the forage carrying capacity may be limiting in local areas, it is my opinion that the unavailability of permanent surface water is more crucial.

The word "unavailable" is chosen judiciously. Less than 30 km from the wet season environs of the migratory zebra, gazelle, and oryx flows the permanent water of the Umba River. Yet is is only rarely that wild ungulates are seen nearby. If water is such a crucial dry season commodity, the question of why the bushland along the Umba remains barren and depauperate of game animals must be posed. Permanent rivers within other East African parks and reserves largely control the dry season animal distributions.

It appears to me that the answer lies almost wholely in the fact that there is heavy usage of this area by illicit Wakwave and Wapare cattle grazers and hunters. As a consequence, two different effects on the game are evident. Approximately 40% of the entire eastern half of the reserve is seriously overgrazed by cattle (see Table 3, Fig. 20b; Hemingway, Cormack, and Robinette 1966). At a recommended stocking rate of 6 ha/beast (McKay 1968, Hemingway et al. 1966) the southern border areas were estimated to be 15 to 20 times overstocked in 1966 (Hemingway et al. 1966). There is little doubt, therefore, that the grazing wild ungulates incur the effects of severe forage competition in these areas.

But several ungulates (e.g., kudu, gerenuk, and giraffe) rarely graze and since cattle do only limited browsing, it would seem that these ungulates would incur little competitive effect from cattle.

Probably more important is the behavioral effect that people (particularly hunters) and domestic stock have on the game populations. Although no quantitative data are available, there is little doubt among Game Department personnel that the southern and eastern borders of the reserve support the greatest illicit hunting pressure. Pienaar, Wyk, and Farrall (1966) have shown that in the Kruger National Park, at least, breeding herds of elephant significantly avoid areas developed for tourism and that the only recent attacks on tourists have occurred in those areas where elephants had no recourse but to encounter tourists.

The results of this study show a significant difference ($P < .05$) in the mean herd size of elephants between the eastern and western sections of the reserve. The eastern elephant population has the greater mean herd size, and although subjective, it appears that the eastern elephants are substantially more truculent than those of the west. Both of these parameters correlate with the greater hostility toward elephants on the part of hunters and grazers in the eastern half of the reserve. Elephants have also shied away from those areas of the Mkomazi in which substantial culling operations were undertaken in 1968 (B. Turner, personal communication).

These observations are summed up as follows. Although zebra, oryx, and gazelle coinhabit the northern half of the eastern end of the reserve with cattle during the wet seasons, they very rarely inhabit the areas along the Umba River. Although their exodus from the reserve is concurrent with, and appears to be a result of, the drying of surface water, they do not utilize the Umba River. Excluding elephants, the 2 to 3 km strip of bushland adjacent to the permanent water of the Umba River supports the lowest game density of any area in the reserve. This density approaches 0 animals/km^2.

Elephants, on the other hand, do utilize the bushland along the Umba; and since in this area of the Mkomazi they are essentially browsers, it is doubtful that much forage competition occurs with the cattle of the area. They too move away from the permanent water of the Umba during the dry season.

With regard to the potential utilization of East African rangelands for game cropping or ranching, considerable literature has been compiled on the relative densities of game and the game carrying capacities of different areas. Comparative values for several areas have been compiled and tabulated by Bourliere and Verschuren (1960), Petrides (1956), Stewart and Zaphiro (1963), Talbot et al. (1965), and Piernaar et al. (1966) (see Talbot et al. 1965 for 28 references prior to 1965).

Although the game density or standing crop of the Mkomazi does not approach the phenomenally high value reported for the higher rainfall areas of eastern Katanga (Congo) or Uganda (ca. 24,000 kg/km^2--Bourliere and Verschuren 1960, Petrides and Swank 1966), the values compare favorably to those reported for other *Acacia-Commiphora* bushland areas under similar rainfall regimes (Table 8). In general, it appears that within the semi-arid bushland association mean annual standing crop values show about a tenfold increase from only a few hundred kilograms per square kilometer in the drier areas (Stewart and Zaphiro 1963) to several thousand under higher rainfall conditions (Potts and Jackson 1952, Talbot 1963*b*). This same range of biomass standing crops occurs in the Mkomazi under apparently similar vegetation conditions and suggests that some measure of overall climatic conditions (e.g., actual evapotranspiration) may be the best correlate for predicting carrying capacity and mean standing crop.

Table 8. Comparative large herbivore densities (no./km^2) and mean annual standing crop biomass (kg/km^2) for different bushland areas of East Africa.

Habitat Type	Location	Density	Standing Crop	Reference
Acacia-Commiphora thornbush	Shinyanga, Tanzania	ca. 4	ca. 2810	Potts and Jackson 1952
Acacia-Commiphora bushland	Kenya-Tanzania, Masailand		5665	Talbot 1963*b*
Dry bush with trees, ca. 50 cm rainfall	Baragoi Plains, Kenya	ca. 1.54	312	Stewart and Zaphiro 1963
Desert grass bush, ca. 65 cm rainfall	Wamba Plains, Kenya	ca. 2	895	Stewart and Zaphiro 1963
Acacia savanna	Tarangire Reserve, Tanzania	ca. 4	ca. 1050	Lamprey 1964
Acacia savanna *Brachystegia* wood	Doma-Mikumi, Tanzania	ca. 4	ca. 1050	Lamprey 1964
Acacia-Commiphora bushland, 38 to 56 cm rainfall	Mkomazi Reserve, Tanzania			
Without cattle		1.91	1200[a]	This study
With cattle		2.36	1303	

[a] The estimated weights used here are considerably less than those generally used elsewhere.

Little mention has been made of the cattle numbers or biomass within the reserve. While conducting the monthly aerial game surveys, cattle numbers and locations were also recorded. From the compiled data the cattle numbers were known to exceed 3,000 during certain rainy seasons, and even during the driest months they numbered in the hundreds. The mean annual number of cattle supported within the reserve was estimated to be 1500 ± 10%. Using a mean weight estimate of 225 kg/individual (Deans et al. 1969), the additional biomass to be included with the wild ungulate standing crop is 337,500 kg or 103 kg/km.

In discussing the severe habitat degradation of the Tsavo National Park of Kenya (contiguous with the Mkomazi), Glover (1963), Bourliere (1965), and Laws (1969) conclude that a density of 0.4 elephants/km^2 (1/mile^2) is approximately the sustained carrying capacity of the semi-arid bushland. Although a considerable area of the Tsavo Park (East) receives less rainfall than the Mkomazi, it is unlikely that the Mkomazi carrying capacity is much greater than 0.5/km^2. But yet the mean annual density of the eastern half is about 1.0/km^2 and in certain areas the density reaches 4/km^2 for several months of the year. It is therefore hoped that the Game Department will pay special attention to the potential problem of too many elephants and pursue a viable management policy as exemplified by the preliminary culling of 300 elephants in 1968.

COMMUNITY STRUCTURE

Tropical ecosytems have long been known for their highly complex structure, the intricate interrelations between components, and their high organismic diversity (Wallace 1878). Although these attributes are most commonly ascribed to the wet tropics, East African ecosystems reflect the same high number of species, and because of the array of large animals, they have gained considerable acclaim.

Much ecological theory has been directed toward the questions of tropical community structure and how these systems support such high diversities (Klopfer and MacArthur 1961, Connel and Orias 1964, Pianka 1966). Without implying causation, most theoretical arguments reduce to the hypothesis that, in general, tropical organisms have narrower niches. In other words, they generally manifest greater specificities for abiotic and biotic conditions than their temperate counterparts.

With specific reference to East Africa, studies by Talbot and Talbot (1962), Vesey-Fitzgerald (1960, 1965), Lamprey (1963), and Field (1968) suggest considerable ecological or niche separation of the large herbivores on the food resource alone. A similar condition exists for the large predatory array (Wright 1960; Kruuk and Turner 1969; Mitchell, Shenton, and Uys 1965; Hirst 1969). Darling (1960) has described other aspects of the ecological separation of the large ungulates, and the work of Lamprey (1963) has provided still further insight. Hofmann (1968) has elucidated internal anatomical differences which correlate with and possibly govern feeding habits.

Although this study was not purposely designed to elucidate the ecological separation of the species array, the quantitative analysis of results provides insight into this phenomenon.

Conceptually, the Mkomazi community may be portrayed by means of a species-environment matrix (Fig. 16). The total area of the reserve has been roughly divided into four habitat types, namely, dry montane and riparian forest, tallgrass savanna (bushed and wooded grassland), open grasslands, and bushland. A measure of species diversity for each habitat provides insight into the large animal constituancy of each.

By considering each species' relative occurrence in each of the major habitats, a crude measure of ecological separation is obtained. However, the utilization of the various habitats is time dependent; and therefore if the total period of study is divided into wet, dry, and transitional periods, an estimate of temporal separation can be made. An index of niche breadth on the "time dimension" will therefore reflect an inverse measure of a species' specificity of seasonal conditions.

Clearly, the number of resources (dimensions) upon which a species' specificity could be evaluated is very large. This line of reasoning soon leads to the Hutchinsonian concept of each species occupying an n-dimensional hyperspace (Hutchinson 1957, 1965).

Finally, it seems clear that all species are not discretely separated (Lamprey 1963, Field 1968) along any dimension. That is, closely related species tend to "overlap" one another with respect to food, habitat utilization, temporal patterns, etc. This leads to the concept of niche overlap or the quantitative expression of the similarity of different species.

Species Diversity

A primary problem associated with the study of community diversity is its measurement. The species diversity of a community or ecosystem may be simply expressed as the number of species present or some complex relationship between the number of species and the numbers of individuals per species. But a simple tally of the species present may show two greatly dissimilar communities to have the same "diversity" since no consideration is given to possibly differing abundances. More sophisticated indices include Fisher's "α" index (Fisher, Corbet, and Williams 1943), Simpson's "λ" index (Simpson 1949), Margalef's "d" indices (Margalef 1957), and others.

Currently, use of the Shannon-Wiener information indices are gaining wide acceptance because of their comprehensive but simplistic nature (Margalef 1963; Pielou 1967; Lloyd, Zar, and Karr 1968). In short, the underlying theory is that of defining the number of "bits" of information or binary choices necessary to fully identify any element in an array. Thus, from an "information" point of view, the index relates to the uncertainty involved in predicting which species will be encountered by a random sample from the community (Lloyd et al. 1968). From this it is established that any monospecific array of elements will have the lowest possible value since only one choice is necessary to identify any element.

It does not hold, however, that an array with the largest number of species of elements will necessarily have the largest index value. For if S species of elements total N individuals, the maximum value would only be achieved if all elements were equitably distributed among the S species, that is, N/S, individuals per species. On the other hand, the minimum value will be achieved when all N-S+1 elements are of the same species and the remaining S-1 species are represented by only one individual each.

Clearly, there are two components to the index: the number of species and the equitability with which individuals are distributed among the species.

The mathematics of the indices are adequately developed and explained by a number of authors including Margalef (1957), Pielou (1967), Lloyd and Gherlardi (1964), and Lloyd et al. (1968). Using Sterling's approximation to large factorials, the equation for individual diversity is:

$$N' = -\sum_{i=1}^{S} P_i \log P_i$$

where P_i = the proportion of the total elements (individuals in this case) which occur in the i^{th}

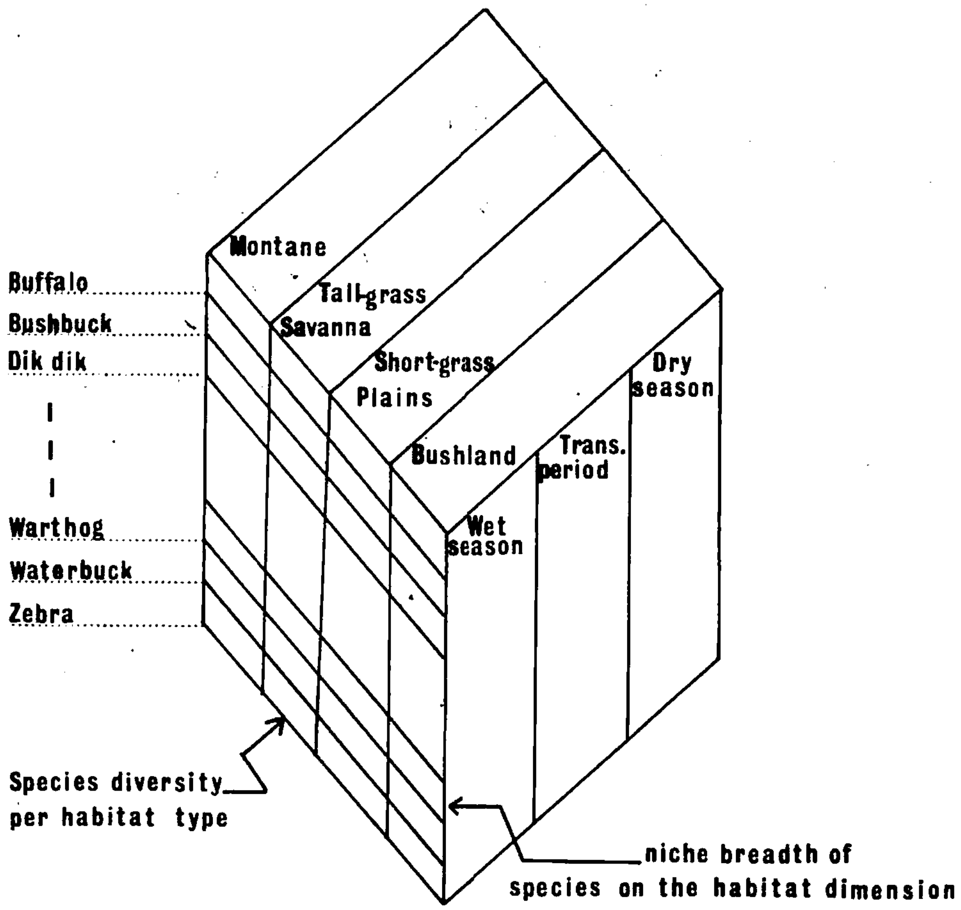


Fig. 16. Conceptualization of the Mkomazi community-environment matrix. The distributions of species in the four major habitat types and three time periods occur in varying proportions. By evaluating the proportions in each habitat type with the formula $\log B' = -\Sigma P_i \log P_i$ (see text), a measure of each species' niche breadth is derived. Using the same formula but now evaluating the proportions of total observations which occurred in each of the three time categories derives a measure of each species' temporal niche breadth. A measure of each habitat's large herbivore species diversity is readily obtainable by considering the proportion of total observations in the habitat contributed by each species (see text).

species of the array. The logarithms may be taken to any convenient base although base 2 is commonly used. This is the case below.

This index is sensitive to unequal sampling, however, and therefore the values reported here are derived by calculating $P_i = \bar{n}_i/\Sigma\bar{n}_i$ where $\bar{n}_i$ = the mean number of the i^{th} species occurring along a game count segment.

The mean numerical species diversity for all game count segments representative of the various habitat types was:

Montane	0.74 ± .10
Bushland	1.12 ± .00
Shortgrass plains	1.46 ± .22
Tallgrass savanna	1.68 ± .10

Although there is no clear diversity gradient with east-west location in the reserve per se, it appears that there is a direct relationship between diversity and utilizable net primary production.

When the size or weight difference between the species of a community is very large, some question may be raised regarding the usage of numbers as opposed to biomass. For example, since an elephant weighs roughly 500 times as much as a dik dik, it seems illogical to treat the two as equals when calculating herbivore diversity. It has been proposed, therefore, that the proportion of total biomass contributed by the i^{th} species be used as the P_i rather than the proportion of total numbers (Dickman 1968). Although consideration of the "clumped" distribution of biomass units and other aspects (Valiela, personal communication) may negate the validity of using biomass proportions in the standard information equations, the mean individual biomass diversities for the various habitats were:

Montane	0.50 ± .00
Bushland	0.74 ± .10
Open grassland	1.18 ± .22
Wooded grassland	1.31 ± .00

The relationship between the different habitat values does not change appreciably, irrespective of whether numerical or biomass values are used. The main difference between the two is that the biomass indices are all reduced substantially from the numerical index values. This reflects a less equitable distribution of biomass between the species than do numbers. However, since the relative values do not change appreciably, it must be that the large species were approximately evenly distributed between the four habitat types. If there had been a greatly disparate distribution of the large species between the habitats, the relative index value of each habitat type would change considerably when biomass proportions were substituted for numbers.

Despite the relative similarity of numerical and biomass index values above, there seem to be marked differences when considering changes in time. Numerical diversity indices for a number of transect areas show a tendency to increase during the wet season. This trend was not universal, however, and it does not hold for the reserve as a whole.

On the other hand, the biomass diversity indices reflect the opposite response. The monthly values calculated for the entire reserve show a marked decrease during several rainy periods. This was undoubtedly due to the ingress of large numbers of elephants and the consequent shift in biomass proportions.

Niche Breadth--Habitats

Whereas the concept of the ecological niche is old (Grinnel 1917), the quantitative evaluation of niche breadths is relatively new (Levins 1968). The contemporary indices of niche breadth are simple expressions which attempt to quantitatively evaluate the specificity of an organism's resource utilization or tolerance. Indeed, any measure which quantitatively evaluates the "spread" or breadth of conditions over which an organism ranges could be used as a niche breadth measure. Along with most measures of dispersion, the index value increases as the breadth of the distribution increases. Therefore, the index represents the inverse of specificity; and if a species has a high niche breadth value for habitats, it would be expected to be a cosmopolitan species.

Again, with minor alteration, the information theory derivate used for the diversity indices may be applied to quantify niche breadth (Levins 1968). Let P_i of the formula

$$\log B' = -\sum_{i=1}^{h} P_i \log P_i$$

represent the proportion of observations on a species made in the i^{th} habitat, as opposed to the proportion of individuals representing the i^{th} species as was the case with the diversity index. Then the result, B', is a measure of the niche breadth of the species on the h different habitats considered. That is, it provides a measure of the uncertainty involved with predicting in which of the h habitats the species will next be encountered. But as mentioned above, unequal sampling obviously biases the value. Therefore, P_i is defined here as $\bar{X}_i/\Sigma\bar{X}_i$ where $\bar{X}_i$ equals the mean number seen per segment per unit time in the i^{th} habitat type.

By taking the antilog of log B', the limits of the index are adjusted to yield a maximum of 4.0 when a species was equitably distributed between the four habitat types and a minimum value of 1.0 when it was only seen in one habitat.

The index values for the large ungulates range from a maximum of 3.42 for rhinoceros to a value of 1.22 for bushbuck (Table 9). The five most cosmopolitan (equitably distributed) species were rhinoceros, eland (3.31), warthog (3.22), giraffe (3.11), and elephant (3.09), while the five most habitat-specific species were bushbuck (1.22), duiker (1.63), buffalo (1.74), wildebeest (1.75), and reedbuck (1.97).

Table 9. Tabulated index values of niche breadth on the habitat and time dimensions for the larger animals of the Mkomazi Reserve. The index values were derived from the formula log B' = $-\Sigma P_i \log P_i$ (see text for terminology).

Niche Breadth on Four Habitat Types ($1 \leq x \leq 4$)		Niche Breadth on Three Seasons ($1 \leq x \leq 3$)	
Rhinoceros	(3.42)	Eland	(2.988)
Eland	(3.31)	Gerenuk	(2.975)
Warthog	(3.22)	Reedbuck	(2.974)
Giraffe	(3.11)	Giraffe	(2.973)
Elephant	(3.09)	Warthog	(2.953)
Gerenuk	(2.92)	Rhinoceros	(2.947)
Dik dik	(2.86)	Ostrich	(2.934)
Hartebeest	(2.79)	Gazelle	(2.933)
Gazelle	(2.54)	Kudu	(2.908)
Zebra	(2.52)	Hartebeest	(2.898)
Ostrich	(2.46)	Elephant	(2.895)
Kudu	(2.45)	Oryx	(2.867)
Impala	(2.36)	Impala	(2.806)
Oryx	(2.31)	Dik dik	(2.679)
Steinbok	(2.10)	Steinbok	(2.568)
Waterbuck	(2.03)	Zebra	(2.509)
Klipspringer	(1.98)	Buffalo	(1.897)
Reedbuck	(1.97)	Waterbuck	(1.708)
Wildebeest	(1.75)	Wildebeest	(1.592)
Buffalo	(1.74)	Duiker	(1.000)
Duiker	(1.63)	Klipspringer	(1.000)
Bushbuck	(1.22)	Bushbuck	(1.000)
Lion	(1.90)	Lion	(1.763)
Jackal	(1.64)	Jackal	(1.000)
Hunting dog	(1.00)	Hunting dog	(1.000)
Hyaena	(1.00)	Hyaena	(1.000)

Niche Breadth--Time

If the proportions of total observations of each species are categorized by season rather than habitat, the niche breadth index reflects the species' temporal distribution. A low index value would suggest that the proportions of total observations made during each season were disparate, and therefore, the species probably reflects large seasonal density fluctuations.

Only patterns applicable to the reserve as a whole can be described here, and consequently, only the aerial transect data were used in the calculations since only they represent the entire reserve.

Because of the few seasonal categories, the limits of the index are 1.0 and 3.0, and several small species which were observed only once or a few times on the aerial transects reflect the lower limit. Thirteen other species showed index values greater than 2.8 (Table 9). Because of this clumped array of values near the upper limit, the index difference between eland which reflected the greatest temporal stability (2.988) and Grant's gazelle (2.933) which was notably migratory is only 0.055.

Habitat Preference

With compensation for unequal sampling and the differential visibility in various habitat types, the relative proportion of times a species was observed in the various habitats should represent a crude index to habitat preference. Correction for unequal sampling may be made by simply reverting to the mean number seen per unit distance, while the differential visibilities can be partially corrected by converting to the number observed per unit area surveyed. Still, it is improbable that the success of sighting animals in different habitats can be completely equalized; and therefore, a relatively constant bias toward the more open vegetation types seems inevitable.

Within the 22 species array of large herbivores, there appears to be a gradient of preferences from montane and riparian forest to open grassland conditions (Fig. 17). Since the observations are here categorized into four major habitat types, 25% of all observations would be expected to occur in each habitat type if no affinities or preferences were operative.

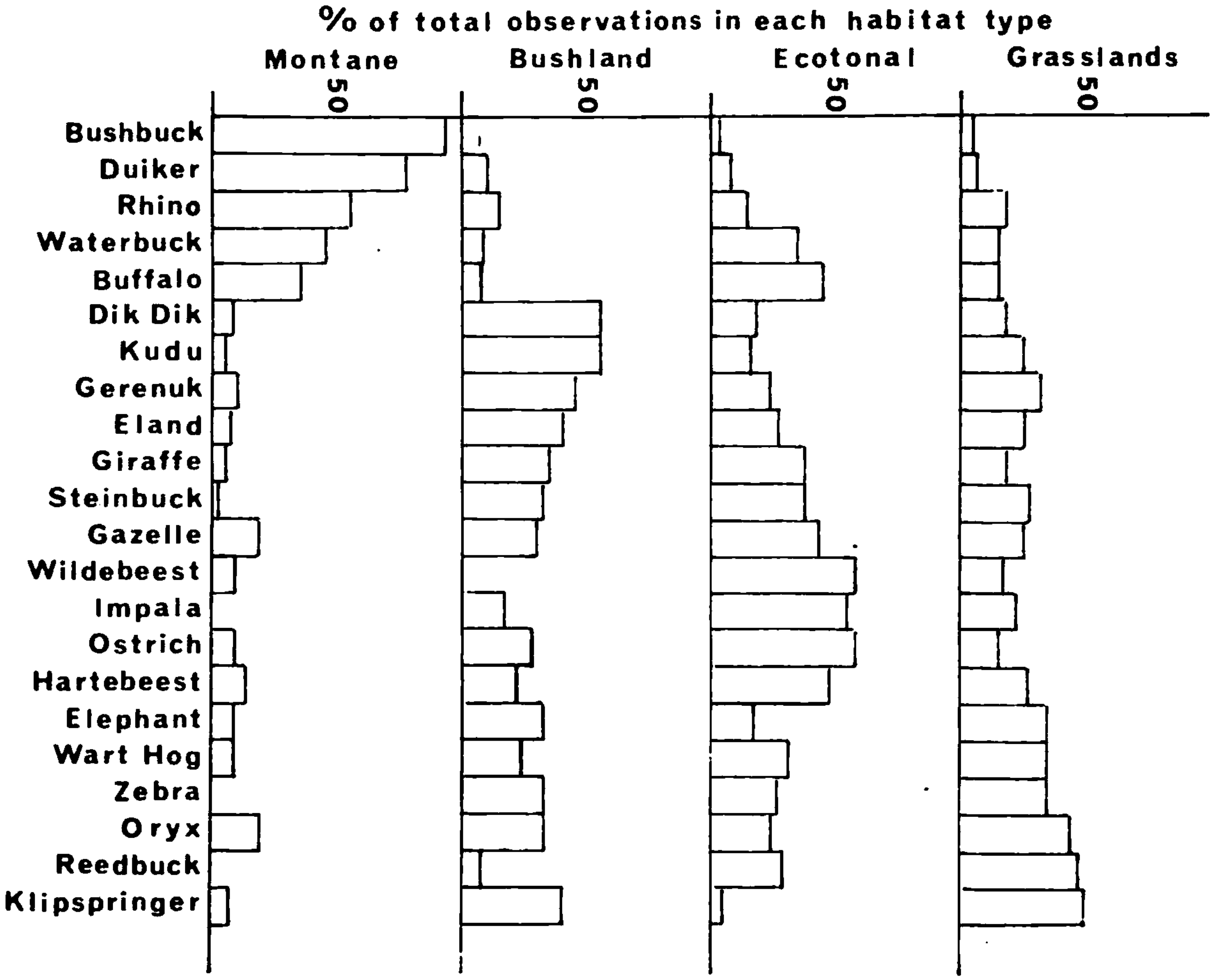


Fig. 17. Observations of the 22 large herbivores occurring in the Mkomazi Reserve show varying degrees of segregation into the different habitat types. There is, however, a general gradient from those which occurred most frequently under montane or riparian conditions (upper left) to those which were observed most frequently in grasslands of varying types (lower right).

Therefore if the proportion of observations made on a species exceeds 25%, some degree of preference is implied. Further, if the majority of observations (proportion >0.5) occurred in a single habitat type, it seems that the species involved was strongly attracted to that habitat type.

Five of the 22 large herbivores (bushbuck, duiker, rhinoceros, waterbuck, and buffalo) were observed in montane or riparian forests greater than 25% of the time. Three of these species (bushbuck, duiker, and rhino) occupied these environs the majority of the time.

Twelve species were observed under bushland conditions more than 25% of the time, but only two species (dik dik and kudu) were found under these conditions the majority of the time. Three other species (gerenuk, eland, and klipspringer) reflected substantial affinities (≥40%) for bushland, but were not recorded there a majority of the time.

Nine species (eland, elephant, gerenuk, hartebeest, kudu, oryx, reedbuck, warthog, and zebra) manifested some degree of affinity for the various types of grasslands, but only klipspringer was observed under these conditions a majority of the time. Klipspringers, although reflecting high proportions of occurrence in the grassland and bushland categories, are very restricted to rock outcrops and small hilltops under relatively open conditions. Since these local conditions are largely contained in surrounding areas of grass or bushland, the reported proportions are artifacts of the necessarily gross categories.

The concept of the "edge effect" or the utilization of the ecotonal area between vegetation types is of great importance in the Mkomazi as elsewhere in East Africa (Lamprey 1963). Impala, ostrich, and the introduced wildebeest were all observed under ecotonal conditions greater than 50% of the time, with greater than 40% of the buffalo, gazelle, and hartebeest observations being recorded under these conditions. Eight other species utilized the transition zones greater than 25% of the time. The many advantages of such behavior are well known, but close proximity to the different food and cover types seems to be a dominant factor.

Species Association and Niche Overlap

Because of the decidedly non-normal frequency distributions, serial correlations, the high incidence of tied observations, and other data peculiarities, standard correlative techniques were generally not valid analytical measures for the data at hand. Therefore, a measure of niche overlap has been applied to the species occurrence frequency distributions.

If two species were found in the same proportion on all game count segments over the entire course of the study, the measure of correlation between the two should approach the maximal limit. Similarly, a measure of niche overlap on the habitat dimension would reflect a maximum value under such conditions.

The equation for niche overlap used here is that of Horn (1966), and his paper should be consulted for the derivation. If the total number of observations made on a species is subdivided into categories representing game count segments upon which the observations were made, then the number occurring on the i^{th} segment is denoted by x_i and the sum of the x_i (representing the total observation) is denoted by X. That is, $\Sigma x_i = X$.

Similarly, when the total observations of a second species are appropriately categorized, the number in each category is denoted y_i and the total observations of species 2 is $\Sigma y_i = Y$. When the observations are categorized in such a manner the "overlap" of the two species (i.e., the degree of similarity in the categorized observations) is given by the equation:

$$R_o = \frac{\Sigma(x_i+y_i)\log(x_i+y_i) - \Sigma x_i \log x_i - \Sigma y_i \log y_i}{(X+Y)\log(X+Y) - X\log X - Y\log Y}$$

Since we are only interested in the ratios of these measures rather than the values themselves, the logarithms may be taken to any convenient base. The limits of overlap deriving from the above equation vary from 0 when the two species being considered are completely distinct with respect to distribution, to 1.0 when the two species are identical with respect to proportional distribution.

A similarity matrix of R_o values representing the degree of overlap between all species combinations is then generated, and since 26 species (22 herbivores and 4 carnivores) are considered here, the matrix is square and of order 26 × 26. Since the degree of overlap between species 1 and species 2 is identical to that between species 2 and species 1, the matrix is symmetrical and only a diagonal half need be considered. Similarly, when the various proportions of a species are compared to itself, they are seen to be identical; and therefore, all elements along the matrix diagonal reflect the limit of 1.0 (Fig. 18).

Biologically, two salient features derive from such a similarity matrix. One, those species pairs reflecting high degrees of overlap tend to exist in the same places in about the same proportions. Such a relationship might imply some positive association or facilitation between the two. Secondly, those species pairs manifesting low index values showed little spacial overlap which might imply antagonism or competitive exclusion.

Not discernable from the matrix given are the potential temporal interactions of species. That is, it may be inferred from a high index value that two species occupied the sample areas in approximately equal proportions. But the reader is cautioned against the inference that they inhabited these areas simultaneously. Analysis of the 33 monthly matrices is required for such interpretation.

The highest overlap value found by this analysis was 0.86 obtained from the occurrence records of impala and hartebeest. Other herbivore associates with hartebeest and impala which reflected a high degree of association were ostrich, steinbok, giraffe, and gazelle (see upper left-hand corner of Fig. 18). Jackal manifested the highest degree of association between a carnivore and the herbivores mentioned

SPECIES		Hartebeest 1	Impala 2	Ostrich 3	Steinbok 4	Giraffe 5	Gazelle 6	Wart hog 7	Dik dik 8	Eland 9	Elephant 10	Gerenuk 11	Zebra 12	Oryx 13	Kudu 14	Rhinoceros 15	Reedbuck 16	Wildebeest 17	Waterbuck 18	Buffalo 19	Duiker 20	Klipspringer 21	Bushbuck 22	Jackal 23	Lion 24	Hyaena 25	Hunting dog 26
Hartebeest	1	1																									
Impala	2	.86	1																								
Ostrich	3	.84	.82	1																							
Steinbok	4	.80	.80	.72	1																						
Giraffe	5	.85	.81	.83	.72	1																					
Gazelle	6	.83	.77	.83	.75	.75	1																				
Wart hog	7	.76	.77	.68	.68	.76	.62	1																			
Dik dik	8	.72	.64	.67	.59	.74	.66	.61	1																		
Eland	9	.68	.69	.62	.51	.71	.68	.46	.54	1																	
Elephant	10	.65	.59	.58	.50	.73	.63	.50	.56	.78	1																
Gerenuk	11	.80	.60	.62	.59	.63	.63	.55	.66	.55	.57	1															
Zebra	12	.72	.60	.62	.53	.69	.79	.52	.54	.69	.74	.50	1														
Oryx	13	.61	.51	.61	.57	.67	.68	.61	.69	.57	.60	.58	.78	1													
Kudu	14	.69	.63	.53	.29	.69	.50	.42	.62	.53	.61	.49	.43	.49	1												
Rhinoceros	15	.74	.66	.52	.41	.67	.53	.45	.35	.51	.69	.35	.50	.34	.40	1											
Reedbuck	16	.77	.75	.54	.48	.66	.53	.46	.33	.39	.52	.34	.38	.26	.40	.71	1										
Wildebeest	17	.70	.64	.44	.27	.53	.51	.20	.04	.47	.63	.05	.49	.12	.04	.46	.43	1									
Waterbuck	18	.64	.57	.40	.29	.48	.39	.32	.34	.42	.66	.33	.48	.34	.34	.45	.34	.35	1								
Buffalo	19	.54	.48	.35	.29	.42	.35	.26	.23	.40	.52	.22	.44	.24	.27	.57	.51	.74	.44	1							
Duiker	20	.53	.45	.38	.32	.46	.35	.37	.28	.36	.67	.27	.41	.34	.26	.46	.30	.20	.61	.38	1						
Klipspringer	21	.60	.59	.07	.14	.31	.25	.22	.23	.28	.39	.24	.20	.41	.55	.14	.13	.04	.38	.19	.23	1					
Bushbuck	22	.40	.23	.18	.12	.26	.12	.18	.10	.21	.51	.05	.24	.10	.15	.47	.25	.11	.54	.30	.67	.13	1				
Jackal	23	.84	.82	.70	.60	.73	.76	.59	.43	.65	.68	.53	.74	.62	.29	.39	.29	.32	.51	.51	.40	.01	.01	1			
Lion	24	.78	.74	.53	.50	.56	.60	.44	.35	.53	.60	.41	.60	.49	.31	.36	.41	.40	.48	.53	.38	.39	.20	.66	1		
Hyaena	25	.67	.73	.61	.57	.60	.58	.59	.54	.27	.35	.57	.11	.41	.47	.44	.55	.00	.19	.13	.26	.12	.09	.13	.22	1	
Hunting dog	26	.51	.16	.14	.10	.14	.49	.05	.03	.14	.57	.05	.64	.48	.06	.27	.07	.16	.08	.16	.02	.00	.01	.07	.12	.00	1

Fig. 18. Elements of the similarity matrix shown here represent the degree of niche overlap as measured by the proportional occurrence on the different segments of the game count grid. For example, species 1 and species 2 (hartebeest and impala) reflect a spacial niche overlap of 0.86 where the limits of the index are 0.0 and 1.0. A value of 0.0 would be obtained if the species were 100% spatially isolated and were never observed on the same game count segment. A value of 1.0, on the other hand, would be obtained if the two species occurred on all segments in exactly the same proportions. The order of the species has been arranged to segregate the ones of greatest niche overlap in the upper left corner of the matrix, while those reflecting little overlap are segregated toward the lower right.

above, while lion reflected only slightly lower index values.

It is a common observation that many ungulates do not scatter or flee from the area when most predators are present. On the other hand, hunting dogs frequently drive the potential prey animals from location upon arrival. The index values between hunting dogs and most herbivores are much lower than the three other carnivores and imply a distinct negative association. Whether or not an antagonistic behavior was actually involved cannot be definitely established from these values however.

Low index values reflecting spacially separated distributions between the large herbivores were conspicuous for a number of species. The values between wildebeest and klipspringer (.04), dik dik (.04), gerenuk (.05), and kudu (.04), as well as between bushbuck and gerenuk (.05), and klipspringer and ostrich (.07) all fell below .10 reflecting a strong lack of overlap in their distribution. Among the dominant species, buffalo seemed to reflect a slight negative association (values <.50) with most other species while elephants manifested about a 60% overlap with most other species. Zebra, oryx, and Grant's gazelle showed 68 to 80% overlap in their distributions.

Discussion

In the preceding sections emphasis has been placed on the description of abiotic and biotic components of the ecosystem. The purpose of the present section is to illustrate patterns of organization within the large animal community.

Of the 22 large herbivores considered, three species were recorded a majority of the time in the montane and riparian forests, two species reflected a majority of observations under bushland conditions, and three species were recorded in ecotonal conditions greater than 50% of the time. Were the observations more discretely classified into vegetation subtypes such as tallgrass, drainageway, bushed and wooded grass, and shortgrass, the description of habitat preferences and ecological separation would be greatly enhanced.

Of the fourteen species which were not recorded more than 50% of the time in any one habitat, examples of both habitat "specialists" and "generalists" exist. Klipspringer, for example, are very discriminating and only occupy rock outcrops. Reedbuck only seem to occupy the rank *Panicum maximum* and *Chloris roxburghiana* grass swards in and around gullies, drainageways, and groundwater seeps. Waterbuck are similarly restricted, but frequently travel considerable distances across open, shorter grasslands in pursuit of water and therefore were frequently recorded under these conditions.

The generalists such as elephant and giraffe may wander freely throughout several major habitat types while maintaining a selective diet of particular species or forage types.

At this level of analysis the complete ecological separation of the species is not possible. Consequently the habitat overlap of many species appears great. For example, the high degree of overlap between impala and hartebeest on the habitat dimension could be greatly refined if food species preference within the habitats were considered.

Superimposed upon the spatial patterning of species is the possibility of temporal patterning. Considering the relatively isothermal environmental conditions and the physiological adaptations to water stress (Taylor 1968, 1969), it appears that great opportunity for temporal patterning exists in tropical communities. Thus a cursory purusal of the game count records shows that the greatest number of large herbivore species ever seen on a single segment (representative of a local area within one habitat type) was 12 and the median number was four ($\bar{x}$ = 4.26). The maximum of 12 occurred around the Dindira Dam area during the dry season when animals were concentrated to the greatest degree.

The pattern of north-south and east-west movements associated with the Mkomazi fauna seems to substantiate a high degree of temporal patterning. Four species (elephant, gazelle, oryx, and zebra) all reflect a dry season exodus from the reserve. Of those animals remaining in the reserve during this period, elephant, zebra, gazelle, eland, giraffe, and buffalo all show marked increases in numbers around Dindira Dam. But, surprisingly, the numbers of hartebeest and impala around Dindira Dam decrease during this period of intense utilization. They move to slightly more distant areas still accessible to the water.

Similarly, there appears to be a temporal interaction between the numbers of impala and gazelle in certain local areas of the northwestern section (e.g., that covered by the Gate-to-Ibaya transect). During periods when impala numbers were high in this area, the numbers of gazelle tended to be low; the obverse also held.

From the habitat point of view, the diversity indices of the four major communities reflect an important overall trend. From the limited data available, there is a strong positive relationship between the mean large herbivore diversity (both biomass and numerical) and the accessible net primary productivity of the major plant communities.

Within the lowland vegetation communities there seems little doubt that the bushed and wooded grasslands of the northwest are generally more productive than the shortgrass plains and that the bushland is least productive of all (see Fig. 8). It may be recalled that the herbivore diversities of the different habitats were significantly different with bushed and wooded grassland being greater than shortgrass which was greater than bushland.

It is further postulated that even though the dry montane forests are surely more productive than the bushed and wooded grasslands, a high percentage of the production is either limited to the canopy and inaccessible to the large herbivores or it is in the form of unutilizable branches and twigs. Therefore, the large herbivore diversity is understandably low.

Connell and Orias (1964) and Pianka (1966) have hypothesized that a positive correlation between productivity and diversity might hold generally, while Margalef (1963, 1968) has presented arguments in favor of an inverse relationship. Confounded within these arguments are the ideas of specific trophic level production and diversity as opposed to the ecosystem as a whole.

It is of considerable importance to mention at this time that although the precision with which biological phenomena can be described is usually enhanced by the use of mathematical formulations, the accuracy of the descriptions is not necessarily increased. This is of particular importance here since an attempt has been made to use quantitative analytical techniques on a body of basically descriptive data. The fact that klipspringers were shown to exist largely in bushland and grassland and have a relatively wide niche breadth on the habitat dimension is not an inadequacy of the analytic techniques, but rather an inadequacy of the sampling design. For optimal results it is essential that the modes of analysis be borne in mind when establishing the sampling regimes.

The onus of the ecologist is the integration of seemingly disjunct facts, figures, and empirical knowledge into a coherent whole which is frequently more meaningful than the sum of the parts. Furthermore, there are a number of factors, influences, and interactions which have meaning when a system is viewed as a whole, but which are not apparent to the autoecologist or even to the population or community analyst.

For example, the analysis of the Mkomazi animal community by itself provided a valuable description of the spacial gradients in density and biomass. Without the insights gained by considering the abiotic, vegetative, and human aspects, however, the factors causing those effects would remain little more than speculation. Similarly, the formulation of ecological questions without a full appreciation of the frame of reference could lead to spurious results. Hopefully, sufficient evidence is presented in the present chapter to substantiate the claim that large-scale ecological surveys must be viewed in an ecosystem context.

Although the concept of species dominance is presently in disfavor among many ecologists (McNaughton and Wolf 1970), it appears that, in general, a relatively few "dominant" species account for the bulk of the numbers and biomass in most communities. In other words, a few species predominantly define the structure. Seemingly of more interest, however, is the concept of "functional arrays" of species or the idea that most ecosystem functions are also mediated through a few species. If this is the case, and we wish to further analogize with physical systems, we might label this subset of species which performs the bulk of the system's function (e.g., energy, nutrient, or mass transfer; productivity; decomposition; etc.) as the "energy processors." Thus, with regard to any particular function (e.g., energy transformation), a few species perform the bulk of the function and all other species might be categorized as a "control" or "signal processing" component. Although this array of "control" organisms plays a minor role in the system's function, it may perform a major control or regulatory activity. These "control" organisms probably constitute the majority of the inherent redundancy characteristic of biological communities. They provide the system's long-term stability similar to the intricate guidance controls of a space vehicle, or in crude form, the furnace thermostat.

Specifically, it is postulated that a few species of the Mkomazi ecosystem dominate the numbers and biomass and, in general, portray the system. It is further hypothesized that a few species process the bulk of the energy, mediate the bulk of the nutrient flow, and exert a major effect upon the environment. These postulates seem substantiated by the following statistics.

During the period of study four large mammal species accounted for between 60 and 90% of the mean annual numbers on the various study areas and on the reserve as a whole (Table 10). Four species also accounted for between 44 and 96% of the total biomass.

Table 10. The percent contribution of the four most dominant species with regard to the mean annual number, the mean annual biomass, and the mean annual metabolism (see text).

Species	% Mean Annual Number				% Mean Annual Biomass				% Mean Annual Metabolism			
	Dindira	Mbula	Mzara	Entire Res.	Dindira	Mbula	Mzara	Entire Res.	Dindira	Mbula	Mzara	Entire Res.
Buffalo	45			12	48			9	49			10
Elephant	9	8		25	38	61	11	72	32	50		67
Gazelle		7	28				12				16	
Giraffe						11	11	5		9		5
Hartebeest	18	24	26	14	5	12	32		8	16	32	5
Impala	16	44	25	10		8			3	14	14	
Ostrich			12		a/			b/			11	
Total Contribution of 4 spp. (%)	88	83	91	61	93	92	66	90	92	89	73	87

a/ 2% contribution by zebra.

b/ 4% contribution by eland.

Since maintenance and sustained work metabolism appear to be linear functions of the basal metabolic costs of homeothermic animals (Brody 1945, Kleiber 1961, Hemmingsen 1960), an index to community metabolism is derivable from the mean weights of the species involved. Even though the standard metabolic function $70\ kg^{.75}$ (Maynard and Loosli 1956, National Academy of Sciences 1966) may underestimate the true fasting catabolism of indigenous East African ungulates (Rogerson 1968), this is of little consequence here since it is only being used as an index to total metabolism. Multiplying the estimated basal metabolism of each species by the appropriate density and summing over all species present yields an estimate of the total large herbivore catabolism. From this it is concluded that four species account for 77 to 91% of the total large herbivore energy transformation throughout the reserve (Table 10). This is further corroborated by the species-specific productivity estimates which are not included at this time.

As previously established, however, spatial and temporal patterning of the total species array suggests that different species dominate the functional processes in different regions and at different times in the same region. Therefore, annual statistics of specific areas or even seasonal statistics derived from large areas are not the most accurate reflection of the month to month or seasonal properties of specific communities.

Although the numbers of four species (buffalo, elephant, hartebeest, and zebra) must be summed to account for 90% of the dry season totals in the Dindira study area, two species (buffalo and elephant) constitute approximately 90% of the total biomass and metabolism (Fig. 19). Buffalo completely abandon this area during the wet season, and impala replace them as an integral species. Along with elephant and hartebeest they constitute approximately 90% of the total numbers and biomass, while the three species process 93% of the energy flow.

From this it seems that the bulk of the Mkomazi large herbivore species do not contribute significantly to the major structural or functional attributes of the system and their role may well be that of signal processors or controllers for the system. Chew and Chew (1970) draw a nearly identical conclusion from their study of mammals in a desert shrub community. They state, "Mammals are not important in the energy turnover--their importance must lie in the specific controlling actions on the plants and other components." This concept does not imply that they are of less importance to the biological system, but only that their role is less obvious and probably more involved with the sytem's homeostasis than in the processing of nutrients or energy. In other words, these species may exert considerable influence on the abiotic component (e.g., soil structure, microrelief, and microclimate) as well as other biotic components (e.g., the control of bush encroachment or vegetation species composition). It is likely that they also have a major influence in balancing the composition of the biological system. For example, aside from the beneficial effects of competition, they undoubtedly play a major role in supporting the predator component which likely serves as the ultimate control on the herbivores (Errington 1963, Buckner 1966, Hirst 1969).

Whatever the relationship between the different species, it seems clear that in reality the large herbivore community is not highly diverse, but rather, a highly dominant community. In addition to the above, recall that the mean number of species seen per game count segment was only 4.26. Further, t should be noted that the large herbivore diversity indices were low relative to values obtained for other tropical communities (Odum and Pigeon 1970). Thus, even though the number of species is great, the individuals are largely contained by a few species, and the overall complexion is one of dominance.

Ranging from nearly imperceptible homeostatic effects under "normal" conditions (Vesey-Fitzgerald 1960, 1963; Paine 1966; Paine and Vadas 1969; Harper 1969) to conspicuous habitat degradation in certain instances (Petrides and Swank 1958, Buechner and Dawkins 1961, Glover 1963), large herbivores effect considerable pressure on their environment. The homeostatic effects are rarely discernable, however, unless the herbivores are reduced in numbers or removed; and therefore, it is difficult to measure or interpret. Evidence for the later effect (i.e., habitat degredation) was available, however, and is presented below.

Although factors are usually confounded in nature to the extent that single-factor-effects are rarely measurable, a form of experimentation can be accomplished by isolating the factors in time or space. By considering all other factors relatively constant, the independent effects of elephants, cattle, and fire can be described.

Elephant densities in the Mkomazi area are relatively high (up to 1/km^2/year in local areas), and there is considerable reason to believe they are a major factor in changing their environment (Buechner and Dawkins 1961, Glover 1963, Bourliere 1965, Pienaar et al. 1966, Lamprey et al. 1967). Under the drier bushland conditions in the Mkomazi, the majority of the elephant foodstuff is browse; and therefore, this animal would be expected to have its greatest effect on the woody component of the biota (Fig. 20a). The effect of trampling on grasses and herbs is restricted to watering points and is negligible. Aside from water holes, there is no area in the Mkomazi where the natural populations of game alone have had a perceivably degrading effect on the grass-forb component. The "elephant-effect" is therefore believed to be mainly restricted to the arborescent vegetation.

The southern three-fourths of the entire eastern half of the reserve (within watering distance (≈15 km) of the Mbaramu-Umba River) has been subjected to intense cattle grazing for over a decade. In the southern border areas there is essentially no game (<<100 kg/km^2), and therefore, any vegetation degradation is certainly due to cattle. Since browse provides only a small percentage of cattle forage the grass-forb component of these areas all manifest the effects of severe overgrazing (Table 3, area 4, and Fig. 20b; Hemingway et al. 1966), while there has been no apparent degratory effect on the woody vegetation (Fig. 20b). It is therefore concluded that the "cattle-effect" is largely limited to the grass-forb component of the vegetation.

In the east central section of the reserve (around Kamakota) the annual density of both cattle (1 cow/3 to 4 ha) and elephants (1.0/km^2) is high. The combined effect is expected to be displayed by both components of the vegetation, therefore, and there is obviously such an effect (Fig. 20b).

The single factor "fire-effect" can be demonstrated by controlled burning in areas where cattle and game have been excluded or by natural fires in areas where animals do not occur. In August 1966 a range fire burned extensively in the Mkomazi, and the fire line representing the point where it was extinguished vividly portrays the effect of one hot fire on bush suppression (Fig. 21a).

The combined effects of cattle, elephants, and fire on the vegetative component of the system

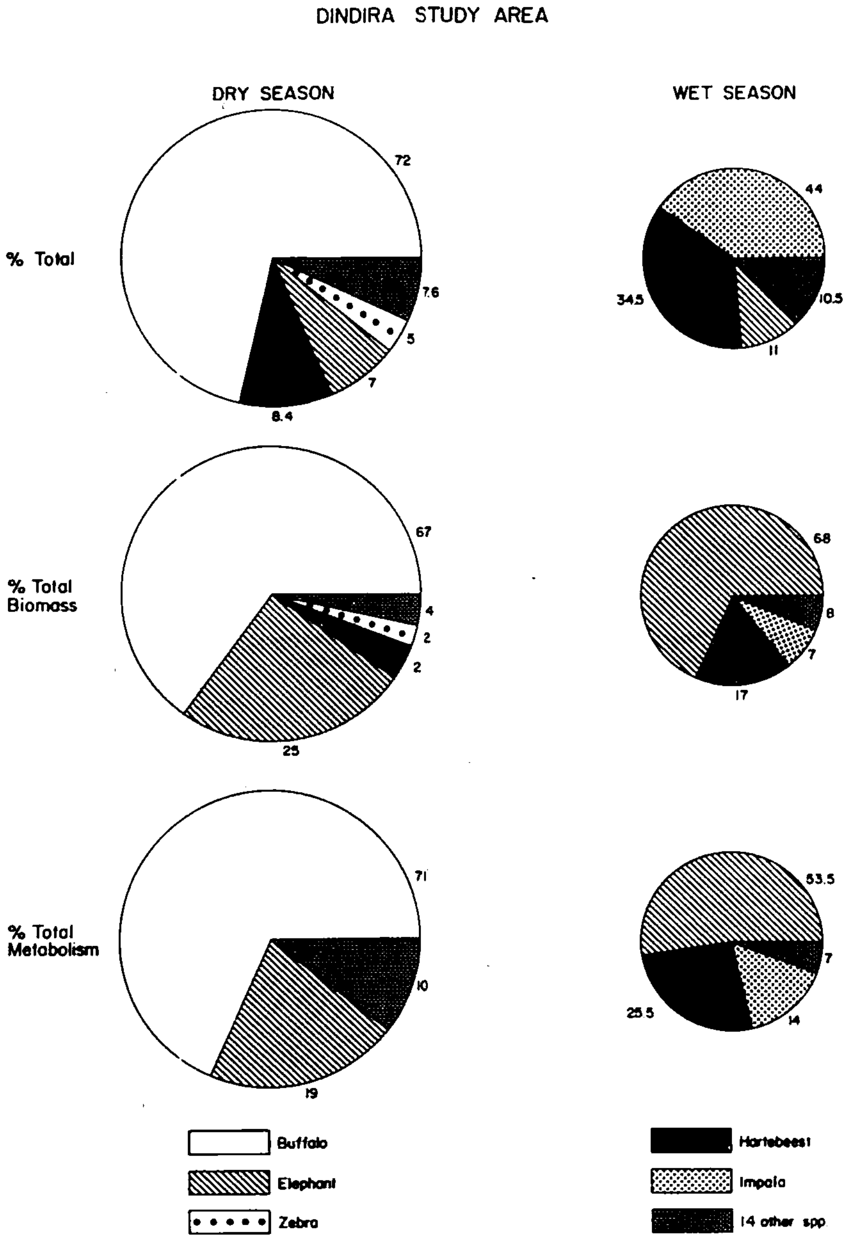


Fig. 19. Mean seasonal species contribution to the numbers, biomass, and large herbivore metabolism of the Dindira study area in the western end of the Mkomazi Reserve. Although the dry season density of animals (numbers) was approximately three times as great as the wet, the dry season biomass density was over six times that of the wet. Importantly, only three or four of the 22 large herbivore species constitute over 90% of the numbers and biomass of the large herbivore community and process an equally high percentage of the energy transfer.

Fig. 20a.

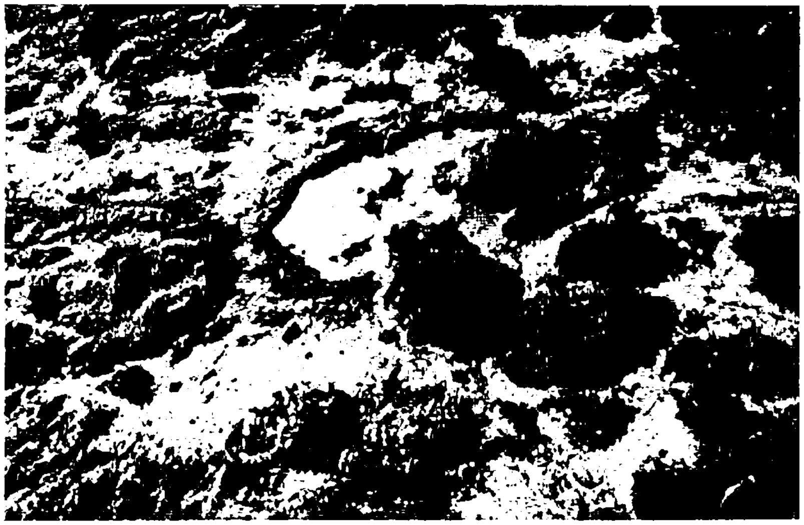


Fig. 20b.

Fig. 20. a. The "elephant-effect" seems to be that of reducing the woody, arborescent component of the vegetation. Although normally less diligent, elephants had felled and completely devoured this baobab (*Adansonia digitata* Bombacaceae) in less the two weeks time. In no area free from cattle grazing was there any substantial degredation of the grass-forb component of the vegetation by elephants or other indigenous herbivores.

b. The "cattle-effect" is that of severely degrading the grass-forb component of the vegetation while having a benign to positive effect on bush standing crop and production. About 750 km^2 along the south central and eastern boundaries of the reserve are overgrazed to the extent shown.

Fig. 21a.

Fig. 21b.

Fig. 21. a. The "fire-effect" is one of obvious bush suppression. Hillsides as steep as that depicted are rarely grazed or browsed by indigenous herbivores, and the depicted effect is that of one fire in August 1966. The sharp fire-line manifests the effect one hot burn may have on bush control.

b. The combined effect of cattle overgrazing and elephant browsing pressure in the central section of the reserve. There is essentially no "fire-effect" involved here as the area will not sustain a bush or grass fire.

are well known to field ecologists in East Africa, but only partial documentation exists. Mr. D. G. Anstey, formerly of the Tanzania Game Division, has kindly provided a series of photographs of the extant vegetation conditions around Dindira Dam at the time of its construction in 1957 (left-hand column, Fig. 22). Matched photographs were taken in 1967 after 10 years of the combined effects of fire and elephant usage (right-hand column, Fig. 22). The over-riding difference is that the area is now more open with considerably less bush and tree cover than was extant in 1957. Mr. Anstey, having known the area intimately for nearly 20 years, assures me that, to a greater or lesser extent, the depicted change applies to the whole reserve.

The management implications of these photos should be obvious; if the bushed and wooded grassland structure is to be maintained, fire, elephant, and possibly other herbivore management will be required.

As previously described, the complex of large herbivores is partitioned temporally as well as by habitat type. There was also shown to be a highly significant interaction between season and area when measured as total biomass density (Table 7). A salient factor in this interaction involves the seasonal differences in the utilization of specific areas. Thus, herds of impala and hartebeest retreat from the Dindira Dam area as buffalo, elephant, eland, and zebra concentrate there during the dry season. Impala and hartebeest move back into the area during the rainy months. Similarly, as many of the impala move onto the Mzukune area (10 to 15 km south of Dindira) during the dry season, Grant's gazelle numbers show a large reduction in this area. In certain areas the pattern of seasonal change in species utilization is so striking as to suggest that an overall "grazing strategy" might be operative.

Working with the interaction between different stocking rates and grazing systems in New Zealand, McMeekan (1960) and McMeekan and Walshe (1963) found that higher dairy cattle productivities per unit area were achieved at high stocking rates than at the low rates, but significant interactions were found to exist. At high stocking rates, best results were obtained from a controlled rotational grazing scheme, while at low stocking rates continuous grazing produced highest productivities. The same significant interaction has now been described for East African domestic stock (Walker 1968, Walker and Scott 1968*a*,*b*).

Within the Mkomazi, the Dindira area represents the most heavily stocked region, and the grazing pattern is cyclical to the point of appearing "rotational." Other areas removed from the permanent water support much lower densities of herbivores, but with different species moving in and out the numbers remain relatively constant throughout the year. The "coincidence" of these patterns seems almost theological and is deserving of further appraisal.

The alternative hypothesis of competitive exclusion in certain areas but not in others is only testable by evaluating a series of interspecific interaction coefficients. Such coefficients are available from my data and are held for future analysis.

It has been postulated that the high species diversity of tropical areas might derive from the inherently greater productivities of this region (Connell and Orias 1964, Pianka 1966). Hypothetically, since net primary production is greater, the areas could support a larger number and a greater array of animals in the higher trophic levels. A similar argument in favor of game cropping asserts that greater forage specificity on the part of each herbivore species allows a greater portion of the net primary production to be channeled upward through the herbivore food chain than is the case in low diversity, high latitude regions.

It is unknown what percentage of the total annual energy budget flowed through the North American bison and allied herbivore component. But within contemporary biotic regimes, it appears that less than 10% of the total net primary production flows through the vertebrate herbivore component in most temperate regions (Odum, Connell, and Davenport 1962; Golley 1960; Chew and Chew 1970; Slobodkin, Smith, and Hairston 1967). Petrides and Swank (1965) estimated that 9.5% of the available net production in a small area of Queen Elizabeth Park, Uganda, was consumed by elephants alone.

In a study of indigenous ungulate energy utilization, Rogerson (1968) states that, "the results suggest that the eland and wildebeest would require from 20 to 30% more metabolizable energy than would cattle, and since the efficiency with which these animals used the digestible energy for metabolic purposes is similar, then a corresponding greater food intake would be required by the eland and wildebeest." Therefore, it seems that the standard food requirements established for domestic cattle might reasonably be used to conservatively estimate the food intake per ruminant stock unit in the Mkomazi Reserve. The standard air dry maintenance diet for range cattle is estimated to be about 2% of body weight per day (Stoddart and Smith 1955). This makes no allowance for growth and reproduction, however, and therefore 25 lb. (11.3 kg)/stock unit/day is used here as an estimate for annual consumption. From this it is estimated that the mean annual standing crop of herbivores on the Dindira study area (5,548 kg/km^2) would consume 50,447 kg of air dry forage per year. The estimated net annual production of this area is about 3×10^5 kg/km^2, and therefore, the percentage of net production consumed by large herbivores alone is 16.8%. But it is well known that elephants are very "rough" feeders and that they consume much greater quantities of forage per unit body weight than do the ruminants (Benedict 1936). This, along with the added grazing pressure of the other small vertebrate herbivores, is likely to raise the percentage utilization to at least 17.5%. This is a substantially greater amount than reported for unmanaged temperate areas.

The idea that a greater percentage of the total energy fixation is transferred through the herbivore-carnivore pathway in East African systems is not surprising to field ecologists of the area. For, surely, one of the most striking features of these systems is the seemingly depauperate decomposer fauna. Studies have shown much lower arthropod numbers in these areas than are commonly found in temperate regions (Salt 1952, Madge 1965), and it seems that chemical oxidation and termites are the major decomposers of the East African semi-arid regions. Hopkins (1966) reports that "wood disappearance was caused by termites rather than microorganisms," and consequently, "wood decay on the savanna site took about half as long as on the forest site." Although the alternating wet and dry conditions are believed to be important

Vegetation changes surrounding an
artificial water supply from 1957 to 1967

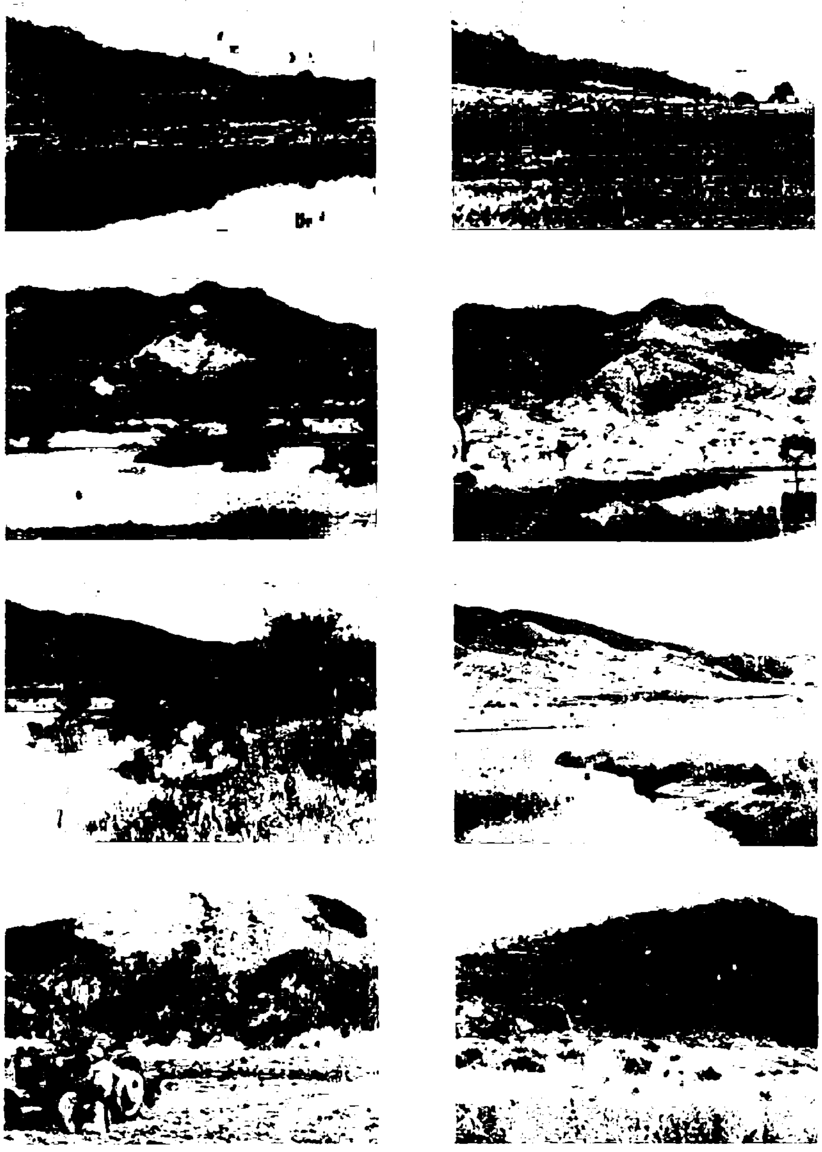


Fig. 22. Ten-year time-lapse photographs illustrating the combined effects of fire and elephants along with dry season concentrations of other herbivores around Dindira Dam. The left-hand column of photographs depict the vegetation as it existed in 1957 during construction of the artificial permanent water supply (photos courtesy of D. G. Anstey). Matched photographs taken in 1967 appear in the right-hand column and illustrate the vegetation condition 10 years later. Although the hillside vegetation appears more substantial in the 1967 photograph of the bottom pair, this is an artifact of a higher power lens and better resolution. The removal of the bush thicket of the foreground is a significant change toward a more open grassland.

factors in limiting the decomposer populations, the full explanation remains obscure (Visser 1969).

Not only are termites of indisputable value in effecting decomposition, but they also play other roles in the ecology of these areas (Kemp 1955; Murray 1938; Pendleton 1941; Hesse 1955; Watson 1962; Glover, Trump, and Wateridge 1964). There is almost always an accumulation of base elements in the area immediately surrounding their mounds. These nutrients have a great effect on local plant associations and may provide centers of radiation from which succession takes place (Thomas 1941, Myers 1936). The termites provide a major source of food for the aardvark (*Orycteropus afer*), and other mammals, as well as many birds, while the mounds are of importance in the territorial behavior of ungulates and a valuable refuge for mongooses and other small mammals. Their direct and indirect importance to the Mkomazi ecosystem cannot be overemphasized.

In conclusion, the interrelations of the various system components cannot be overly stressed. Although there is a slight gradient of solar energy input to the system from west to east, it is doubtful that this is of direct importance to the overall functioning of the system. The solar input of about 1.65×10^6 kcal/m^2/year provides the driving force behind the system's structure and function, while obvious gradients in the other abiotic components provide the major constraints within which the biological components must function. Water, essentially the carrier of nutrients and energy up the trophic ladder, seems to be the major constraint both directly and indirectly. Just as there is a difference between food consumption and food utilization, so is there a difference between the quantity of precipitation and the quantity of utilizable water.

The distribution and intensity of rainfall as well as temperature, soil runoff, permeability, and the other soil parameters which affect the water retention capacity play major roles in determining the system's characteristics. Being dependent upon the climatic patterns and pedogenesis, the exchangeable ion profiles provide the second major constraint upon the biological components. It was pointed out that manganese is localized in the upper few centimeters of the soil profile and is likely to be deficient in several sodium-saturated vertisolic soils. On the other hand, manganese is probably the most important micro-element affecting animal productivity. The symptoms of only mild deficiencies are lowered milk production, retarded growth, and ataxia as well as lowered reproduction per se.

Manifestations of these abiotic constraints on the biological components of the system appear at the first trophic level. Along with the gradient in physiognomic form from west to east, net primary production and general range conditions followed the same pattern. Now, along with the greater water stress from west to east, the herbivore component is further limited by lower primary productivities. As a result, herbivore density, diversity, energy transferral, and annual length of occupancy of the central and eastern areas was considerably reduced.

The interrelations of abiotic and biotic components are not unidirectional, however. The herbivores have considerable influence on the structure of the vegetative and soil components. This is a clear example of "feedback" or "control" and adds validity to the analogy between biological and physical systems. Man's interference with the energetics of biological systems (e.g., the increase of productivity) will most probably necessitate an involvement with control. Thus, just as the utilization of monospecific agronomic practices usually requires the concurrent use of pesticide controls, so will the construction of artificial water supplies and other production oriented game management activities require concurrent controls. The 1968 elephant culling operation in the Mkomazi was just such a "control." Hopefully, such foresight will continue to be a part of the overall systems management strategy.

SUMMARY

The Mkomazi Game Reserve of semi-arid northeastern Tanzania was established in 1951 as a *quid pro quo* negotiation for the former Pare Reserve which was "dereserved" in 1950. Since its establishment, the boundaries have twice been retracted and human pressure continues to be high.

An elevational gradient from 230 m above sea level in the southeast to about 800 m in the northwest underlies much of the biological variation of the area. Superimposed upon, and partly a consequence of, the elevational gradient there is a decline in annual precipitation from about 55 to 60 cm in the northwest to only 35 to 40 cm in the east central section. The annual rainfall pattern is sharply bimodal, and although precipitation is by far the most important climatic factor, sufficient importance is attached to temperature, wind, and solar radiation to warrant utilization of some more descriptive climatic index. Using Thornthwaite's measure as a comparative index, the climate of the east central section of the reserve was estimated to be at least 50% more arid than that of the northwestern section.

Along with the elevational and climatic gradients, soil profile depth, organic matter content, permeability, and water retention capacity all generally decrease from west to east. No general soil fertility gradient was elucidated. Most of the bottomland soils are saturated with sodium salts, and along with seasonal waterlogging these highly expansive montmorillonite clays appear to be of less overall value than the more freely drained but lower mineral status soils higher on the slopes. While many of the upland soils contain only marginal levels of calcium (by domestic livestock standards), several of the lowland vertisols contain only marginal phosphorus reserves. The high sodium levels may induce microelement deficiencies in the lowland soils.

The vegetation was categorized into four major types with dry montane covering the mountain tops and bushed and wooded grasslands occupying the freely drained fan slopes of the northwestern section of the reserve. *Acacia-Commiphora* bushland replaces the bushed and wooded grassland in areas receiving less than about 50 cm annual precipitation. Covering approximately 70% of the total area, this community typifies the reserve. Open corridors of seasonally inundated grasslands occupy the bottomland vertisols and constitute nearly 20% of the reserve area.

Annual net primary production follows the abiotic gradients and varies from about 400 g/m^2 in the higher rainfall areas of the northwest to approximately 170 g/m^2 in the east central section. Judging from plant density, ground cover, and other indices, rangeland condition is also substantially better in the northwest.

In concordance with the abiotic and vegetation production gradients, animal density also varies from west to east. The mean annual large herbivore biomass density of the northwest is approximately 5,550 kg/km^2, while that of the central and eastern sections drops to about 1,000 kg/km^2. There was a shift in species composition from west to east however, and although elephants constituted less than 50% of the total large herbivore biomass in the northwest, about 90% of the eastern section biomass was contributed by elephants. Consequently, although the difference in biomass density from west to east was only fivefold, there was nearly a 12-fold difference in numbers of herbivores per unit area. The disproportionately large seasonal fluctuations in elephant numbers also caused seasonal shifts in total biomass composition. Whereas only 46% of the dry season biomass was contributed by elephants, they constituted 82% of the wet season biomass.

There appeared to be a direct relationship between utilizable primary production and herbivore diversity. The bushed and wooded grasslands of the northwest supported the greatest diversity, while the open grassland, bushland, and dry montane supported successively lower diversities.

Based on the relative frequency of occurrence in four general habitat types, the total species array was found to be segregated by habitat preferences. Spatial and temporal patterning was further elucidated by means of a niche breadth equation. Of the total herbivore community, rhinoceros were found to be the most equitably distributed among the various habitat types, and thus this species reflected the greatest index value of niche breadth on the habitat dimension. Eland, warthog, giraffe, and elephant were the next most broadly distributed species. Eland observations were found to be the most equitably distributed in time while gerenuk, reedbuck, giraffe, and warthog were next in order. Certain of the species reflected seasonal migration patterns (e.g., elephant, buffalo, zebra, oryx, and gazelle), and along with generally lower niche breadths on the time dimension, these species are largely responsible for a highly significant interaction effect of season and space on biomass density. Areas which support the greatest wet season densities generally support the lowest dry season densities and vice versa.

A measure of niche overlap was used as a quantitative expression of species association. From the similarity matrix of association (overlap) coefficients for all two-species combinations it was found that hartebeest and impala reflected the greatest overlap on the habitat dimension, while klipspringer and bushbuck reflected the least overlap. Of the predators, jackals manifested the greatest distributional overlap with herbivores, while hunting dogs showed the least overlap.

Since only four species of large herbivores accounted for 80 to 90% of the total numbers and biomass and 85 to 90% of the energy exchange, it was concluded that the system's major structural and functional attributes were dominated by a very few species. Further, since collectively the 16 to 18 "nondominant" large herbivores accounted for only 10 to 15% of the consumer level numbers, biomass, productivity, and energy exchange, it is hypothesized that they function mainly as "signal processing" or "control" mechanisms for the system.

In closing, this study has explicitly shown the interrelations of abiotic and biotic gradients in an ecological system and suggests how they may affect large herbivore behavioral patterns such as migration and grazing. The concept of dominance of ecological systems by a few species were verified. And finally, support is given to the whole-systems approach to ecological problems since considerable insight was gained by describing and evaluating the various components concurrently.

ACKNOWLEDGEMENTS

Many individuals and organizations too numerous to mention assisted the study in various ways. The following, however, seemed to go beyond their roles as professionals and deserve special credit.

In Tanzania, Mr. David Anstey, Senior Warden of the Tanzania Game Division, was instrumental in initiating the study, while Messrs. William Dick and E. O. Charlton, also Northern Region wardens, provided valuable logistic assistance in carrying out the study. Mr. H. S. Mahinda, the Chief Warden of the Game Division, provided encouragement throughout and has kindly authorized publication of the data. Dr. H. F. Lamprey and Messrs. G. S. Child, P. Hemmingway, A. Hecker, and W. L. Robinette of The College of African Wildlife Management gave stimulating advice on a number of occasions. Although D. G. Anstey piloted the airplane on all but one aerial survey, G. S. Chile and P. Hemmingway also assisted in this capacity.

I am grateful for the field assistance and friendship of Game Scouts, V. M. Mushi, H. R. Mwamba, W. George, and J. Kirindo. For them, "Nashakuru sana." Desmond Vesey-Fitzgerald, Scientific officer, Tanzania National Parks, and G. S. Child provided identifications of bird, mammal, and reptile specimens.

George A. Petrides, R. H. Baker, W. E. Cooper, S. N. Stephenson, and E. P. Whiteside, all of Michigan State University, have commented on the manuscript, and Mrs. W. H. Burke deserves credit for work on the figures.

Financial support for the work was derived from the U.S. Peace Corps and the Tanzania Game Division. Fellowships and grants from the U.S. Department of Health, Education and Welfare, the National Science Foundation, The Wildlife Federation, the office of Research Development of Michigan State University, and the Society of Sigma Xi supported the analytical phase.

Typing and publication was supported by National Science Foundation Grants GB-13096 and GB-31862X to the Grassland Biome, U.S. International Biological Program, for "Analysis of Structure, Function, and Utilization of Grassland Ecosystems."

LITERATURE CITED

Ahlgren, I. F. and C. E. Ahlgren. 1960. Ecological effects of forest fires. Bot. Rev. 26:483-533.

Aldous, A. E. 1934. Effect of burning on Kansas bluestem pastures. Kansas Agr. Exp. Sta. Tech. Bull. 38, Manhattan. 65 p.

Aldous, A. E. 1935. Management of Kansas permanent pastures. Kansas Agr. Exp. Sta. Tech. Bull. 272, Manhattan. 44 p.

Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. Principles of animal ecology. W. B. Saunders Co., Philadelphia. 837 p.

Anderson, B. 1963. Soils of Tanganyika. Tanganyika Min. Agr. Bull. 16, Tanganyika. 36 p.

Anderson, G. D. 1968. A reconnaissance survey of the land use potential of the Mkomazi Game Reserve and an appraisal of factors affecting present and potential land use and productivity in its environs. Tanzania Min. Agr., Tanzania. 41 p. (Mimeo).

Anderson, G. D. and Z. Naveh. 1968. Promising pasture plants for northern Tanzania. V. Overall comparisons of promising plants. E. Afr. Agr. Forest. J. 34(1):84-105.

Anderson, G. D. and L. M. Talbot. 1965. Soil factors affecting the distribution of the grassland types and their utilization by wild animals on the Serengeti Plains, Tanganyika. J. Ecol. 53:33-56.

Anstey, D. G. 1956. Mkomazi Game Reserve. Oryx 3(4):183-185.

Aubréville, A. 1965. Principes d'une systématique des formations végétales tropicales. Adansonia 5(2):153-196.

Banage, W. B. and S. A. Visser. 1967. Soil moisture and temperature levels and fluctuations in one year in a Uganda soil catena. E. Afr. Agr. Forest. J. 32(1):450-455.

Benedict, F. G. 1936. The physiology of the elephant. Carnegie Inst. Publ. 474. Washington, D. C. 302 p.

Best, G. A., F. Edmond-Blanc, and R. C. Witting [Ed.] 1962. Rowland Ward's records of big game. 11th ed. (Africa). Rowland Ward, London.

Blancou, L. 1962. Mensurations et poids de quelques ongules de Tchad et de la Republique centre-Africaine. Mammalia 26(1):84-106.

Boaler, S. B. 1966. The ecology of *Pterocarpus angolensis* D.C. in Tanzania. Min. Overseas Development, Overseas Res. Pub. No. 12, London. 128 p.

Bourlière, F. 1965. Ecological notes on the Tsavo. Afr. Wildlife 19:47-107.

Bourlière, F. and I. Verschuren. 1960. Exploration de Parc National Albert. Fax 1. Brussels.

Bradley, J. V. 1968. Distribution-free statistical tests. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 388 p.

Braun, H. M. 1969. Grassland productivity, p. 15-17. *In* Serengeti Research Institute annual report. Tanzania National Parks, Arusha.

Bredon, R. M. 1963. The chemical composition and nutritive value of grasses from semi-arid areas of Karamoja as related to ecology and types of soils. E. Afr. Agr. Forest. J. 28(3):134-142.

Brockington, N. R. 1961. Studies of the growth of a *Hyparrhenia* dominated grassland in Northern Rhodesia. J. Brit. Grassland Soc. 16(1):54-64.

Brody, S. 1945. Bioenergetics and growth with special reference to the efficiency complex in domestic animals. Reinhold Publ. Corp., New York. 1023 p.

Buckner, C. H. 1966. The role of vertebrate predators in the biological control of forest insects. Annu. Rev. Entomol. 11:449-470.

Buechner, H. K. and H. C. Dawkins. 1961. Vegetation change induced by elephants and fire in Murchison Falls National Park, Uganda. Ecology 42(4): 752-766.

Burtt, B. D. 1929. A record of fruits and seeds dispersed by mammals and birds from the Singida District of Tanganyika Territory. J. Ecol. 17(2):351-355.

Burtt, B. D. 1942. Some East African vegetation communities. J. Ecol. 30:67-146.

Calhoun, J. B. 1959. Revised sampling procedure for the North American Census of Small Mammals (NACSM), Population Dynamics of Vertebrates. U.S. Dep. Health, Educ., Welfare, Admin. Pub. Release No. 10. Washington, D. C. (Mimeo).

Calton, W. E. 1954. An experimental pedological map of Tanganyika, p. 237-240. *In* 2nd Inter-Afr. Soils Conf., Proc., Comptes Rendus (Leopoldville). Sci. Council Afr. S. of Sahara, Brussels.

Carter, D. B. 1954. Climates of Africa and India according to Thornthwaite's 1948 classification. Pub. Climatol. 7(4):453-479.

Chenery, E. M. 1954. Minor elements in Uganda soils, p. 1157-1160. *In* 2nd Inter-Afr. Soils Conf., Proc., Comptes Rendus (Leopoldville). Sci. Council Afr. S. of Sahara, Brussels.

Chew, R. M. and Alice E. Chew. 1970. Energy relationships of the mammals of a desert shrub (*Larrea tridentata*) community. Ecol. Monogr. 40(1):1-21.

Commonwealth Bureau of Pastures and Field Crops. 1951. Management and conservation of vegetation in Africa. Commonwealth Bur. Pastures Field Crops Bull. 41. 97 p.

Connell, J. H. and E. Orias. 1964. The ecological regulation of species diversity. Amer. Natur. 98(903):399-414.

Curtis, J. T. and M. L. Partch. 1950. Some factors affecting flower production in *Andropogon gerardi*. Ecology 31:488-489.

Dagg, M. 1965. A rational approach to the selection of crops for areas of marginal rainfall in E. Africa. E. Afr. Agr. Forest. J. 30(3):296-300.

Dames, T. W. G. 1959. The soils of Pangani Valley. F.A.O. Rep. No. 970 to Tanganyika Gov., F.A.O., Rome.

Darling, F. F. 1960. Wild life in an African territory. Oxford Univ. Press, London. 160 p.

Daubenmire, R. 1968. Ecology of fire in grasslands, p. 209-266. *In* J. B. Cragg [Ed.] Advances in ecological research 5. Academic Press, New York.

Deans, R. J., C. M. Teague, L. G. Signell, B. M. John, and M. E. Knickerbocker. 1969. Livestock and range improvement in Masailand: Tanzania. U.S. Dep. Agr. and U.S. Agency for Int. Development. Washington, D. C. 156 p.

Decken, C. C. von der. 1869. Reisen in Ost-Afrika in den Jahren 1859 bis 1965, bearbeitet von Otto Kersten. 4 vol. Leipzig and Heidelburg, Germany.

D'Hoore, J. L. 1964. Soil map of Africa with explanatory monograph. C.C.T.A. (Commission for the Technical Cooperation in Africa South of the Sahara). Lagos, Nigeria. 205 p.

De Vos, A. 1969. Ecological conditions affecting the production of wild herbivorous mammals on grasslands, p. 137-183. *In* J. B. Cragg [Ed.] Advances in ecological research 6. Academic Press, New York.

Dickman, M. 1968. Some indices of diversity. Ecology 49:1191-1193.

Donahue, R. L. 1970. Soils of equatorial Africa and their relevance to rational agricultural development. Inst. Int. Agr., Michigan State Univ., East Lansing. 52 p.

Ehrenreich, J. H. 1959. Effect of burning and clipping on growth of native prairie in Iowa. J. Range Manage. 12:133-137.

Elwell, H. M., H. A. Daniel, and F. A. Fenton. 1941. The effects of burning pasture and native woodland vegetation. Oklahoma Agr. Exp. Sta. Bull. B-247. 14 p.

Ellerman, J. R. 1940. The families and genera of living rodents. 3 vol. Brit. Mus. Natur. Hist., London.

Errington, P. L. 1963. The phenomenon of predation. Amer. Sci. 51(2):180-192.

Evans, A. C. 1963*a*. Soil fertility studies in Tanganyika. II. Continued applications of fertilizer on the red and red-brown loams of the Nachingwea series. E. Afr. Agr. Forest. J. 28(1):228-230.

Evans, A. C. 1963*b*. Soil fertility studies in Tanganyika. III. Improvement to crop and grass production on a leached sandy soil in Bukoba. E. Afr. Agr. Forest. J. 27(1):189-196.

Evans, A. C. and H. W. Mitchell. 1962. Soil fertility studies in Tanganyika. I. Improvement to crop and grass production on a leached sandy soil in Bukoba. E. Afr. Agr. Forest. J. 27(1):189-196.

Field, C. R. 1968. A comparative study of the food habits of some wild ungulates in the Queen Elizabeth National Park, Uganda, preliminary report. Symp. Zool. Soc. London 21:135-151.

Fisher, R. A., A. S. Corbet, and C. B. Williams. 1943. The relationship between the numbers of species and the number of individuals in a random sample of an animal population. J. Anim. Ecol. 12:42-58.

Forbes, S. A. 1887. The lake as a microcosm. Bull. Peoria Sci. Assoc., p. 77-87. Reprinted in Illinois Natur. Hist. Soc. Survey Bull. 15 1925. p. 537-550.

Fuggles-Couchman, N. R. 1948. The habitat-distribution of birds of northern, eastern, and central Tanganyika with field keys. IV. Birds of the thorn-bush. Tanganyika Notes Rec. 38:31-68.

Gillman, C. 1949. A vegetation-types map of Tanganyika territory. Geogr. Rev. 39(1):7-37.

Gittins, R. 1968. Trend-surface analysis of ecological data. J. Ecol. 56(3):845-869.

Glover, J. 1963. The elephant problem at Tsavo. E. Afr. Wildlife J. 1:30-39.

Glover, P. E., E. C. Trump, and L. E. D. Wateridge. 1964. Termitaria and vegetation patterns on the Loita plains of Kenya. J. Ecol. 52:367-377.

Golley, F. B. 1960. Energy dynamics of a food chain of an old field community. Ecol. Monogr. 30:187-206.

Golley, F. B. 1965. Structure and function of an old-field broomsedge community. Ecol. Monogr. 35(1):113-137.

Griffiths, J. F. 1962. The climate of East Africa, p. 77-87. *In* E. W. Russell [Ed.] The natural resources of East Africa. D. A. Hawkins Ltd., Nairobi, Kenya.

Grinnell, J. 1917. The niche relationships of the California thrasher. Auk 34:427-433.

Gwynne, M. D. and R. H. V. Bell. 1968. Selection of vegetation components by grazing ungulates in the Serengeti National Park. Nature 220(5165):390-393.

Hadley, E. B. and B. J. Kieckhefer. 1963. Productivity of two prairie grasses in relation to fire frequency. Ecology 44:389-396.

Hahn, H. C., Jr. 1949. A method of censusing deer and its application in the Edwards Plateau of Texas. Texas Game, Fish, Oyster Comm., Austin. 24 p.

Hahnel, L. von. 1890. Ostaquatorial--Afrika zwischen Pangani und dem neuentclecten Rudolph--See; Ergebnisse der Graf S. Telekischen expedition 1887-1888. Petermann's Mitteilungen, Gotha, East Germany.

Harker, K. W. 1961. A comparison of standing hay production from grasses at Entebbe. E. Afr. Agr. Forest. J. 27(1):49-51.

Harper, J. L. 1969. The role of predation in vegetational diversity. Symp. Brookhaven Nat. Lab. 22:48-62.

Harris, L. D. 1968. Population dynamics of the African elephant in the Mkomazi Game Reserve, Tanzania, East Africa. M.S. Thesis. Michigan State Univ., East Lansing. 54 p.

Hemmingsen, A. M. 1960. Energy metabolism as related to body size and respiratory surfaces, and its evolution. Steno Memorial Hospital and Nordisk Insulinlaboratorium Rep. 9(II):1-110.

Hemingway, P., A. Cormack, and W. L. Robinette. 1966. Appraisal of range condition on the Kalimawe controlled area, p. 7-9. *In* D. G. Anstey. Kalimawe in relation to Mkomazi Game Reserve. Rep. to Regional Development Comm. Kilimanjaro Region, Moshi, Tanzania. Ref. No. TA/G/GR/MR.

Hesse, P. R. 1955. A chemical and physical study of the soils of termite mounds in East Africa. J. Ecol. 43(2):449-461.

Hirst, S. M. 1969. Populations in a transvaal lowveld nature reserve. Zool. Afr. 4(2):199-230.

Hofmann, R. R. 1968. Comparisons of the rumen and omasum structures in East African game ruminants in relation to their feeding habits. Symp. Zool. Soc. London 21:179-194.

Holdridge, L. R. 1967. Life zone ecology. Tropical Science Center, San Jose, California. 206 p.

Hopkins, B. 1966. Vegetation of the Olokemeji Forest Reserve, Nigeria. IV. The litter and soil with special reference to their seasonal changes. J. Ecol. 54:687-703.

Hopkins, H. H. 1954. Effects of mulch upon certain factors on grassland environments. J. Range Manage. 7:255-259.

Hopkins, H. H., F. W. Albertson, and A. Riegel. 1948. Some effects of burning upon a prairie in west-central Kansas. Kansas Acad. Sci., Trans. 51:131-141.

Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies. Amer. Natur. 100:419-424.

Howe, G. M. 1953. Climates of the Rhodesias and Nyasaland according to the Thornthwaite classification. Geogr. Rev. 43(4):525-539.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symp. 22:415-427.

Hutchinson, G. E. 1965. The ecological theater and the evolutionary play. Yale Univ. Press, New Haven, Connecticut. 139 p.

Huxley, J. 1961. The conservation of wildlife and natural habitats in central and east Africa. UNESCO. Place de Fontenay, Paris. 113 p.

Jackson, G. 1954. Preliminary ecological survey of Nyasaland, p. 679-690. *In* 2nd Inter-Afr. Soils Conf., Proc., Comptes Rendus (Leopoldville). Sci. Council Afr. S. of Sahara, Brussels.

Janzen, D. H. 1966. Coevolution of mutualism between ants and *Acacias* in Central America. Evolution 20(3):249-275.

Janzen, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. Evolution 21:620-637.

Jowett, D. and P. O. Eriaku. 1966. The relationship between sunshine, rainfall, and crop yields at Serere Research Station. E. Afr. Agr. Forest. J. 31(4):439-440.

Keay, R. W. J. and A. Aubréville. 1959. Vegetation map of Africa south of the Tropic of Cancer. Oxford Univ. Press, Oxford. 24 p.

Kelly, J. M., P. A. Opstrup, J. S. Olson, S. I. Auerbach, and G. M. Van Dyne. 1969. Models and seasonal primary productivity in eastern Tennessee *Festuca* and *Andropogon* ecosystems. Oak Ridge Nat. Lab. 4310, U.S. Atomic Energy Comm., Biol. and Med. UC-48. 305 p.

Kemp, P. B. 1955. The termites of north-eastern Tanganyika: their distribution and biology. Bull. Entomol. Res. 46:113-135.

Kimble, G. H. T. 1960. Tropical Africa, Vol. 1, Land and livelihood. Doubleday and Co., Inc., Garden City, New York. 2 vol.

Kleiber, M. 1961. The fire of life. John Wiley & Sons, Inc., New York. 454 p.

Klopfer, P. H. and R. H. MacArthur. 1961. On the causes of tropical species diversity: niche overlap. Amer. Natur. 95:223-226.

Kruuk, H. and M. Turner. 1969. Comparative notes on predation by lion, leopard, cheetah and wild dog in the Serengeti area, East Africa. Mammalia 31(1):1-27.

Kucera, C. L., R. C. Dahlman, and M. R. Koelling. 1967. Total net productivity and turnover on an energy basis for tallgrass prairie. Ecology 48:536-541.

Lamprey, H. F. 1963. Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika. E. Afr. Wildlife J. 1:63-92.

Lamprey, H. F. 1964. Estimation of the large mammal densities, biomass and energy exchange in the Tarangire Game Reserve and the Masai Steppe in Tanganyika. E. Afr. Wildlife J. 2:1-46.

Lamprey, H. F., P. E. Glover, M. I. M. Turner, and R. H. V. Bell. 1967. Invasion of the Serengeti National Park by elephants. E. Afr. Wildlife J. 5:151-161.

Lang-Brown, J. R. and J. F. Harrop. 1962. The ecology and soils of the Kibale grasslands, Uganda. E. Afr. Agr. Forest. J. 27(1):264-273.

Laws, R. M. 1968. A preliminary report [to the Tanzania Government] on three hundred elephant culled in the Mkomazi Game Reserve in March and April 1968. Tanzania Government. 5 p. (Typescript).

Laws, R. M. 1969. The Tsavo research project. J. Reprod. Fertilization, Suppl. 6:495-531.

Lawton, R. M. 1968. The value of browse in the dry tropics. E. Afr. Agr. Forest. J. 34(1):227-230.

Lay, D. W. 1956. Effects of prescribed burning on forage and mast production in southern pine forests. J. Forest. 54:582-584.

Ledger, H. P. 1968. Body composition as a basis for a comparative study of some East African mammals. Symp. Zool. Soc. London 21:289-310.

LeRoy, A. 1893. Au Kilimanjaro. [Transl. from French.] Sanard et Deragean, Paris.

Levins, R. 1968. Evolution in changing environments, some theoretical explorations. Princeton Univ. Press, Princeton, New Jersey. 120 p.

Lloyd, M. and R. J. Ghelardi. 1964. A table for calculating the "equitability" component of species diversity. J. Anim. Ecol. 33:217-225.

Lloyd, M., J. H. Zar, and J. R. Karr. 1968. On the calculation of information-theoretical measures of diversity. Amer. Midland Natur. 79(2):257-272.

Mackworth-Praed, C. W. and C. H. B. Grant. 1957. Birds of Eastern and Northeastern Africa. 2 vol. Longmans, Green and Co., New York.

Madge, D. S. 1965. Leaf fall and litter disappearance in a tropical forest. Pedobiologia 5: 273-288.

Makin, J. 1969*a*. The use of identification keys in distinguishing individual soil categories. E. Afr. Agr. Forest. J. 34(4):416-418.

Makin, J. 1969*b*. A feature card system for data retrieval and its application to soil research. E. Afr. Agr. Forest. J. 34(4):418-421.

Marcus, L. F. and J. H. Vandermeer. 1966. Regional trends in geographic variation. Syst. Zool. 15(1):1-13.

Margalef, R. 1957. Lateoria de la informacion en ecologia. Mem. R. Acad. Barcelona 32(13):373-449. [Transl. from Spanish by W. Hall, 1957]. *Also* Information theory in ecology. Gen. Syst. 3:36-71.

Margalef, R. 1963. On certain unifying principles in ecology. Amer. Natur. 97:357-374.

Margalef, R. 1968. Perspectives in ecological theory. Univ. Chicago Press, Chicago. 111 p.

Maynard, L. A. and J. K. Loosli. 1956. Animal nutrition. McGraw-Hill Book Co., Inc., New York. 484 p.

McCulloch, J. S. C. 1965. Tables for the rapid computation of the Penman estimate of evaporation. E. Afr. Agr. Forest. J. 30:286-295.

McKay, A. D. 1968. Rangeland productivity in Botswana. E. Afr. Agr. Forest. J. 32(2):178-193.

McMeekan, C. P. 1960. Grazing management, p. 21-26. *In* 8th Int. Grassland Congr., Proc. Alden Press, Oxford. 764 p.

McMeekan, C. P. and M. J. Walshe. 1963. The interrelationships of grazing method and stocking rate in the efficiency of pasture utilization by dairy cattle. J. Agr. Sci. 61:147-163.

McNaughton, S. J. and L. L. Wolf. 1970. Dominance and the niche in ecological systems. Science 167(3915):131-139.

Mehlich, A., R. J. Kempton, A. Pinkerton, and W. Robertson. 1962. Mass analysis methods for soil fertility evaluation. Scott Agr. Lab., Kenya Dep. Agr., Nairobi.

Meinertzhagen, R. 1938. Some weights and measurements of large mammals. Zool. Soc. London, Proc., A. 108:433-439.

Mills, W. R. 1954. A review of recent trials with fertilizers in Uganda, p. 1133-1141. *In* 2nd Inter-Afr. Soils Conf., Proc., Comptes Rendus (Leopoldville). Sci. Council Afr. S. of Sahara, Brussels.

Milne, G. 1936. A provisional soil map of East Africa. Crown Agents Colony, London. 34 p.

Milne, G. 1947. A soil reconnaissance journey through parts of Tanganyika Territory, Dec. 1935 to Feb. 1936. J. Ecol. 35:192-265.

Mitchell, B. L., J. B. Shenton, and J. C. M. Uys. 1965. Predation on large mammals in the Kafue National Park, Zambia. Zool. Afr. 1(1):297-318.

Moreau, R. E. 1935. A synecological study of Usambara, Tanganyika Territory, with particular reference to birds. J. Ecol. 23(1):1-43.

Morison, C. G. T., A. C. Hoyle, and J. F. Hope-Simpson. 1948. Tropical soil-vegetation catenas and mosaics. J. Ecol. 36:1-84.

Murray, T. M. 1938. An investigation of the interrelationships of the vegetation, soil and termites. S. Afr. J. Sci. 35:288-297.

Myers, J. G. 1936. Savannah and forest vegetation of the interior Guiana plateau. J. Ecol. 24:163-184.

Naik, A. H. 1965. Mineral status of grasses and soils of part of Mbulu district of Tanzania in relation to animal health. E. Afr. Agr. Forest. J. 30(3):175-182.

National Academy of Sciences, National Research Council. 1966. Biological Energy interrelationships and glossary of energy terms. Nat. Acad. Sci. Nat. Res. Council Pub. 1411. Washington, D. C. 35 p.

Naveh, Z. 1968*a*. The determination of agroecological site potentials of Tanzania Masailand--a challenge for the International Biological Program. Symp. Recent Adv. Trop. Ecol., Proc. p. 601-611.

Naveh, Z. 1968*b*. The ecological basis of pasture production in northern Tanzania. Symp. Recent Adv. Trop. Ecol., Proc. p. 685-696.

Odum, E. P. 1962. Relationships between structure and function in the ecosystem. Jap. J. Ecol. 12(3):108-118.

Odum, E. P., C. E. Connell, and L. B. Davenport. 1962. Population energy flow of three primary consumer components of an old-field ecosystem. Ecology 43:88-96.

Odum, H. T. 1967. Energetics of world food production, p. 55-94. *In* The world food problem. President's Sci. Advisory Comm. III. Washington, D. C.

Odum, H. T. and R. F. Pigeon. 1970. A tropical rain forest, a study of irradiation and ecology at El Verde, Puerto Rico. Div. Tech. Information, U.S. Atomic Energy Comm., Washington, D. C. ca. 1600 p.

O'Leary, M., R. H. Lippert, and O. T. Spitz. 1969. FORTRAN IV and map program for computation and plotting of trend surfaces for degrees 1 through 6. State Geol. Survey, Univ. Kansas, Lawrence. 48 p.

Paine, R. T. 1966. Food web complexity and species diversity. Amer. Natur. 100:65-75.

Paine, R. T. and R. L. Vadas. 1969. The effects of grazing by sea urchins on benthic algal populations. Limnol. Oceanogr. 14:710-719.

Pendleton, R. L. 1941. Some results of termite activity in Thailand soils. Thailand Sci. Bull. 3(2):28-53.

Penfound, W. T. 1964. Effects of denudation on the productivity of grassland. Ecology 45:838-845.

Penman, H. L. 1948. Natural evaporation from open water and grass. Roy. Soc. (London), Proc., A. 193:120-146.

Petrides, G. A. 1956. Big game densities and range carrying capacities in East Africa. N. Amer. Wildlife Conf., Trans. 21:525-537.

Petrides, G. A. and W. G. Swank. 1958. Management of the big game resource in Uganda, East Africa. N. Amer. Wildlife Conf., Trans. 23:461-477.

Petrides, G. A. and W. G. Swank. 1965. Population densities and the range-carrying capacity for large mammals in Queen Elizabeth National Park, Uganda. Zool. Africana 1(1):209-225.

Petrides, G. A. and W. G. Swank. 1966. Estimating the productivity and energy relations of an African elephant population, p. 831-842. *In* 9th Int. Grassland Conf., Proc. Alarico Ltd., San Paulo, Brazil.

Phillips, J. F. V. 1929. Some important vegetation communities in the central province of Tanganyika. S. Afr. J. Sci. 26:332-372.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. Amer. Natur. 100(910):33-46.

Pielou, E. C. 1967. The use of information theory in the study of the diversity of biological populations. 5th Berkeley Symp. Math. Statis. Problems, Proc. 4:163-177.

Pienaar, U. de V., P. van Wyk, and N. Farrall. 1966. An aerial census of elephant and buffalo in the Kruger National Park, and the implications thereof on intended management schemes. Koedoe 9:40-107.

Potts, W. H. and C. H. N. Jackson. 1952. The Shinyanga game destruction experiment. Bull. Entomol. Res. 43:365-374.

Pratt, D. J. P., J. Greenway, and M. D. Gwynne. 1966. A classification of East African rangeland, with an appendix on terminology. J. Appl. Ecol. 3(2):369-382.

Quick, H. 1965. Ecology of the African elephant. Biol. Sci. Curric. Study Pamphlet 21. D. C. Heath & Co., Boston.

Robinette, W. L. 1963. Weights of some of the larger mammals of Northern Rhodesia. The Puko 1:207-215.

Rogerson, A. 1968. Energy utilization by the eland and wildebeest. Symp. Zool. Soc. London 21: 153-161.

Sachs, R. 1967. Liveweights and body measurements of Serengeti game animals. E. Afr. Wildlife J. 5:24-36.

Salt, G. 1952. The arthropod population of the soil in some East African pastures. Bull. Entomol. Res. 43:203-220.

Scott, R. M. 1962*a*. The soils of East Africa, p. 67-76. *In* E. W. Russell [Ed.] The natural resources of East Africa. D. A. Hawkins, Ltd., Nairobi, Kenya.

Scott, R. M. 1962*b*. Exchangeable bases of mature, well drained soil in relation to rainfall in East Africa. J. Soil Sci. 13:1-9.

Semb, G. and J. B. D. Robinson. 1969. The natural nitrogen flush in different arable soils and climates in East Africa. E. Afr. Agr. Forest. J. 34(1):350-369.

Shantz, H. L. 1947. The use of fire as a tool in the management of the brush ranges of California. California State Div. Forest., Sacramento. 156 p.

Shantz, H. L. and C. F. Marbut. 1923. The vegetation and soils of Africa. Amer. Geogr. Soc. Res. Ser. No. 13, New York. 263 p.

Simpson, E. H. 1949. Measurement of diversity. Nature 163:688.

Smith, G. D. 1965. Lectures on soil classification. Pedologie, Spec. No. 4. Leningrad.

Slade, N. A. and R. D. Anderson. 1970. Is wildlife management an ecological science? Wildlife Soc. News 129:38.

Slobodkin, L. B., F. E. Smith, and N. G. Hairston. 1967. Regulation in terrestrial ecosystems, and the implied balance of nature. Amer. Natur. 101:109-124.

Sneath, P. H. A. 1967. Trend-surface analysis of transformation grids. J. Zool. 151:65-122.

Sokal, R. R. 1965. Statistical methods in systematics. Biol. Rev. 40:337-391.

Spurr, A. M. M. 1954. A basis of classification of the soils of areas of composite topography in Central Africa, with special reference to the soils of the southern highlands of Tanganyika, p. 175-190. *In* 2nd Int. Afr. Soils Conf., Proc., Comptes Rendus (Leopoldville). Sci. Council Afr. S. of Sahara, Brussels.

Stewart, D. R. M. and D. R. P. Zaphiro. 1963. Biomass and density of wild herbivores in different East African habitats. Mammalia 27:483-496.

Stoddart, L. A. and A. D. Smith. 1955. Range management. McGraw-Hill Book Co., Inc., New York. 433 p.

Swynnerton, C. F. M. 1936. The tsetse flies of East Africa. Roy. Entomol. Soc., London.

Swynnerton, G. H. and R. W. Hayman. 1951. A check list of the land mammals of the Tanganyika territory and the Zanzibar protectorate. J. E. Afr. Natur. Hist. Soc. 20(6-7):274-394.

Sys, C. 1967. The concept of ferallitic and fersiallitic soils in central Africa--their classification and their correlation with the 7th approximation. Pedologie 17(3):284-325.

Sys, C. 1968. Suggestions for the classification of tropical soils with lateritic materials in the American classification. Pedologie 18:189-198.

Talbot, L. M. 1963*a*. The biological productivity of the tropical savanna ecosystem, p. 88-97. *In* Ecosystems and biological productivity. 9th Tech. Meeting, Proc., IUCN, Nairobi, Kenya. Morges, Switzerland.

Talbot, L. M. 1963*b*. Comparison of the efficiency of wild animals and domestic livestock in utilization of East African rangelands. Publ. N.S. 1:328-335, IUCN, Morges, Switzerland.

Talbot, L. M. 1964. The concept of biomass in African wildlife research. Mammalia 28(4): 613-619.

Talbot, L. M. and Martha H. Talbot. 1962. Food preferences of some East African wild ungulates. E. Afr. Agr. Forest. J. 27:131-138.

Talbot, L. M., W. J. A. Payne, H. P. Ledger, Lorna D. Verdcourt, and Martha H. Talbot. 1965. The meat production potential of wild animals in Africa, a review of biological knowledge. Commonwealth Bur. Animal Breeding Genetics. Tech. Commun. 16. 42 p.

Tanganyika Atlas. 1955. Government Printer, Dar Es Salaam, Tanganyika.

Tanganyika Game and Tsetse Division. 1933. Annual Report. Government Printer, Dar Es Salaam, Tanganyika.

Tanganyika Game and Tsetse Division. 1935. Annual Report. Government Printer, Dar Es Salaam, Tanganyika.

Tanganyika Game and Tsetse Division. 1950. Annual Report. Government Printer, Dar Es Salaam, Tanganyika.

Tanganyika Game and Tsetse Division. 1955. Annual Report. Government Printer, Dar Es Salaam, Tanganyika.

Tanganyika Ministry of Lands, Forests and Wildlife, Survey Division. 1963. Geological Survey maps. Dodoma, Tanganyika.

Taylor, C. R. 1968. The minimum water requirements of some East African bovids. Symp. Zool. Soc. London 21:195-206.

Taylor, C. R. 1969. The eland and the oryx. Sci. Amer. 220(1):88-95.

Thomas, A. S. 1941. The vegetation of the Sese Islands Uganda--an illustration of edaphic factors in tropical ecology. J. Ecol. 29:330-353.

Thompson, B. W. 1965. The climate of Africa. Oxford Univ. Press, Oxford.

Thornthwaite, C. W. 1948. An approach toward a rationale classification of climate. Geogr. Rev. 38:51-94.

Thornthwaite, C. W. and F. K. Hare. 1965. The loss of water to the air. Meteorol. Monogr. 6(28): 163-180.

Trapnell, C. F. and I. Langdale-Brown. 1962. The natural vegetation of East Africa, p. 92-102. *In* E. W. Russell [Ed.] The natural resources of East Africa. D. A. Hawkins, Ltd., Nairobi, Kenya.

Trapnell, C. G. and J. F. Griffiths. 1960. The rainfall-altitude relation and its ecological significance in Kenya. E. Afr. Agr. Forest. J. 25:207-213.

U.S. Deparmtent of Agriculture. 1951. Soil survey manual. USDA Handbook No. 18, U.S. Government Printing Office. Washington, D. C. 503 p.

U.S. Department of Agriculture. 1960. Soil classification--a comprehensive system 7th approximation. Soil Conserv. Service. Washington, D. C. 265 p.

U.S. Department of Agriculture. 1967. Supplement to soil classification system 7th approximation. Soil Conserv. Service. Washington, D. C. 207 p.

U.S. Forest Service. 1968. Range environmental analysis handbook. Rocky Mountain Region (Denver, Colorado), FSH 2209.21.

Vandermeer, J. H. 1966. Statistical analysis of geographical variation of the flathead minnow, *Pimephales promelas*. Copeia 3:457-466.

Vesey-Fitzgerald, D. F. 1960. Grazing succession among East African game animals. J. Mammal. 41: 161-172.

Vesey-Fitzgerald, D. F. 1963. Grasslands in ecosystems and biological productivity. 9th Tech. Meeting, Proc., IUCN, Nairobi, Kenya. Morges, Switzerland.

Vesey-Fitzgerald, D. F. 1965. The utilization of natural pastures by wild animals in the Rukwa Valley, Tanganyika. E. Afr. Wildlife J. 3:38-48.

Visser, S. A. 1969. Environmental factors influencing the occurrence, distribution and activity of micro-organisms in soils, with special reference to waterlogged environments. E. Afr. Agr. Forest. J. 34:336-341.

Voisin, A. 1959. Grass productivity. Phil. Libr., New York. 355 p.

Walker, B. 1968. Grazing experiments at Ukiriguru, Tanzania. II. Comparisons of rotational and continuous grazing systems on natural pastures of hardpan soils using an "extra-period Latin-square change-overdesign." E. Afr. Agr. Forest. J. 34(2):235-244.

Walker, B. and G. D. Scott. 1968*a*. Grazing experiments at Ukiriguru, Tanzania. I. Comparisons of rotational and continuous grazing systems on natural pastures of hardpan soils. E. Afr. Agr. Forest. J. 24(2):224-234.

Walker, B. and G. D. Scott. 1968*b*. Grazing experiments at Ukiriguru, Tanzania. III. A comparison of three stocking rates on the productivity and botanical composition of natural pastures of hardpan soils. E. Afr. Agr. Forest. J. 34(2):245-255.

Walker, T. W. and A. F. R. Adams. 1958. Studies on soil organic matter. I. Influence of phosphorus content of parent materials on accumulations of carbon, nitrogen, sulphur, and organic phosphorus in grassland soils. Soil Sci. 85:307-318.

Wallace, A. R. 1878. Animal life in the tropical forests, p. 270-311. *In* A. R. Wallace [Ed.] Tropical nature and other essays. Reprinted in Natural selection and tropical nature. 1895. The MacMillan Co., New York.

Watson, J. P. 1962. The soil below a termite mound. J. Soil Sci. 13(1):46-51.

Watson, R. M., I. S. C. Parker, and T. Allan. 1969. A census of elephant and other large mammals in the Mkomazi region of northern Tanzania. E. Afr. Wildlife J. 7:11-26.

Weber, N. A. 1959. Isothermal conditions in tropical soil. Ecology 40(1):153-154.

Weiss, P. A. 1958. Condensed transcript of the conference, p. 184. *In* R. W. Gerard [Ed.] Concepts of biology. Publ. 560 Nat. Acad. Sci., Nat. Res. Council. Washington, D. C.

West, O. 1965. Fire in vegetation and its use in pasture management with special reference to tropical and subtropical Africa. Commonwealth Bur. Pastures Field Crops Pub. 1. 53 p. (Mimeo).

Wiegart, R. G. and F. C. Evans. 1964. Primary production and the disappearance of dead vegetation on an old field in southwestern Michigan. Ecology 45:49-63.

Willoughby, J. C. 1889. East Africa and its big game. Longmans, Green and Co., London.

Wright, B. S. 1960. Predation on big game in East Africa. J. Wildlife Manage. 24(1):1-15.

APPENDIX I

I.1. Composite monthly rainfall statistics (in cm) for the eight stations in the Mkomazi Reserve and the Same Meteorological Station from March 1965 to June 1967.

Station									Month	Year
Kamakota	Maori	Kisima	Mzara	Ndea	Mbula	Dindira	Ibaya	Same		
							3.3	9.1	Mar.	
						4.3	1.5	3.6	Apr.	
						2.0	6.6	3.8	May	
						.0	1.8	.0	June	
						.0	.0	.0	July	
						1.0	1.5	1.3	Aug.	1965
		.0	.0	.0	.0	.0	.3	.3	Sep.	
		.0	.0	.0	.0	1.5	2.5	3.6	Oct.	
		2.0	.0	2.8	.0	8.9	6.6	9.7	Nov.	
		19.3	4.8	14.2	14.2	24.4	11.7	7.9	Dec.	
		21.3	4.8	17.0	14.2	42.1	35.8	39.3		
.0	2.3	4.8	.0	3.3	2.5	3.0	3.0	3.3	Jan.	
12.2	7.1	4.1	3.8	3.0	7.9	3.6	7.1	6.6	Feb.	
8.1	11.7	15.2	14.2	11.4	22.6	21.1	19.8	14.7	Mar.	
8.6	9.9	13.7	19.8	6.4	2.8	6.6	2.3	3.8	Apr.	
5.6	1.8	4.8	.8	1.0	1.5	7.4	6.1	9.6	May	
.0	.0	5.1	6.3	5.1	1.0	2.8	.5	1.5	June	
.8	.5	.0	.8	.0	.5	.0	.0	.0	July	1966
.0	.5	.8	.0	.0	.0	.0	.0	1.0	Aug.	
.0	.0	.2	.0	.8	.0	.0	.0	.7	Sep.	
.0	1.3	.0	.0	.5	.0	.0	7.1	9.1	Oct.	
.0	6.1	8.1	.0	4.8	4.8	13.0	3.0	2.3	Nov.	
.0	.0	4.6	4.9	3.8	1.5	4.1	3.6	.8	Dec.	
35.3	41.2	61.4	50.6	40.1	45.1	61.6	52.5	53.4		
2.3	1.8	1.3	3.0	.8	.5	.0	.0	.0	Jan.	
.0	.0	5.6	.0	6.6	8.1	28.2	19.0	2.3	Feb.	
.5	5.1	4.1	4.1	5.3	10.2	8.6	7.9	1.8	Mar.	
21.8	12.4	29.5	7.9	32.5	13.5	20.3	20.3	18.0	Apr.	1967
10.7	9.1	8.1	6.4	7.9	18.3	16.0	16.8	18.0	May	
1.3	1.0	1.0	1.5	1.3	.0	.8	.5	.8	June	
36.6	29.4	49.6	22.9	54.4	50.6	73.9	64.5	40.9		

I.2. Long-term rainfall statistics for four stations within 10 km of the Mkomazi Game Reserve (in cm).

Year	Station			
	Mnazi	Gonja	Kisiwani	Same
1950			59.69	
1951			101.34	
1952		80.01	38.60	
1953		79.24	81.02	
1954		42.67	40.89	
1955		132.08	98.8	
1956		106.17	68.32	
1957	155.44	116.58	81.53	91.94
1958	84.83	106.68	74.16	54.10
1959	66.08	75.69	33.02*	40.38
1960	52.32	49.78	45.21	62.73
1961	79.5	113.28	143.25	69.34
1962	72.13	110.23	160.52	45.46
1963	103.63	103.88	100.58	100.58
1964	68.83	70.86	66.04	51.05
1965	74.16	67.81	49.27	45.72
1966	46.99	74.93	44.95	53.59
Mean	80.77	88.64	75.69	57.65

* July to December only.

I.3. Mean monthly maxima, minima, and mean monthly temperatures for the Same Meteorological Station (°C).

Month	Mean Maxima		Mean Minima		Mean Monthly	
	1965	1966	1965	1966	1965	1966
Jan.	29.63	32.30	18.25	19.53	23.97	25.91
Feb.	33.57	31.85	18.64	19.64	26.14	25.75
Mar.	32.74	29.58	19.09	19.31	25.91	24.47
Apr.	29.41	29.08	18.75	18.59	24.08	23.86
May	25.53	27.36	16.59	16.98	21.09	22.20
June	26.58	25.36	18.75	15.65	22.69	20.53
July	25.58	26.36	14.48	14.87	20.03	20.64
Aug.	26.47	27.32	14.76	15.09	20.64	21.25
Sep.	26.08	29.08	15.65	15.76	20.86	22.42
Oct.	29.24	29.97	16.98	16.70	23.14	23.36
Nov.	29.24	30.35	18.37	18.37	23.80	21.58
Dec.	30.85	30.58	19.20	19.09	25.03	24.86

I.4. Monthly absolute maxima, minima, and the absolute temperature range recorded during 1965-66 at the Same Meteorological Station (°C).

Month	Absolute Maxima		Absolute Minima		Absolute Range	
	1965	1966	1965	1966	1965	1966
Jan.	33.96	34.74	16.59	17.76	17.4	17.0
Feb.	35.63	35.52	16.76	16.65	18.9	18.9
Mar.	34.96	32.46	17.37	17.48	17.6	15.0
Apr.	32.96	30.85	17.31	16.87	15.6	14.0
May	30.58	32.41	15.20	13.98	15.4	18.4
June	29.30	28.30	12.21	13.59	17.1	15.3
July	28.74	28.30	11.37	10.87	17.4	17.6
Aug.	29.30	30.69	11.98	11.98	17.3	18.7
Sep.	30.58	32.19	13.26	12.21	17.3	20.0
Oct.	32.19	32.35	15.20	13.48	17.0	18.9
Nov.	36.74	34.35	16.76	16.09	15.0	18.3
Dec.	32.91	31.74	17.20	17.98	15.7	13.8

I.5. Absolute maxima, minima, and mean monthly relative humidity values calculated from the 1600 hours wet and dry bulb thermometer readings of the Same Meteorological Station.

Month	Absolute Maxima		Absolute Minima		Mean Monthly	
	1965	1966	1965	1966	1965	1966
Jan.					51	38
Feb.	68	68	22	28	41	44
Mar.					41	58
Apr.	98	91	40	43	55	57
May					52	60
June	63	96	33	44	46	58
July					46	52
Aug.	93	70	33	34	46	46
Sep.					44	46
Oct.	81	98	32	31	47	46
Nov.					52	48
Dec.	75	80	32	33	47	46

I.6. Monthly values of aridity coefficients calculated by the Thornthwaite method (1948). A value of -1.0 means that no rainfall occurred and the rainfall deficit equalled the potential evapotranspiration (P.E.). A value of 0.0 implies that precipitation equalled the P.E., while positive values reflect a positive balance of precipitation over P.E. All values are negative unless otherwise marked.

Station							Month	Year
Kamakota	Maori	Mzara	Ndea	Mbula	Ibaya	Same		
					.75		Mar.	1965
					.88	.70	Apr.	
					.42	.66	May	
					.83	1.0	June	
					1.0		July	
					.86	.88	Aug.	
		1.0	1.0	1.0	.97	.97	Sep.	
		1.0	1.0	1.0	.80	.71	Oct.	
		1.0	.78	1.0	.46	.21	Nov.	
		1.0	0.0	+ .05	.13	.41	Dec.	
1.0	.84	1.0	.76	.81	.77	.75	Jan.	1966
.14	.47	.72	.77	.36	.42	.46	Feb.	
.46	.20	.03	.18	.68	+ .47	+ .10	Mar.	
.38	.25	+ .48	.50	.77	.93	.69	Apr.	
.55	.85	.93	.91	.86	.55	.15	May	
1.0	1.0	1.0	.57	.91	.95	.86	June	
.93	.95	.93	1.0	.95	1.0	1.0	July	
1.0	.95	1.0	1.0	1.0	1.0	.91	Aug.	
1.0	1.0	1.0	.93	1.0	1.0	.93	Sep.	
1.0	.90	1.0	.96	1.0	.44	.28	Oct.	
1.0	.53	1.0	.63	.61	.75	.81	Nov.	
1.0	1.0	.66	.73	.88	.73	.94	Dec.	
.84	.87	.79	.94	.96	1.0	1.0	Jan.	1967
1.0	1.0	1.0	.50	.34	+ .53	.81	Feb.	
.95	.65	.72	.62	.23	.41	.86	Mar.	
+ .56	.06	.40	+1.51	+ .08	+ .62	.45	Apr.	
.15	.27	.49	.35	+ .59	+ .42	.92	May	
.89	.91	.87	.89	1.0	.95	.97	June	

APPENDIX II

A listing of the Mkomazi soils as classified by the American 7th Approximation to a comprehensive soil classification system (USDA 1960, 1967).

A_1	Fine, mixed, isohyperthermic, Typic Camborthid
A_2	Fine, mixed, isohyperthermic, Typic Paleargid
A_3	Fine, montmorillonitic, isohyperthermic, Chromic Pellustert
A_4	Fine, montmorillonitic, isohyperthermic, Typic Pellustert
B_1	Fine, mixed, isohyperthermic, Mollic Paleargid
B_2	Fine, mixed, isohyperthermic, Mollic Paleargid
B_3	Fine loamy, mixed, isohyperthermic, Typic Paleargid
B_4	Fine, mixed, isohyperthermic, Typic Paleargid
B_5	Very fine, montmorillonitic, isohyperthermic Entic Pellustert
D_1	Fine loamy, mixed, isohyperthermic, Typic Paleargid
D_2	Fine, montmorillonitic, isohyperthermic, Mollic Camborthid
D_3	Very fine, montmorillonitic, isohyperthermic, Udic Pellustert
E	Fine, mixed, acid, isohyperthermic, Typic Paleargid
F	Fine loamy, mixed, isohyperthermic, Typic Camborthid
G_1	Sandy skeletal, mixed, isohyperthermic, Lithic Torripsamment
G_2	Fine loamy, mixed, isohyperthermic, Typic Haplargid

APPENDIX III

A vegetation species list compiled from specimens collected in the Mkomazi Reserve and identified by the East African Herbarium, Nairobi.

Gramineae
Andropogon schinzii Hack.
Aristida adscensionis L.
Aristida lommelii Mez
Bothriochloa glabra (Roxb.) A. Camus
Bothriochloa radicans (Lehm.) A. Camus
Brachiaria defloexa (Schumach.) Hubb.
Brachiaria eruciformis Griseb.
Brachiaria lachnantha (Hochst.) Stapf
Brachiaria leucacrantha (K. Schum.) Stapf
Brachiaria serrifolia (Hochst.) Stapf
Cenchrus ciliaris L.
Chloris mossambicensis K. Schum.
Chloris roxburghiana Schult.
Chloris virgata Sw.
Cymbopogon afronardus Stapf
Cymbosetaria sagittifolia (A. Rich.) Schweickt.
Cynodon dactylon (L.) Pers.
Cynodon plectostachyus (K. Schum.) Pilg.
Dactyloctenium aegyptium (L.) Beauv.
Dichanthium pappilosum (A. Rich.) Stapf
Digitaria macroblephara (Hack.) Stapf
Digitaria mombasana C. E. Hubb.
Digitaria remotigluma (Forsk.) Beauv.
Digitaria rivae (Chiov.) Stapf
Digitaria setivalva Stent
Dinebra retroflexa (Vahl) Panz.
Echinochloa haploclada (Stapf) Stapf
Enneapogon cenchroides (Roem. & Schult.) C. E. Hubb.
Enneapogon elegans (Nees) Stapf
Enneapogon sp.
Enteropogon macrostachyus (A. Rich.) Benth.
Eragrostis aethiopica Chiov.
Eragrostis aspera (Jacq.) Nees
Eragrostis caespitosa Chiov.
Eragrostis rigidior Pilg.
Eragrostis superba Peyr.
Eriochloa meyeriana (Nees) Pilg.
Eriochloa nubica (Steud.) Thell.
Eustachys paspaloides (Vahl) Lanza & Mattei
Heterocarpha haareri Stapf & C. E. Hubb.
Heteropogon contortus (L.) Roem. & Schult.
Ischaemum afrum (J. F. Gmel.) Dandy
Latipes senegalensis Kunth
Leptocarydion vulpiastrum (De Not.) Stapf
Leptochloa obtusiflora Hochst.
Leptochloa panicea (Retz.) Ohwi
Lintonia nutans Stapf
Microchloa kunthii Desv.
Panicum coloratum L.
Panicum deustum Thunb.
Panicum infestum Anderss.
Panicum maximum Jacq.
Panicum sp.
Pennisetum mezianum Leeke
Rhynchelytrum repens (Willd.) C. E. Hubb.
Rhynchelytrum setifolium (Stapf) Chiov.
Rhynchelytrum villosum (Parl.) Chiov.
Rottboellia exaltata L.f.
Schmidtia bulbosa Stapf
Schoenefeldia transiens (Pilg.) Chiov.
Setaria homonyma (Steud.) Chiov.
Setaria incrassata (Hochst.) Hack.
Setaria sphacelata (Schumach.) Stapf & C. E. Hubb.
Sorghum versicolor Anderss
Sorghum verticilliflorum (Steud.) Stapf
Sporobolus consimilis Fresen.
Sporobolus festivus A. Rich.
Sporobolus filipes Napper
Sporobolus fimbriatus Nees var. *latifolius* Stent
Sporobolus pyramidalis Beauv.
Sporobolus sp. near *pyramidalis* Beauv.
Tetrapogon bidentatus Pilg.
Tetrapogon tenellus (Roxb.) Chiov.
Themeda triandra Forsk.
Tragus berteronianus Schult.
Tripogon abyssinicus Steud.
Urochloa mosambicensis (Hack.) Dandy
Urochloa sp.

Cyperaceae
Cyperus alopecuroides Rottb.
Cyperus bulbous Vahl
Cyperus distans L.f.
Cyperus exaltatus Retz
Cyperus obtusiflorus Vahl
Kyllinga oblonga C.B.Cl.
Mariscus circumclusus C.B.Cl.
Mariscus leptophyllus (Hochst.) C.B.Cl.
Mariscus pseudovestitus (C.B.Cl.) Kukenth.
Mariscus taylori C.B.Cl. var. *taylori*

Commelinaceae
Aneilema aequinoctiole (P. Beauv.) Kunth
Commelina sp.

Liliaceae
Aloa sp.
Anthericum ?moniliforma Rendle
Asparagus asiaticus L.
Asparagus racemosa Willd.
Gloriosa simplex L.
Ornithogalum donaldsonii Rendle
Ornithogalum sp.

Velloziaceae
Vellozia aequatorialis Rendle
Vellozia spekei Bak.

Moraceae
Ficus pretoriae B. Davy
Ficus spp.

Polygonaceae
Oxygonum sinuatum (Meisn.) Dammer

Amaranthaceae
Achyranthes sp.
Aerva lanata Juss.
Aerva persica (Burm.) Merr.
Alternanthera sessilis R. Br.
Centemopsis rubra (Lopr.) Schinz
Cyathula erinaceae Schinz
Digera muricata (L.) Mart.
Pupalia lappacea Juss.
Sericocomopsis grisea Suessenguth
Sericocomopsis pallida (S. Moore) Schinz

Aizoaceae
Gisekia pharnaceoides L.

- Portulacaceae
  - *Calyptrotheca taitensis* (Pax & Vatke) Brenan
  - *Talinum caffrum* Eck. & Zey.

- Capparidaceae
  - *Boscia angustifolia* A. Rich.
  - *Boscia salicifolia* Oliv.
  - *Cadaba farinosa* Forsk.
    - subsp. *adenotricha* Gilg & Bened.
  - *Cadaba ruspolii* Gilg
  - *Cadaba* sp.
  - *Capparis tomentosa* Lam.
  - *Cleome stenopetala* Gilg & Benedict
  - *Maerua grantii* Oliv.
  - *Maerua* Kirkii
  - *Thylachium africanum* Lour.

- Mimosaceae
  - *Acacia ancistroclada* Brenan
  - *Acacia brevispica* Harms
  - *Acacia bussei* Harms ex Sjostedt
  - *Acacia etbaica* Schweinf.
    - subsp. *platycarpa* Brenan
  - *Acacia mellifera* (Vahl) Benth.
  - *Acacia senegal* (L.) Willd. var. *senegal*
  - *Acacia seyal* Del. var. *fistula* (Schweinf.) Oliv.
  - *Acacia stuhlmannii* Taub.
  - *Acacia tortilis* (Forsk.) Hayne
    - subsp. *spirocarpa* (Hochst. ex A. Rich.) Brenan
  - *Acacia zanzibarica* (S. Moore) Taub.
  - *Acacia* sp. no flowers or pods
  - *Albizia anthelmintica* Brongn.
  - *Albizia harveyi*
  - *Albizia petersiana* (Bolle) Oliv.
  - *Albizia* sp.
  - *Dichrostachys cinerea*
  - *Newtonia hildebrandtii* (Vatke) Torre var. *hildebrandtii*

- Caesalpiniaceae
  - *Afzelia cuanzensis* Welw.
  - *Cassia abbreviata* Oliv.
    - subsp. *beareana* (Holmes) Brenan
  - *Cassia longiracemosa* Vatke
  - *Cassia mimosoides* L.
  - *Cassia singueana* Del.
  - *Delonix elata* (L.) Gamble
  - *Tamarindus indica* L.
  - *Tylosema fassoglensis* (Kotschy ex Schweinf.) Torre & Hillcoat

- Papilionaceae
  - *Abrus schimperi* Hochst. ex Bak.
    - subsp. *africanus* (Vatke) Verdc.
  - *Craibia brevicaudata* (Vatke) Dunn.
    - subsp. *brevicaudata*
  - *Crotalaria* sp.
  - *Dalbergia melanoxylon* Guill. & Perr.
  - *Erythrina* sp.
  - *Indigofera schimperi* J. & S. var. *baukeana* (Vatke) Gillett
  - *Indigofera spinosa* Forsk.
  - *Indigofera zenkeri* Bak. f.
  - *Indigofera* sp.
  - *Lonchocarpus eriocalyx* Harms
  - *Lonchocarpus* sp.
  - *Neorautenenia pseudopachyrhiza* (Harms) M. Redh.
  - *Ostryoderris stuhlmanni* (Taub.) Bak. f.
  - *Platycelyphium voense* (Engl.) H. Wild.
  - *Sesbania sesban* (L.) Merrill var. *nubica* Chiov.
  - *Tephrosia ?interrupta* Hochst. & Steud ex E. Engl.
  - *Tephrosia pumila* (Lam.) Pers.
  - *Tephrosia villosa* (L.) Pers var. *incana* (Roxb.) Bak.
  - *Vigna fragrans* Bak. f.
  - *Vigna reticulata* Hook. f.

- Zygaphyllaceae
  - *Tribulus terrestris* L. (specimen without flowers)

- Balanitaceae
  - *Balanites* sp.

- Rutaceae
  - *Calodendrum capense* (L.f.) Thub.
  - *Fagara* sp.
  - *Vepris uguenensis* Engl.

- Burseraceae
  - *Commiphora caerulea*
  - *Commiphora campestris* Engl.
  - *Commiphora schimperi*
  - *Commiphora* sp. aff. *C. mollis* (Oliv.) Engl.
  - *Commiphora* sp.

- Meliaceae
  - *Melia volkensii* Guerke
  - *Trichilia* sp.

- Malpighiaceae
  - *Acridocarpus zanzibaricus* A. Juss.

- Euphorbiaceae
  - *Acalypha ciliata* Forsk.
  - *Acalypha fruticosa* Forsk.
  - *Croton dichogamus* Pax
  - *Euphorbia systyloides* Pax
  - *Phyllanthus amarus* Schum. & Thonn.
  - *Phyllanthus maderaspatensis* L.
  - *Ricinus communis* L.

- Anacardiaceae
  - *Lannea alata* Engl.
  - *Lannea stuhlmannii* (Engl.) Engl.

- Salvadoraceae
  - *Dobera loranthifolia* (Warb.) Warb. ex Harms
  - *Salvadora persica* L.

- Icacinaceae
  - *Pyrenacantha malvifolia* Engl.

- Sapindaceae
  - *Haplocoelum foliolosum* (Hiern) Bullock

- Rhamnaceae
  - *Ziziphus mucronata* Willd.

- Vitaceae
  - *Cissus rotundifolia* (Forsk.) Vahl

Tiliaceae
Corchorus trilocularis L.
Grewia bicolor A. Juss.
Grewia fallax K. Schum.
Grewia tembensis Fres. var. *kakothamnos* (K. Schum.) Burret
Grewia tenax (Forsk.) Fiori
Grewia villosa Willd.

Malvaceae
Abutilon guineense (Schum.) Bak. f.
Hibiscus micranthus L.
Hibiscus vitifolius L.
Sida cordifolia L.

Sterculiaceae
Hermannia exappendiculata (Mast.) K. Schum.
Hermannia oliveri K. Schum.
Melhania ferruginea A. Rich.
Sterculia africana (Lour.) Fiori
Sterculia appendiculata K. Schum.

Passifloraceae
Adenia globosa Engl.

Thymelaeceae
Gnidia latifolius (Oliv.) Brenan

Rhizophoraceae
Cassipourea malosana (Bak.) Alston

Combretaceae
Combretum aculeatum Vent.
Combretum molle R. Br. ex G. Don.
Terminalia kilimandscaharica Engl.
Terminalia prunioides Laws
Terminalia spinosa Engl.
Vernonia cinerascens Sch. Bip.

Plumbaginaceae
Plumbago zeylanica L.

Loganiaceae
Strychnos spp. material on loan

Apocynaceae
Adenium obesum (Forsk.) Roem & Schult

Convolvulaceae
Astripomoea hyoscyamoides (Vatke) Verdcourt
Ipomoea pestigridis L. var. *longibracteata* Vatke
Impomoea wightii (Wall.) Choisy

Bombacaceae
Adansonia digitata

Boraginaceae
Cordia ovalis R. Br.
Cordia rothii Roem. & Schult
Ehretia amoena Klotzsch
Ehretia teitensis Guerke
Heliotropium eduardii Martelli

Verbenaeceae
Clerodendrum hildebrandtii Vatke
Lantana rhodesiensis Moldenke
Premna oligotricha Bak.
Premna resinosa (Hochst.) Schauer
Premna sp.
Vitex strickeri Vatke & Hildbr.

Labiatae
Aeolanthus repens Oliv.
Basilicum polystachion (L.) Moench.
Hemizygia fischeri Guerke
Hostundia opposita Vahl
Leucas glabrata R. Br.
Orthosiphon parvifolius Vatke
Pycnostachys umbrosa (Vatke) Perk.

Solanaceae
Solanum incanum L.
Solanum sp. near *taitense* Vatke

Scrophulariaceae
Striga asiatica (L.) O. Ktze
Striga latericea Vatke

Acanthaceae
Barleria diffusa (Oliv.) Lindau
Barleria ramulosa C. B. Cl.
Barleria sp.
Blepharis integrifolia (L.f.) E. May.
Crossandra mucronata Lindau
Dyschoriste hildebrandtii Lindau
Justicia flava Vahl
Justicia glabra Roxb.
Pseuderanthemum hildebrandtii Lindau
Thunbergia affinis S. Moore

Rubiaceae
Gardenia sp.
Pentanisia auranogyne S. Moore
Pentas parvifolia Hiern
Psychotria kirkii Hiern
Rytigynia sp.

Compositae
Aspilia mossambicensis (Oliv.) Wild
Brachylaena hutchinsii Hutch.
Haarera alternifolia (O. Hoffm.) Hutch. & E. A. Bruce
Helichrysum glumaceum DC.
Lactuca capensis Thunb.
Microglossa oblongifolia O. Hoffm.
Vernonia cinerascens Sch. Bip.
Vernonia pauciflora Less.

APPENDIX IV

IV.1. Recorded bird species for the Mkomazi Reserve.

Struthionidae
- Ostrich

Podicipidae
- African little grebe

Phalacrocoracidae
- White-necked cormorant
- Long-tailed cormorant

Pelecanidae
- White pelican
- Pink-backed pelican

Ardeidae
- Grey heron
- Black-headed heron
- Purple heron
- Great white egret
- Buff-backed heron
- Squacco heron
- Night heron
- Little bittern

Scopidae
- Hammerkop

Ciconiidae
- European white stork
- European black stork
- Woolly-necked stork
- Open-bill stork
- Saddle-bill stork
- Marabou stork

Threskiornithidae
- Wood ibis
- Sacred ibis
- African spoonbill

Anatidae
- African pochard
- Red-bill duck
- Knob-billed duck
- Egyptian goose
- Spur-winged goose

Sagittariidae
- Secretary bird

Aegypiidae
- Ruppell's griffon vulture
- White-backed vulture
- Lappet-faced vulture
- White-headed vulture

Falconidae
- European lesser kestrel
- Pygmy falcon
- Tawny eagle
- Wahlberg's eagle
- African hawk-eagle
- Martial eagle
- Crowned hawk-eagle
- Long-crested hawk-eagle
- Lizard buzzard
- Black-chested harrier eagle
- Grasshopper buzzard
- Bateleur eagle
- African fish eagle
- Augur buzzard
- Gabar goshawk
- Pale chanting goshawk
- Montagu's harrier
- Harrier hawk

Phasianidae
- Crested francolin
- Scaly francolin
- Yellow-necked spurfowl
- Helmeted guinea-fowl
- Kenya crested guinea-fowl
- Vulturine guinea-fowl

Otididae
- Kori bustard
- Jackson's bustard
- Buff-crested bustard
- Black-bellied bustard
- Hartlaub's bustard
- Crested bustard

Burhinidae
- Spotted stone curlew

Jacanidae
- African jacana

Charadriidae
- Three-banded plover
- Crowned lapwing
- Senegal plover
- Blacksmith plover
- Black-winged stilt

Scolopacidae
- Little stint
- Green sandpiper
- Wood sandpiper
- Greenshank

Glareolidae
- Heuglin's courser
- Bronze-winged courser

Pteroclididae
- Black-faced sandgrouse

Columbidae
- Pink-breasted dove
- Red-eyed dove
- Ring-necked dove
- Laughing dove
- Namaqua dove
- Emerald-spotted wood dove
- Green pigeon

Cuculidae
- Cuckoo
- Red-chested cuckoo
- White-browed coucal

Musophagidae
- Violet-crested touraco
- White-bellied go-away-bird

Psittacidae
- Orange-bellied parrot

Coraciidae
- European roller
- Lilac-breasted roller
- Rufous-crowned roller
- Broad-billed roller

Alcedinidae
- Giant kingfisher
- Brown-hooded kingfisher
- Striped kingfisher

Meropidae
- European bee-eater
- Madagascar bee-eater
- Carmine bee-eater
- Little bee-eater

Bucerotidae
- Trumpeter hornbill
- Black and white-casqued hornbill
- Grey hornbill
- Red-billed hornbill
- Yellow-billed hornbill
- Von der Decken's hornbill
- Jackson's hornbill
- Crowned hornbill
- Ground hornbill

Upupidae
- African hoopoe

Phoeniculidae
- Green wood hoopoe
- Scimitar-bill
- Abyssinian scimitar-bill

Strigidae
- Scops owl
- Pearl-spotted owlet
- Spotted eagle owl

Caprimulgidae
- European nightjar
- Donaldson-Smith's nightjar
- Freckled nightjar
- Gaboon nightjar

Coliidae
- Blue-naped mousebird

Capitonidae
- Brown-throated barbet
- Spotted-flanked barbet
- Red-and-yellow barbet
- D'Arnaud's barbet

Indicatoridae
- Greater honey-guide

Picidae
- Nubian woodpecker
- Cardinal woodpecker
- Bearded woodpecker

Apodidae
- Common swift

Alaudidae
- Singing bush lark
- Red-winged bush lark
- Rufous-naped lark
- Flappet lark
- Fawn-coloured lark

Notacillidae
- African pied wagtail
- Eastern yellow wagtail
- Golden pipit

Pycnonotidae
- Dark-capped bulbul
- White-eared bulbul

Muscicapidae
- Spotted flycatcher
- South African black flycatcher
- Puff-back flycatcher
- Paradise flycatcher

Turdidae
- Olive thrush
- Red-tailed ant thrush
- European rock thrush
- European wheatear
- Pied wheatear
- Capped wheatear
- Cliff chat
- Stone chat
- Red-capped robin chat
- Spotted morning warbler
- White-winged scrub robin
- White-starred bush robin

Sylviidae
- Olivaceous warbler
- European wood warbler
- Red-capped forest warbler
- Crombec
- Grey-backed camaroptera
- Zitting cisticola
- Rattling cisticola
- Winding cisticola
- Tiny cisticola

Hirundinidae
- European swallow
- Red-rumped swallow
- Mosque swallow
- Striped swallow

Campephagidae
- White-breasted cuckoo-shrike

Dicruridae
- Drongo

Prionopidae
- Straight-crested helmet-shrike

Laniidae
- White-crowned shrike
- Long-tailed fiscal shrike
- Red-backed shrike
- Red-tailed shrike
- Slate-coloured boubou
- Black-backed puff-back shrike
- Black-headed bush shrike
- Blackcap bush shrike
- Sulphur-breasted bush shrike
- Black-fronted bush shrike
- Grey-headed bush shrike
- Rosy-patched shrike
- Nicator shrike

Paridae
- White-breasted tit

Oriolidae
  European golden oriole
  African golden oriole
  Black-headed oriole

Corvidae
  Cape rook
  White-necked raven

Sturnidae
  Wattled starling
  Golden-breasted starling
  Red-wing starling
  Fischer's starling
  Hildebrandt's starling
  Superb starling
  Yellow-billed oxpecker
  Red-billed oxpecker

Zosteropidae
  Yellow white-eye

Nectariniidae
  Variable sunbird
  Amethyst sunbird
  Scarlet-chested sunbird
  Collared sunbird

Ploceidae
  Buffalo weaver
  Red-billed buffalo weaver
  White-headed buffalo weaver
  Stripe-breasted sparrow weaver
  White-browed sparrow weaver
  Grey-headed sparrow
  Parrot-billed sparrow
  Yellow-spotted petronia
  Layard's black-headed weaver
  Chestnut weaver
  Black-necked weaver
  Red-headed weaver
  Red-billed quelea
  Cardinal quelea
  Yellow bishop
  White-winged widow-bird
  Green-winged pytilia
  African fire-finch
  Red-rumped waxbill
  Black-rumped waxbill
  Cordon bleu
  Red-cheeked cordon-bleu
  Pin-tailed whydah
  Fischer's whydah
  Paradise whydah
  Broad-tailed whydah

Fringillidae
  Brimstone canary

IV.2. Recorded mammal species for the Mkomazi Reserve.

Taxonomic Name	Common Name
Insectivora	
Macroseelididae	
Elephantulus sp.	Spectacled elephant shrew
Rhynehocyon cirnei	Chequered elephant shrew
Soricidae	
Crocidura sp.	Shrew
Crocidura sp.	Shrew
Chiroptera	
Pteropodidae	
Rousettus angelensis	Rousette bat
Epomopherus sp.	Epauletted fruit bat
Nycteridae	
Nycteris thebaica	Large-eared hollow-faced bat
Hipposideridae	
Hipposideros caffer	Lesser leaf-nosed bat
Molossidae	
Tadarida aegyptica	Mastiff bat
Primates	
Lorisidae	
Galago senegalensis	Bush baby
Cercopithecidae	
Papio cynocephalus	Yellow baboon
Cercopithecus aethiops johnstoni	Kilimanjaro green monkey
Cercopithecus mitis kibonotensis	Kilimanjaro blue monkey

Taxonomic Name	Common Name
Hominidae	
Homo sapiens	Modern man
Pholidota	
Manidae	
Manis temminckii	Ground pangolin
Lagomorpha	
Leporidae	
Lepus capensis abbotti	Abbott's cape hare
Rodentia	
Bathyrgidae	
Heliophobius spalax	Blesmol
Hystricidae	
Hystrix galeata	
Sciuridae	
Paraerus ochraceus	African bush squirrel
Xerus rutibus sativiatus	African ground squirrel
Gliridae	
Graphiurus murinus	African dormouse
Muridae	
Lemniscomys barbarus	Taita striped grass mouse
Lemniscomys griselda	Taita single-striped grass mouse
Mastomys natalensis	Shamba rat
Mus minutoides	Pygmy mouse
Acomys wilsoni	Spiny mouse
Acomys cahitinus	
Gerbillus pusillus	Taita pygmy gerbil
Tatera robusta	Gerbil
Taterillus osgoodi	Gerbil
Carnivora	
Canidae	
Canis familiaris	Domesticated dog
Canis adustus notatus	East African side-striped jackal
Lycaon pectus lupinus	East African wild dog
Otocyon megalotis	East African bat-eared fox
Carnivora	
Mustelidae	
Mellivara capensis sagulata	East African honey badger
Viverridae	
Genetta genetta	Neumann's genet
Civettietis civetta civetta	African civit
Herpestes ichneumon	Greater grey mongoose
Herpestes sanguineus	Lesser mongoose
Helogale undulata	Dwarf mongoose
Munges murgo colonus	East African banded mongoose
Ichneumia albicauda ibeana	East African white-tailed mongoose
Hyaenidae	
Proteles cristatus termes	Masailand aardwolf
Crocuta crocuta	Spotted hyaena
Hyaena hyaena dubbah	Stripped hyaena
Pelidae	
Felis lybica taitae	Taita wild cat
Caracal caracal nuficus	Caracal
Leptailurus serval hindei	Ukamba serval
Panthera pardus fusca	Bengal leopard
Panthera leo massaicus	Masai lion
Acinonyx jubatus	Cheetah

Taxonomic Name	Common Name
Tubulidentata	
Orycteropodidae	
Orycteropus afer	Aardvark
Proboscidea	
Elephantidae	
Loxodenta africana knochenhaueri	East African elephant
Hyracoidea	
Procavidae	
Procavia johnstoni	Rock hyrax
Perissodactyla	
Equidae	
Equus asinus	Domesticated ass
Equus burchellii	Burchell's zebra
Rhinoceratidae	
Diceros bicornis	Cape black rhinoceros
Artiodactyla	
Suidae	
Potamochoerus porcus	Bush-pig
Phacochoerus aethiopicus	Warthog
Giraffidae	
Giraffa camelopardalis	Tanganyika giraffe
Bovidae	
Strepsiceros imberbis	Lesser kudu
Tragelaphus scriptus	Bushbuck
Taurotragus oryx	East African eland
Bos indicus	Domesticated cow
Syncerus caffer	Cape buffalo
Sylvicapra grimmia	Bush duiker
Kobus ellipsiprymnus	Swahili common waterbuck
Redunca redunca	Bohor reedbuck
Oryx beisa	Fringe-eared oryx
Alcelaphus buselaphus	Coke's hartebeest
Oreotragus oreotragus	Klipspringer
Raphicerus campestris	Tanganyika steinbok
Rhynchotragus kirkii	Taita dik dik
Aepyceros melampus	Tanganyika impala
Litocranius walleri	Gereruk
Gazella granti	Grant's gazelle
Capra hireus	Domesticated goat
Ovis aries	Domesticated sheep

IV.3. Size specific weight estimates (kg) for the larger species of the Mkomazi Reserve. Although the values given are less than those generally used in the literature for biomass calculations, they represent the best estimates obtainable from the literature. Values are only given for the size classes used in this work.

Species	Class I	Class II	Class III	Adult Male	Adult Female	Unclass. Adult	Unclass. Age
Buffalo	---	---	---	650	500	575	450
Bushbuck	---	---	---	----	----	----	50
Dik dik	---	---	---	----	----	----	4.5
Duiker	---	---	---	----	----	----	13
Eland	40	90	150	550	425	490	340
Elephant	---	---	---	----	----	----	1725
Gazelle	15	30	40	60	45	50	40
Gerenuk	10	20	25	35	30	32	24
Giraffe	150	300	500	1100	800	950	750
Hartebeest	35	60	90	150	130	140	120
Impala	10	20	35	60	45	50	40
Klipspringer	---	---	---	----	----	----	14
Kudu	20	40	60	100	80	90	70
Oryx	40	80	100	175	160	170	140
Ostrich	10	25	50	135	130	132	75
Reedbuck	10	20	30	60	45	55	40
Rhinoceros	225	500	750	1250	1250	1250	1025
Steinbok	---	---	---	13	13	13	13
Warthog	10	25	40	85	60	70	50
Waterbuck	40	80	120	225	185	205	175
Wildebeest	---	---	---	210	190	200	200
Zebra	50	90	120	260	250	255	200
Lion	30	60	80	150	135	142	120
Hyaena	15	30	50	66	60	63	60
Cheetah	10	20	40	62	55	58	50
Jackal	---	---	---	----	----	----	8
Hunting dog	---	---	---	----	----	----	30