

SOME STRUCTURAL AND FUNCTIONAL ATTRIBUTES
OF A SEMI-ARID EAST AFRICAN ECOSYSTEM

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ABSTRACT

SOME STRUCTURAL AND FUNCTIONAL ATTRIBUTES OF A SEMI-ARID EAST AFRICAN ECOSYSTEM

By

Lawrence Dean Harris

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; 1) dry montane forest, 2) bushed and wooded grassland, 3) seasonally inundated grassland, and 4) bushland. Grass-forb above-ground standing crop values ranged from approximately 600 gm/m^2 in the 500 mm rainfall regions of the bushed and wooded grassland to about 200 gm/m^2 in the 350 mm rainfall regimes of the central-section bushland. Annual above-ground net production was found to vary from about 400 gm/m^2 on previously unclipped plots in the northwest to about 170 gm/m^2 in the

east-central section while denuded plot productivities were about 300 and 150 gm/m² 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/km² (5,548 kg/km²) in the northwest to about 0.5 km² (700 kg) in the central and eastern sections, the dry season densities ranged from 23.7 animals/km² (12,705 kg/km²) to much less than 1/km² in the eastern sections. Seasonal biomass distribution patterns reflect 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 density gradient is nearly extinguished during the wet seasons.

Both spacial 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), wart hog (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). Jackals (Canis adustus) reflected the greatest 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 above-ground primary production (in terms of biomass) was estimated to be channelled through the herbivore-carnivore pathway. The independent effects of elephants, cattle (Bos taurus) and fire on the vegetation are illustrated as are the combined effects of elephants and cattle and herbivores and fire.

SOME STRUCTURAL AND FUNCTIONAL ATTRIBUTES
OF A SEMI-ARID EAST AFRICAN ECOSYSTEM

By

Lawrence Dean Harris

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<u>Species</u>	<u>Number</u>
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impala	2
ostrich	3
steinbok	4
giraffe	5
gazelle	6
wart hog	7
dik dik	8
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19. (cont.)

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gerenuk	11
zebra	12
oryx	13
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rhinoceros	15
reedbuck	16
wildebeest	17
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I N T R O D U C T I O N

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 description, 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 communities.

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 failed 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 1) composition of the biological community; the species, numbers (and thus diversity), biomass, spacial and temporal patterning, and life history phenomena of the component species; 2) the quantity, quality, and distribution of abiotic elements such as water, nutrients, climatic properties, and fire; and, importantly, 3) the gradients of conditions extant in the system.

Systems function 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; 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 inter-relate structure and function since systems structure is 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, they constitute a high proportion of the natural area remaining in Africa today. As such, these lands are economically important to the controlling states because of the great tourist attraction and potential for game utilization. Moreover, they 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.

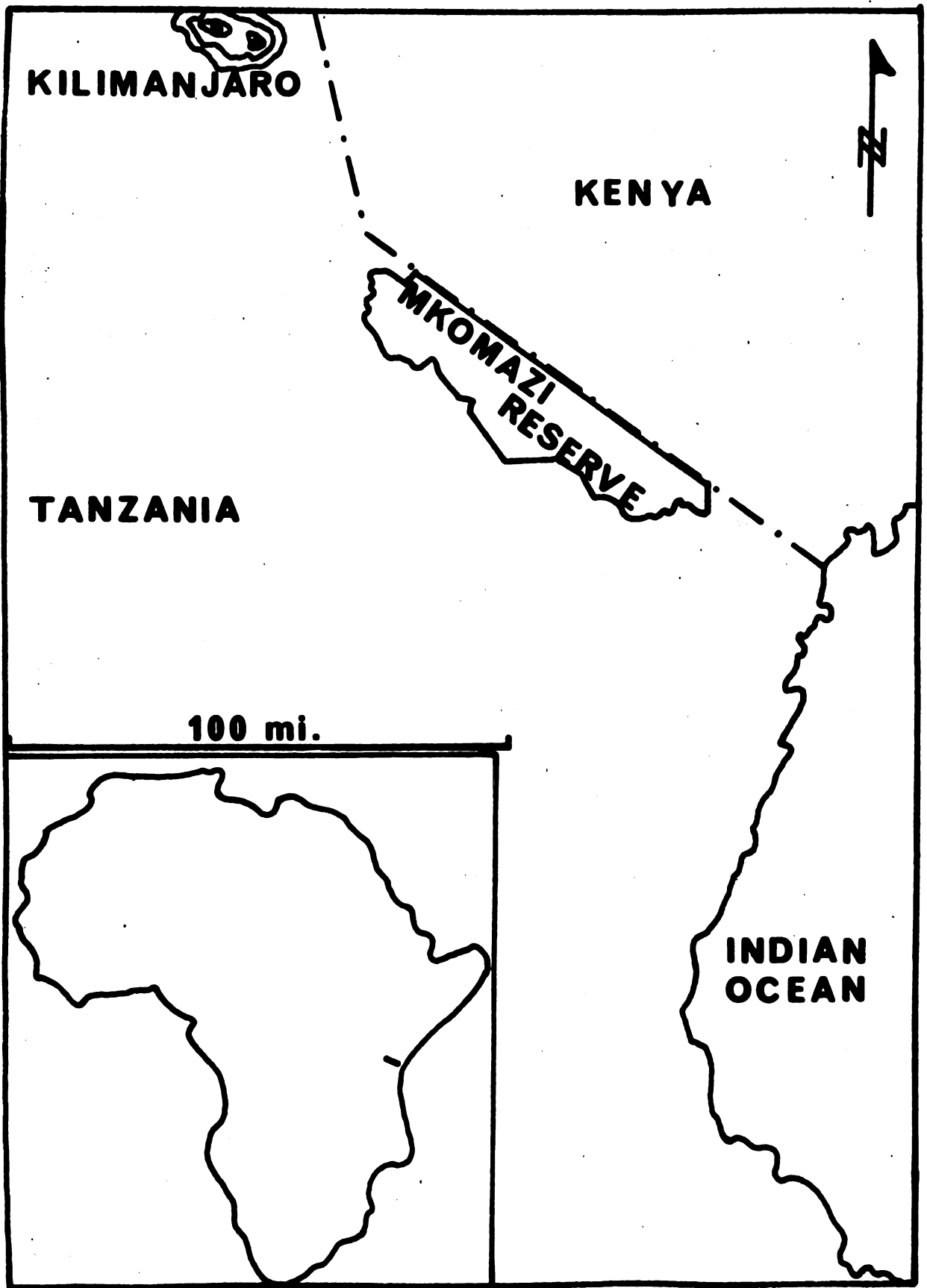
LOCATION AND HISTORY OF THE AREA

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 Uмба River in the southeast, the reserve includes most of the area between the Usambara mountains and the border. More precisely, it lies between $3^{\circ} 47' 30''$ and $4^{\circ} 33'$ south latitude; and $37^{\circ} 45'$ and $92^{\circ} 12'$ east longitude.

The Reserve comprises 3,276 square kilometers 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 the First World War, 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.

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



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, some effort was 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 are 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 jurisdiction and the recommendation of a UNESCO adviser (Huxley 1961) that the Mkomazi area should be included in the park system as a representative semiarid area, the Tanzania Parks administration seems to have given the area low priority for inclusion in the system.

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 meters above sea level and several other peaks exceed 1,225 m. The area covered by these mountains is approximately 130 km², 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 600 m above the plain and approach mountain stature. These hill ranges, grouped in six general masses, occupy an area of approximately 200 km². 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

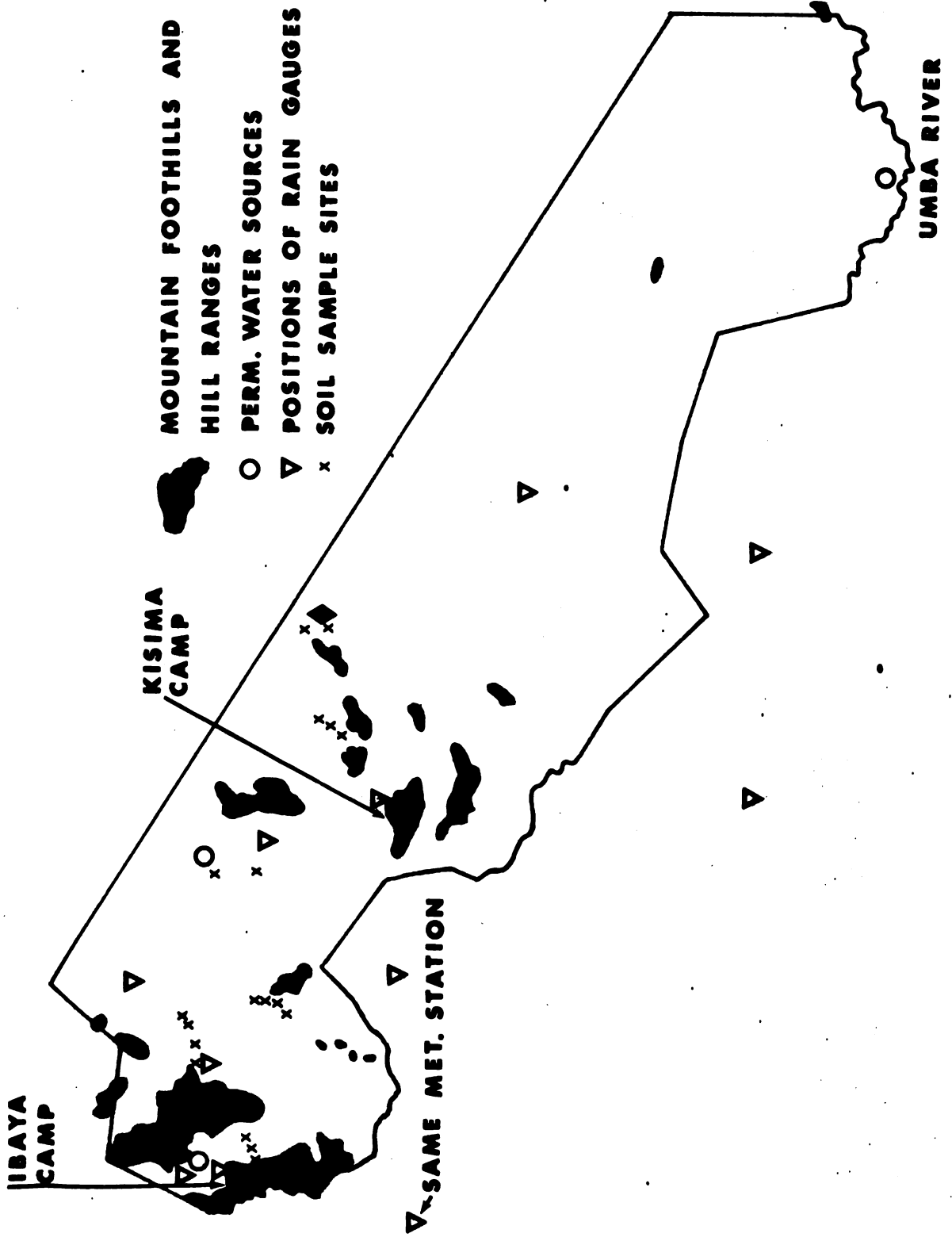
gullies cut and wind their way through the middle of these seasonally waterlogged drainageways. In general the drainageways are directed southeastward, but along the Kenya border they tend to lie in an east-west direction.

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 Uмба Rivers. Since block faulting and tilting movements in the Pare Mountains have created barriers to easterly drainage (Tanganyika Geological Survey 1963), the only naturally-occurring permanent water in the reserve is the Uмба 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 maintains permanent water sources by catching the seasonal runoff (see Figure 2).

The North Pare Mountains are formed of metamorphic rock assigned to the Usagaran system of the Precambrian (Tanganyika Geological Survey 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

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



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 Geological Survey, 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 Geological Survey, 1963).

C L I M A T E

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 Intertropical Convergence Zone (ITCZ), a zone of low pressure at the confluence of the N.E and S.E 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 can not 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 assume 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 75-100 cm isohyet zone. According to the Thornthwaite classification, the area falls within the megathermal

climatic type (A^{*}) with a moisture index (D) of -40 to -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 4 inches above the surface and the surrounding vegetation which might intercept rain was consistently removed. Two gauges (at Ibya 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 Ibya camp in the western end of the reserve (915 m elevation). The thermometers were housed in a standard Stevenson screen which, along with the raingauge, 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 the 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 short-grass prairie around

Maori (20 km further east) received only 40-45 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 raingauges were positioned in the eastern half of the reserve, observations of storm patterns and vegetation conditions suggest a slight increase to 40-45 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, 65 and 66 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, Bradley 1968, pp 174-179).

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.

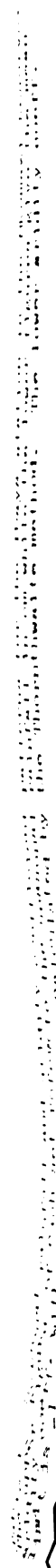


Table 1. Seasonal rainfall and aridity coefficient patterns for the Ibaya station in the Mkomazi Reserve. The upper figure of each set refers to the seasonal rainfall in cm while the lower figures give the mean aridity coeff. with standard error as calculated by the Thornthwaite method. The lower aridity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

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

To substantiate this pattern the long-term data of the outside stations was referred to. But before such reference is valid it must first 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 stations 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 Bindira 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.

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°.

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 hr.) 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 (1965-66) was 23.1° with a mean annual minimum of 17.5° and maximum of 29.0° (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°.

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

In accordance with Chapman's Rule (a change in the mean annual temperature of approximately 6° for each 1000 meters of elevational change, Allee et al. 1949) it is hypothesized that the central section of the reserve averages 2.5° higher and that the eastern end has temperatures about 4° 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/m²/day respectively. The maximal daily values of about 5.7×10^3 , 5.6×10^3 and 5.5×10^3 occur in February while the annual daily minima of about 3.4×10^3 , 3.5×10^3 and 3.6×10^3 Kcal/m²/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 hr 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-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 S E and N E trade winds from the Indian Ocean. The S E trades are more noticeable and normally blow over the area from May to October, whereas the N E trades have only a mild effect from November to May. Significant air movement is usually not initiated until around 1200 hrs., but by 1600 hrs. the winds are considerable and gusts up to 15 Kph: 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 moisture storage and others produces an overall effect which is greater than the sum of the parts (Jowett et al. 1966). For instance,

a week in June with no rainfall is climatologically very different than a similar period in October. Soil moisture 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 classification (1948) 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 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) requires meteorological statistics not commonly available. Furthermore, these equations have also been criticized as inadequate (Holdridge 1967).

In spite of its admitted defects (Thorntwaite and Hare 1965), the Thorntwaite 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-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 ($-.71 \pm .10$) was nearly 50% greater than that of the Ibaya station ($-.49 \pm .14$).

From this I conclude that the general climatic conditions in the center of the reserve are about 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, nearly 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 6 - 8 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 is 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 in the east versus the 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.

S O I L S

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 1962a).

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 1969b, USDA 1960, 1967), and the American 7th Approximation to a Comprehensive Soil Classification System (USDA 1960, 1967) is gaining wide recognition and support (Makin 1969a, 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 Figure 2). All pits exceeded a 3 ft. depth and most were dug to 6 ft. 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 from 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 adsorbed 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). 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, Burt 1942, Morison et al. 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.

Figure 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 are listed in Appendix II.

THE RED AND REDDISH BROWN SOILS

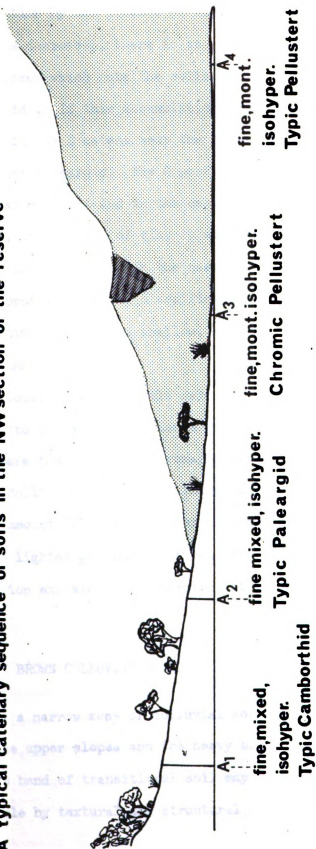
The predominant soils of the Mkomazi are the medium-textured red earths (aridisols) which occupy most hills, ridges and fan slopes, and are characteristic of the freely drained areas (Milne 1936, Dames 1959). Ranging from rather heavy sandy clays to lighter-textured sandy and silty loams they are all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

Figure 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.

A typical catenary sequence of soils in the NW section of the reserve



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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

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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 (200-300 mmh/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 drainage-ways 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 C₁) 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 flocculation 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 A₃, A₄, B₅, and D₃ 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 = 5-6). This was a freely drained profile under short grass prairie and the pH is not unlike that of temperate prairie soils.

The mean total milliequivalents of exchangeable bases per 100 grams (cation exchange capacity) 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 ($\times 1.72$ = organic matter) for all horizons and all profiles of the red soils was $0.45 \pm .05$. There is a significant reduction from the upper horizons ($0.74 \pm .1$) to the lower horizons ($0.21 \pm .03$) 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 $0.098 \pm .000$ while the top 10 cm samples have a mean of $0.14 \pm .05$ and the 30-40 cm horizon has a mean of $0.06 \pm .00$. Although there is not an appreciable change

in the percentage N from red soils high on the slopes to those lower down, the vertisols of the valley bottoms have significantly more ($0.102 \pm .00$) than the aridisols in the upper catenary positions. The carbon/nitrogen ratio of the red aridisols ($7.5 \pm .52$) is also significantly lower than that of the clay vertisols ($12.2 \pm .50$) 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 B₄, 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.

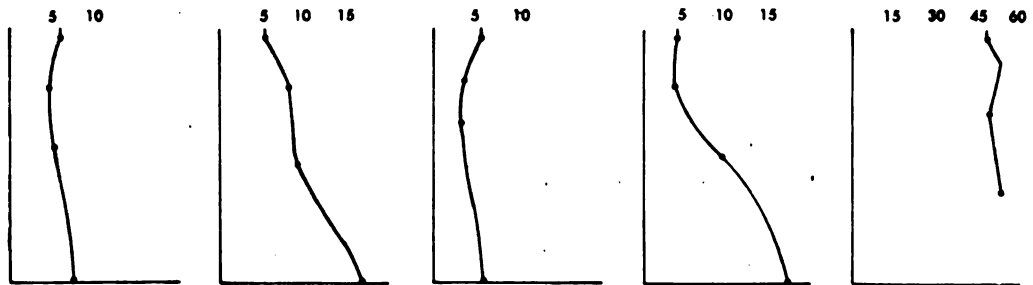
The vertisols of the bottomlands are very rich in total base elements; but as the exchange capacities, base saturations and percentages of organic matter and clay particles increase, so does the

Figure 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 cm while the horizontal axis represents the exchangeable cation level measured as milli-equivalents per 100 gm of soil. The five graphs of each tier correspond to the 5 profiles sampled in the B catena near the Mbula Study area. B₁ was a typical aridisol highest on the slope while B₅ represents the vertisolic clay of the valley bottom.⁵

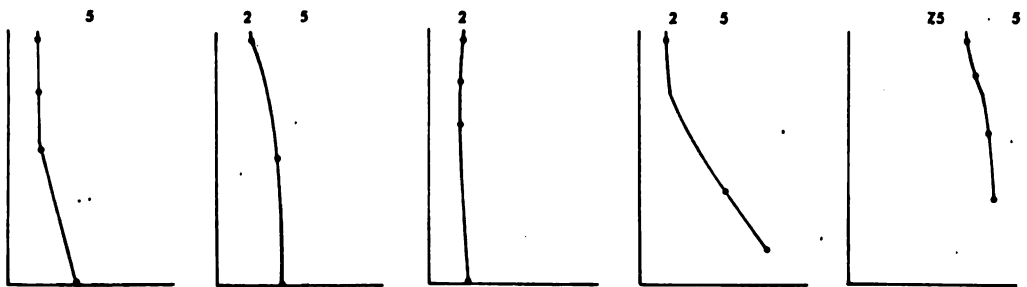
EXCHANGEABLE CATION PROFILES

m.e./100 gm.

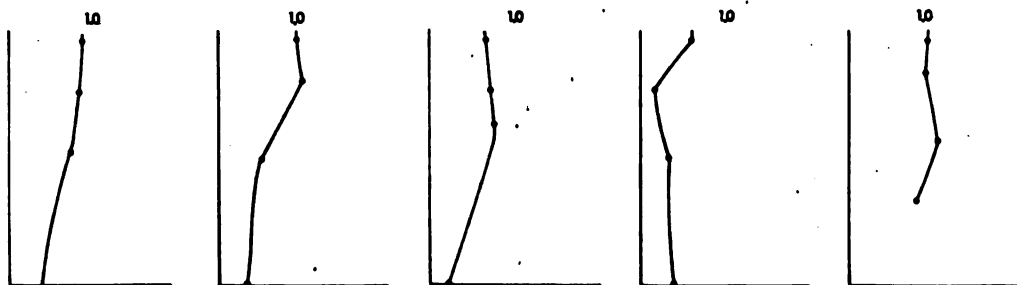
Calcium



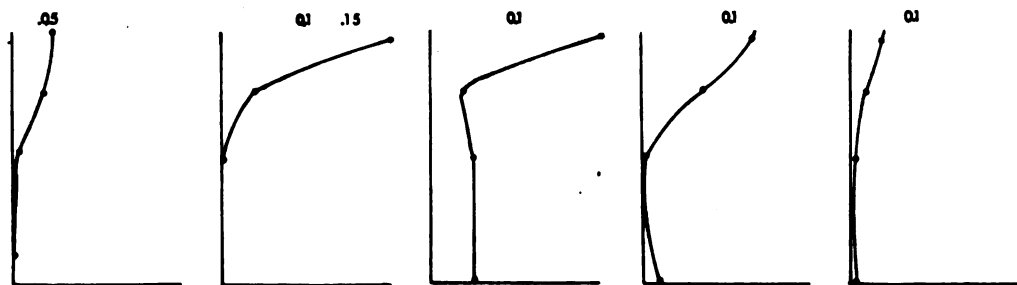
Magnesium



Potassium



Manganese



B1

B2

B3

B4

B5

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 C₂ is restricted to the lower horizon, profile C₁ 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 Mn is generally low (or not measurable as in D₃), 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 1932, 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).

This is neither the place for a detailed probe, nor am I fully qualified to interpret many intricate fertility relationships. But a general discussion is presented relating the results of this study with the overall ecology of the area and with the results of other East African soils work.

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).

As a general condition for East African livestock, Naik (1965) gives minimal levels of calcium and phosphorus as 5 m.e.% and 10 ppm respectively. Based on these levels only two profiles analyzed are deficient in Ca 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 P 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. Semb 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.

Scott (1962b) 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 presumed rainfall gradient as Scott demonstrated for East Africa in general.

Other gradients are more clear: (1) The profile depths of the northwestern foothill area greatly exceed those of the east and (2) the surface hardness and impermeability also increase markedly from west to east. In spite of no consistent gradient in organic matter content, (3) the bushland soils of the east and central sections generally contain less than those of the west. 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. Finally,

(5) 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.

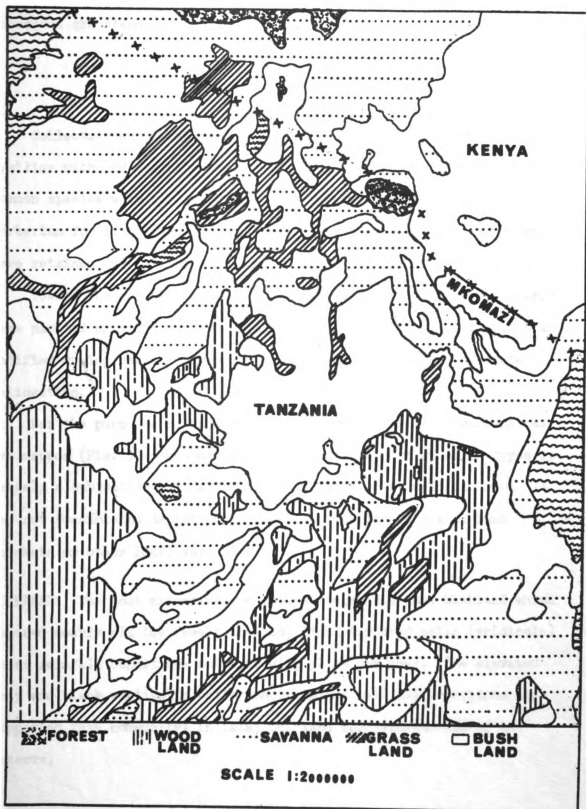
VEGETATION

Several lucid descriptive studies of East African vegetation communities (Shantz and Marbut 1923, Phillips 1929, Burt 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 et al. 1966, and Aubréville 1966), 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 or 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.

Figure 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". Reproduced from the Division of Overseas Survey D.O.S. 299E.



Riparian woodland and dense thicket are interspersed throughout the reserve whereas the heavy clay drainageways support open, seasonally inundated grasslands.

COMMUNITY DESCRIPTIONS

Collection and preservation of plant specimens was done to become familiar with and describe the important species. 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.

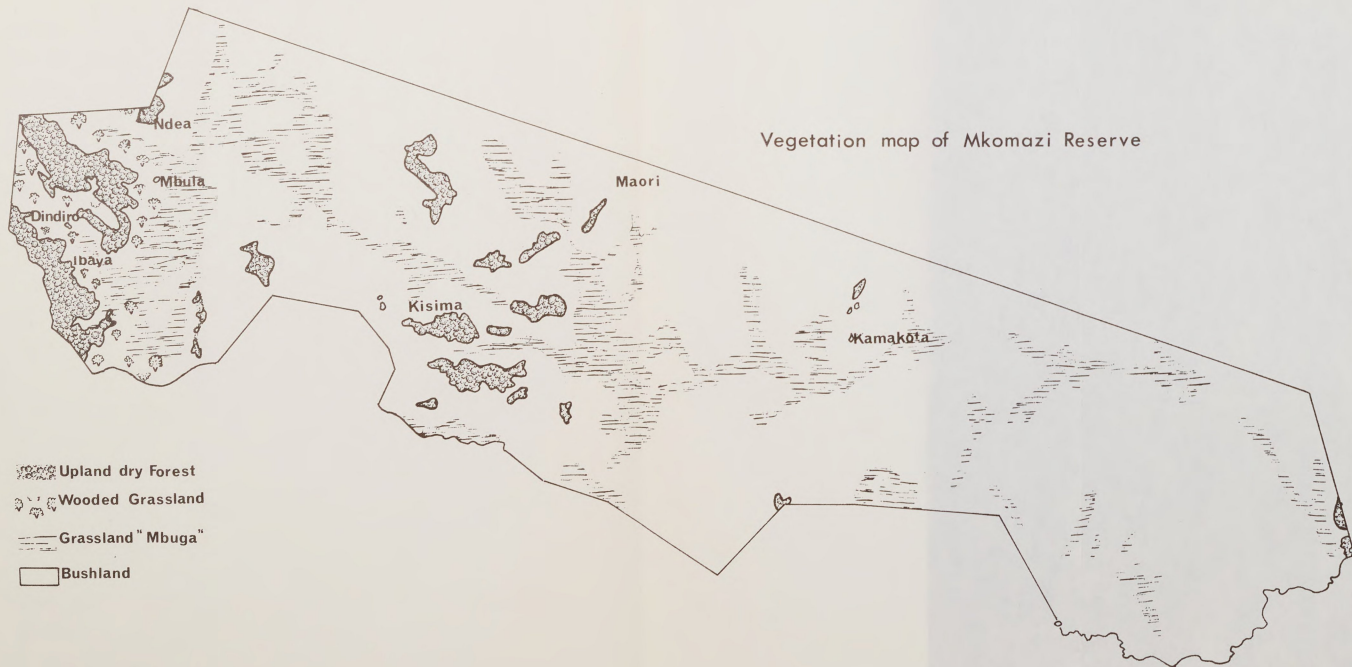
Toward the end of the study community type locations and boundaries were plotted on 1:50,000 maps. These were then reduced to 1:250,000 and modified during aerial surveys of the area to provide more accurate delineation.

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.

Figure 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 follow the distribution of the vertisolic clay drainageways.

Vegetation map of Mkomazi 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) can not stand beneath it. Ground cover exceeds 20%, but is usually less than 40% unless approaching thickets (see Figure 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 Delonix 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 schimperi 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 Hermanaia most frequently seen.

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

Figure 7a. Typical Commiphora schimperi and C. campestris bushland with Cassia spp., Cordia spp. and Grewia spp. sub-dominants in the central section of the reserve.

Figure 7b. A typical association of bushed and wooded grassland (near the Dindira Study Area) in the western end of the Mkomazi Reserve.

Figure 7c. Open Pennisetum 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.



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 10-12 m high (Figure 7b). The more common tree species are Acacia tortilis var. spirocarpa, A. etbaica, A. senegal, Platycephalum 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, partly because of the added runoff water from above. It 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.

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 (Figure 7c). The dominant grass of these areas is Pennisetum mezianum, while other species such as Dicaanthium papillosum, Dactyloctenium aegyptium, Schoenfeldia transiens, Ischaemum afrum, Sorghum verticilliflorum and S. versicolor, Panicum spp. and Bracharia spp. also occur widely.

Open grasslands also appear on the higher, more freely drained fersialitic soils, but usually only as seral stages or fire disclimaxes. These grasslands are very different from the seasonally waterlogged ones; and since they occur locally (e.g. around Maori) among the bush-land 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 15-20 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 dominant the canopy; while Croton dichogamus, Hoslundia opposita, Maerua kirkii, Haplocaelum 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 Figure 6) that this forest type is of considerable extent, in fact, all the closed forests have 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 ground-water 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 Tamarandus indica, Azelia cuanzensis, Newtonia hildebrandtii, Terminalia kilimandscharica, T. prunioides and Zizyphus mucronata while the understory species are commonly Vitex strickerii, Hoslundia opposita, Grewia bicolor, G. villosum, Ehretia taitensis and Haplocaelum foliolosum. All these species seem to provide palatable 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 D₃) 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 above-ground 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. 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 x 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 2-3 m separated the plots from the exclosure wire. Each of the plots was then divided into 12, 4 x 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 above ground standing crop was removed and weighed. Above-ground 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 corrugated 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 above-ground standing crop of the 24 subplots in each exclosure over a 12-month period, the exclosures

were reestablished 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 above ground standing crop on unclipped plots varied between 200 and 600 gm/m² (x 10 = Kg/ha) depending on the month of measurement, but with a growing-season asymptote of slightly less than 600 gm/m² (Fig. 8). This figure fell to approximately 250 gm/m² in the short grass prairie area in the west central section and to approximately 200 gm/m² in the central section.

The cumulative (seasonal) net production on denuded and unclipped plots also follows the same trend. Net above ground production on the denuded plots reached an asymptotic level of about 300 gm/m² in the northwest, approximately 200 in the west-central and only 150 gm/m² in the central section.

Mean daily productivities (monthly accrual/# days) for the different areas, seasons and plots have also been calculated (Table 2). Although short duration daily rates exceeded 6 gm/m²/day in certain plots the overall rainy season mean is $1.93 \pm .30$ gm/m²/day. There is no significant difference between the rainy season daily productivities for the different exclosures nor 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 gm/m² in the three areas from west to east, the respective values for the unclipped plots were approximately 400, 240 and 170 gm/m².

These values are corroborated by the general trend depicted in Table 2. Even though the denuded plots show higher mean daily

Figure 8. Graphs representing the seasonal changes in the above ground grass and forb standing crop (gm/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.

Grassland standing crop and net productivity

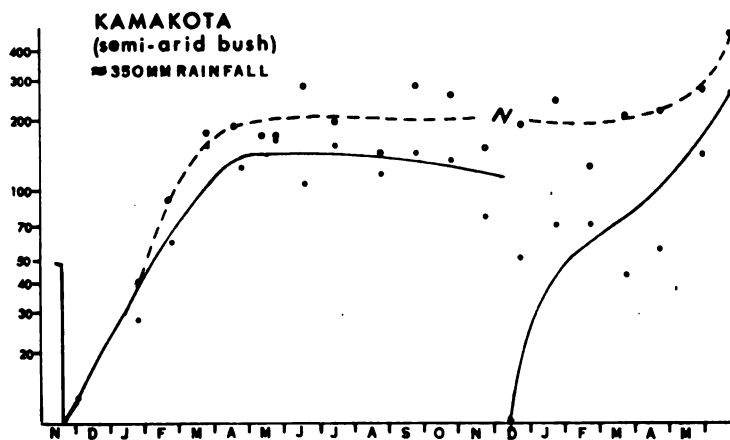
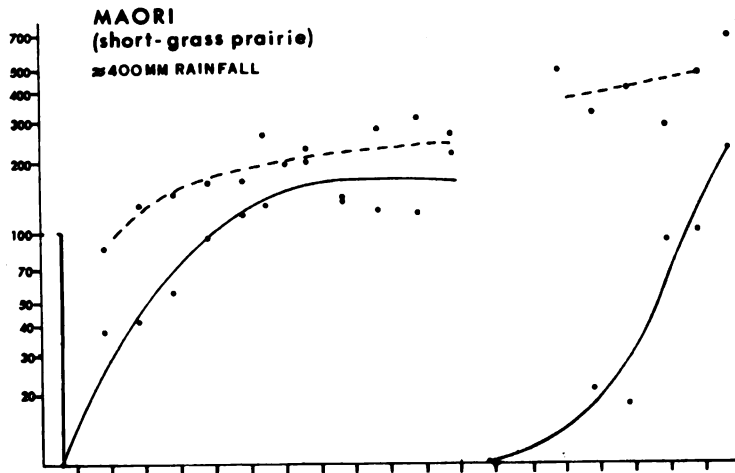
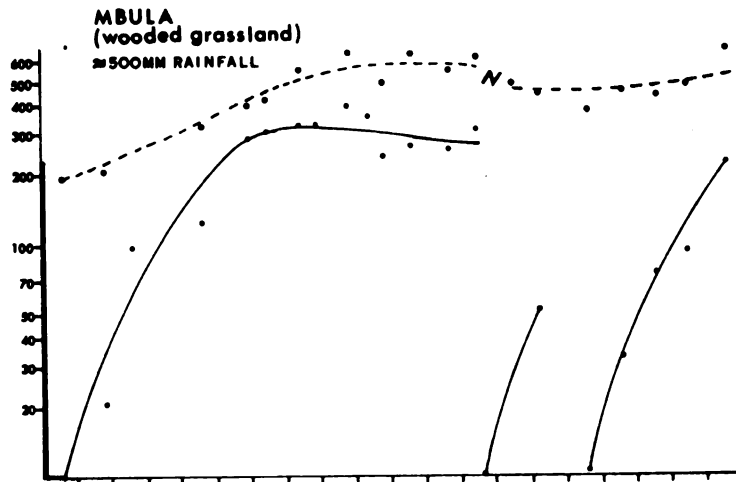


Table 2. Mean daily net above-ground primary production for different seasonal periods, rainfall regimes and clipping treatments. The first area receives about 500 mm of rainfall annually while the second and third receive about 400 and 350 mm respectively. All values are reported as grams/m².

Treatment combination	Seasonal period			
	Nov-Jan	Feb-Apr	May-Jun	Jul-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

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 at the bottom of a small hill (near Kisima) in the west central section.

The asymptotic standing crop of unclipped plots in this area during the growing season was 780 gm/m^2 (± 89.8) while the seasonal productivity reached an asymptote at $415 \pm 26.5 \text{ gm/m}^2$. 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 (Range Analysis Handbook, Region 2, 1968) were utilized. The technique involves using a .75-inch (1.9 cm) diameter

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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 diam.) 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 each from 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 per 100 points.

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

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

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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 over-grazing 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 et al. 1966). From these ratings (excellent, good, fair, poor and v. 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. Because of asynchronous growth patterns of the different species and the inherent inadequacy of a monthly sampling interval, the true seasonal production values are likely to be about 10% greater than seasonal asymptotic values (Weigart and Evans 1964, Golley 1965, Kelly et al. 1969). A crude correction factor of plus 10% may be used if comparison to more accurate estimates by rigorous sampling techniques is desired.

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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 1968a, 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 above-ground 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 et al. 1967). The fact that this effect was not observed under these conditions is of both pragmatic and heuristic interest and is discussed later.

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.

The relationships between the different plant communities and the large herbivores are discussed in the penultimate chapter. However, it is important to stress that primary production per se., or even the

vegetation community structure, does not fully explain the inter-relations with the large herbivores. Grazing and browsing successions do exist (Vesey-Fitzgerald 1960, 1965, Talbot 1963a, 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., Burt 1929, Lawton 1968) and the many alkaloids of the Solanaceae. Whereas species of Solanum are rarely browsed in the neotropics, (D. H. Janzen, pers. comm.) 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.

The effects of fire on the environment are of major concern to range ecologists the world over. I do not propose to discuss the pros and cons of burning rangelands in any detail here and the interested reader should consult the excellent review articles and over 1000 literature citations included by Shantz (1947), Comm. Bur. Past. Res. (1951), Ahlgren and Ahlgren (1960), West (1965), and Daubermire (1968).

Aside from the almost undisputed effect upon bush encroachment there seems to be one other concept 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 about 50-60 cm of annual precipitation there is a positive relationship 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 et al. 1941, Hopkins et al. 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 4 years (Hadley and Kieckhefer 1963). Lay (1956) reported a five-fold increase in dry matter the first year after burning, but this had declined to a two-fold increase by the third year.

Two explanations may account for such a relationship. One, where annual productivity potentially exceeds decomposition, the positive relationship will hold (Olson 1963). Therefore, in the higher rainfall temperate areas it is predicted that there will be a "burning" or "clipping" effect since the removal of standing crop facilitates further production. In the lower rainfall regimes (frequently with concurrently higher temperatures) where decomposition potentially exceeds annual production there will be no clipping or burning effect. Thus in 26 years of annual burning trials in central Kansas, Mc Murphy and Anderson (1963) recorded reduced productivities 16 times. These 16 years of reduced production correlated with the years of below average annual rainfall.

A second, equally plausible explanation, is that a subtle shift from moisture to space limitation occurs as the higher rainfall regimes are approached. 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.

Within the Mkomazi, the effect of fire on bush encroachment is well established (see Figure 22a, p. 148). Furthermore, from the vegetative exclosure experiments it is clear that there was no positive "clipping effect". From this it is concluded that annual fires in the Mkomazi are likely to have a degrading effect on production while a 4-5 year burning cycle may be necessary for bush control and the maintenance of highly diverse vegetation communities.

A N I M A L S

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 (Taurotragus 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 (Panthera 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, Mungos mungo and Ichneumia albicauda), gerbils (Tatera robusta, Taterillus osgoodi), 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 is that of Mackworth-Praed and Grant 1952. The mammal nomenclature largely follows Swynnerton and Hayman 1951 with reference to Ellerman 1940 for rodents and Best et al. 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 species 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 success rates (1-2 per 100 trap nights) suggest that small-mammal densities are very low compared to temperate areas where success rates ten times greater 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. Observations of the greater kudu (Strepsiceros strepsiceros) were made by D. G. Anstey, Game Ranger, in 1952 (Anstey, pers. field notes); and also by the acting warden in official letter no. 451/8/46 of 17 October, 1955. This, along with my finding of a greater kudu horn in the reserve, supports that species' former presence in the reserve.

Both the colobus monkey (Colobus angolensis) and the corcodile (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 km 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 pers. comm.). 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 Uмба 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 is apparently suitable for this species.

NUMBERS, DENSITIES AND BIOMASS

TECHNIQUES

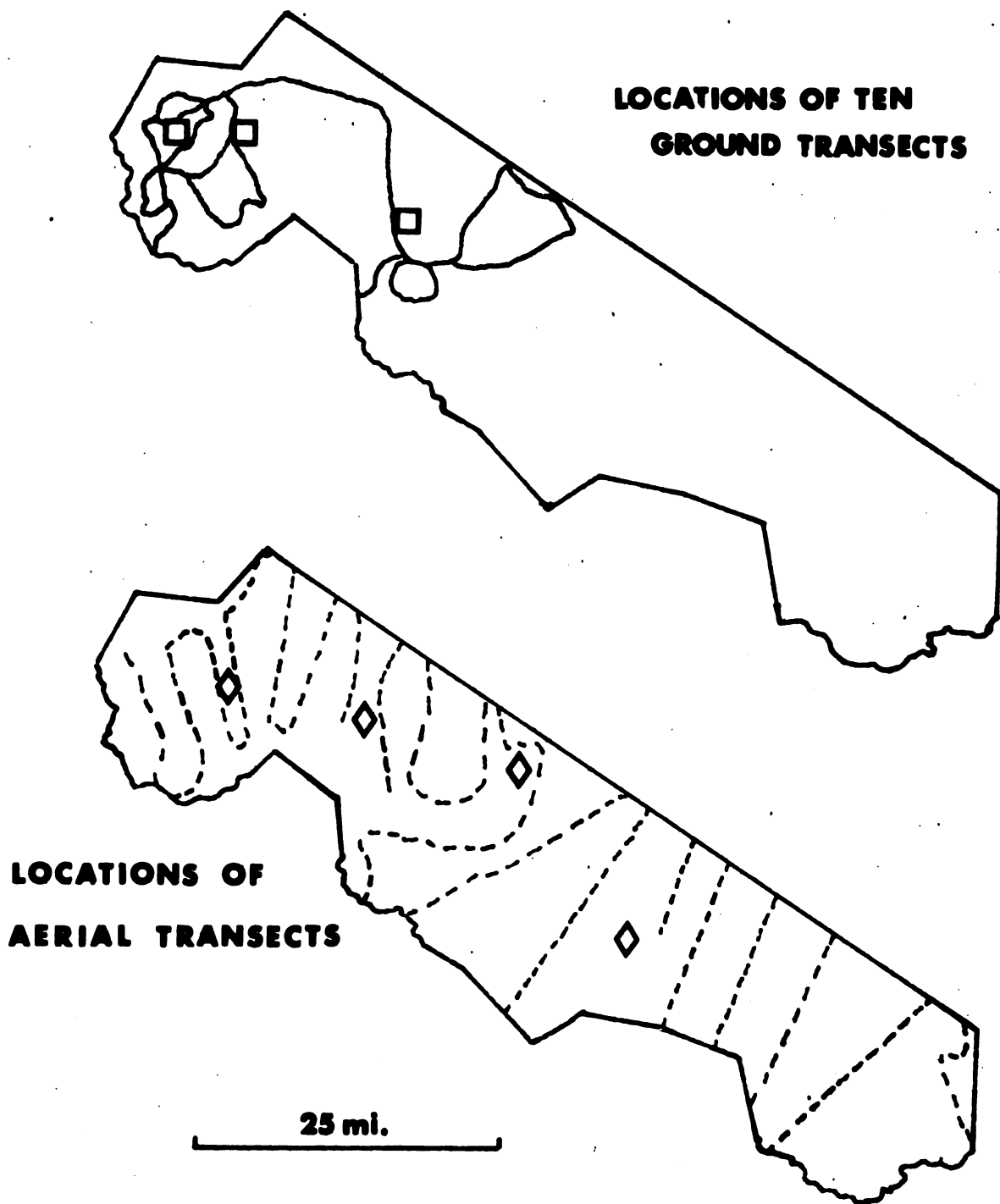
Four techniques were utilized to estimate numbers and densities of the larger mammal species of the reserve. These were: 1) ground transects with associated visibility profiles; 2) aerial transects; 3) demarcated sample study areas; and 4) sight-recording maps for the less abundant species.

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 ten 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 of non-functional transport. In total, 377 counts were conducted along the ten 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, 7x42 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.

Figure 9a. 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. The locations of the three sample plot areas are also depicted by the symbol □.

Figure 9b. 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. Also included are the locations of the four vegetation exclosures for the study of net primary above-ground productivity and standing crop.



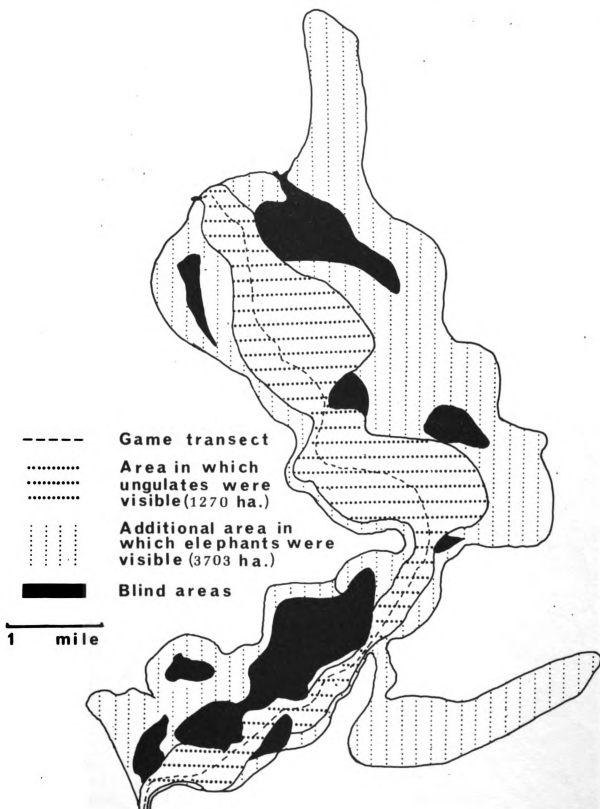
UPPER MAP, □ SAMPLE PLOT AREAS

LOWER MAP, ◇ VEGETATION ENCLOSURES

Visibility Profiles: To convert the number of animals seen to density figures some estimate of the area surveyed was necessary. Visibility profiles (Figs. 10 and 11) 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 obscured 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 wierd-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 water-holes, drainage ditches, rock outcrops, or artificial markers along the reserve boundary. Similar features, as well as peculiar trees,

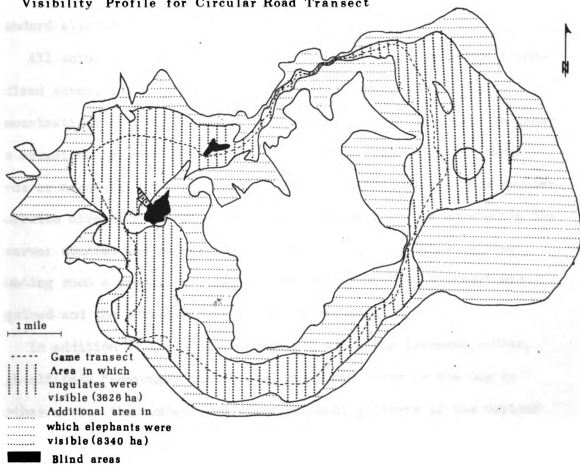
Figure 10. Visibility profile for the Gate-to-Ibaya ground transect. The inner profile was used to estimate the density of the small to medium sized herbivores, while the outer profile of considerably greater extent allowed the calculation of density for the larger species such as elephants and herds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



VISIBILITY PROFILE FOR GATE TO IBAYA TRANSECT

Figure 11. Visibility profile superimposed upon the circular-road ground transect. Again, because of the greater visibility of large species such as elephant, giraffe and herds of eland and buffalo an additional area of visibility was calculated for these species. The expanded area of visibility in the upper left and upper right hand corners resulted from ascending to hill tops during the transect counts.

Visibility Profile for Circular Road Transect



vegetation community boundaries and compass bearings also were used as route markers.

Since the total linear distance of the transects was about 560 km and required a flying time of more than $4\frac{1}{2}$ 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 $1\frac{1}{2}$ hours after sunrise. Flying speed was held constant at 120 km per 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 counter-clockwise 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 can not 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 km² 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. 12). 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.

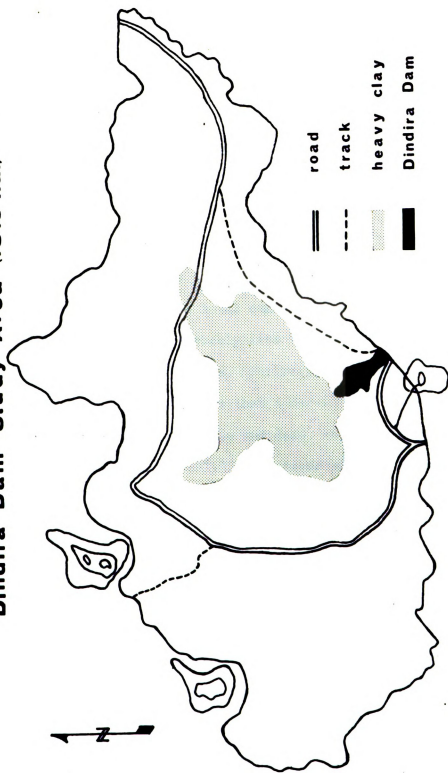
Monthly counts (biweekly for Dindira) of these areas were carried out for over a year using a censusing technique similar to that of Petrides (1956). After initial surveillance, the landrover with observers was driven back and forth over the area at approximately 50 m intervals until it was certain that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

Figure 12. The Dindira Dam Study Area consisted of a 15.1 km 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.

Dindira Dam Study Area (1510 ha.)



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 probably 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.

All weight estimates were taken from the literature. Even though great variation exists between the estimates reported for different areas and by different personnel, it is believed that modal values have yielded a suitably accurate approximation. When several estimates 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) have provided the basis of the weight estimations.

Analysis: Subsequent to the collection of data on standard forms, a tabulated computer codification scheme was established. This 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 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.

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 ran 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 per km² (Table 4). The density decreased rapidly, however, in all directions. Ten km to the south and east the mean annual densities were 7.2 and 6.3 animals/km² respectively. The overall density dropped to less than 6 animals/km² in the west central section and the bushland of the central

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 km of transect while the study plot data represent the mean density per km².

Counting method	Distance from the western boundary in km				
	0-10	10-20	20-40	40-55	55-80 80-125
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		

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 range from less than 1 to about 3.5 animals per km^2 (Table 5). The densities for all species combined ranged from dry season values of 23.7/ km^2 around the permanent water of the northwest to 3.4 in the west-central and much less than 1/ km^2 in the eastern sections (Table 5).

Absolute numbers: Estimates of the absolute numbers of large animals present in the reserve (Table 6) were deduced from a synthesis of:

1) the monthly totals observed from the aerial surveys and sight recording maps; 2) extrapolations from seasonal mean densities for the different habitats and areas; 3) long term sight records of relatively short-ranging species such as rhino and waterbuck; and 4) empirical knowledge resulting from over 5000 hours of field observations in the area. Even though approximate, a high degree of confidence is attached to these estimates.

Elephants were the most numerous animals (Table 6) while hartebeest, buffalo, impala and eland followed in that order. No other non-migratory 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 kg 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

Table 5. Numbers and biomass per km² 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	12705.2	1451.5	260.6	2081.6	3637.6	751.6

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

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. 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 et al. 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 representing the mean biomass per Km^2 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 treated 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 3-dimensional space. It will take the form of:

$$\hat{Y} = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \epsilon$$

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 % 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. 13), cubic (Fig. 14), quartic (Fig. 15), etc.] the greater will be the % variation explained by the equation (X and Y with their powers and products). The % 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.

To evaluate the hypotheses that there was: 1) a dominant east-west biomass gradient; 2) a subdominant north-south gradient, and; 3) a

Figure 13.

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 (0-9) depicts an arbitrary density isopleth whose value in kg/km^2 is given as "Ref. con." along with the plot. Density isopleths (contours) denoted by numerals (0-9) represent values higher than the reference contour; explicitly an increase in density by the stated interval 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 $30 \text{ kg}/\text{km}^2$ 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 $3 \text{ kg}/\text{km}^2$). Therefore the band or contour of 1's represents an isopleth of density between 33 and 36 kg per 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 example, 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 18-21 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 2nd 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.

QUADRATIC RESPONSE

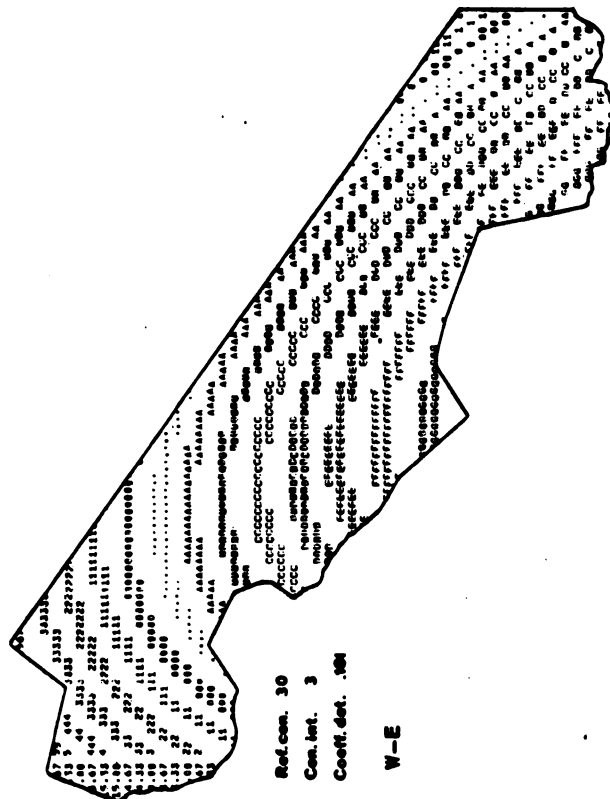
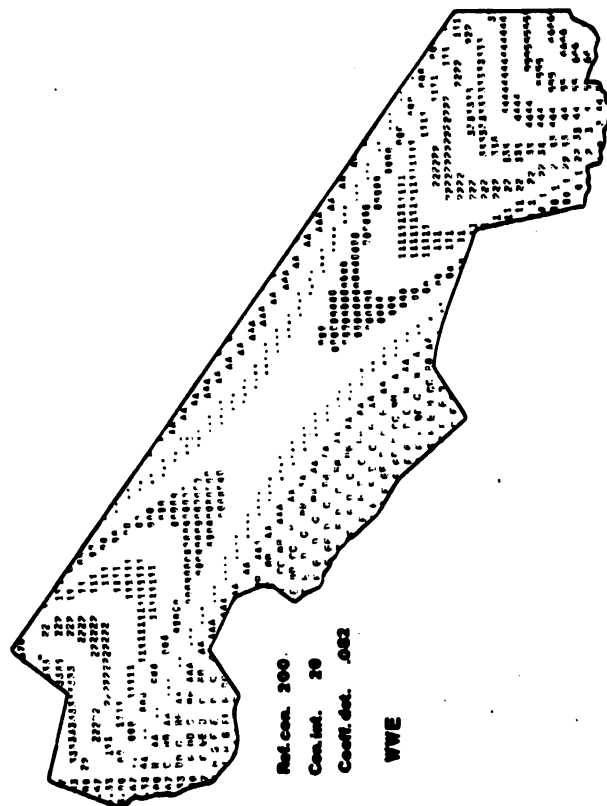
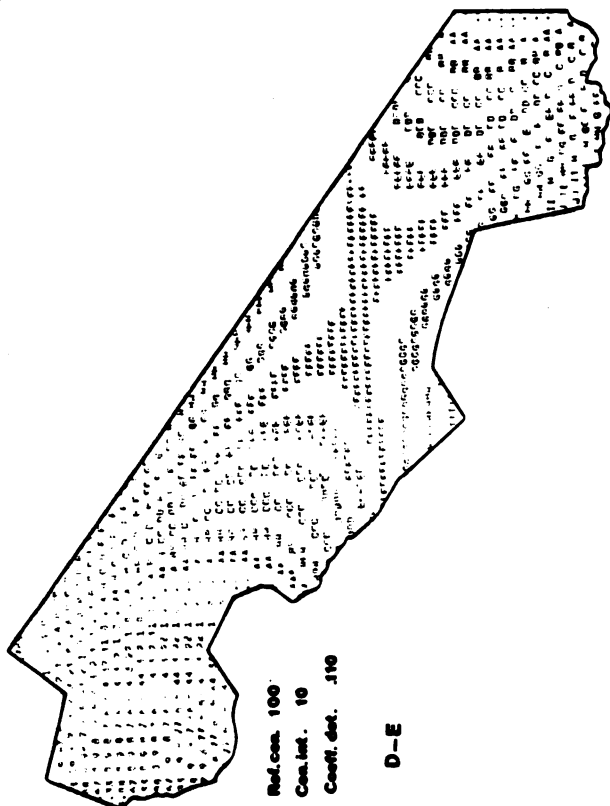
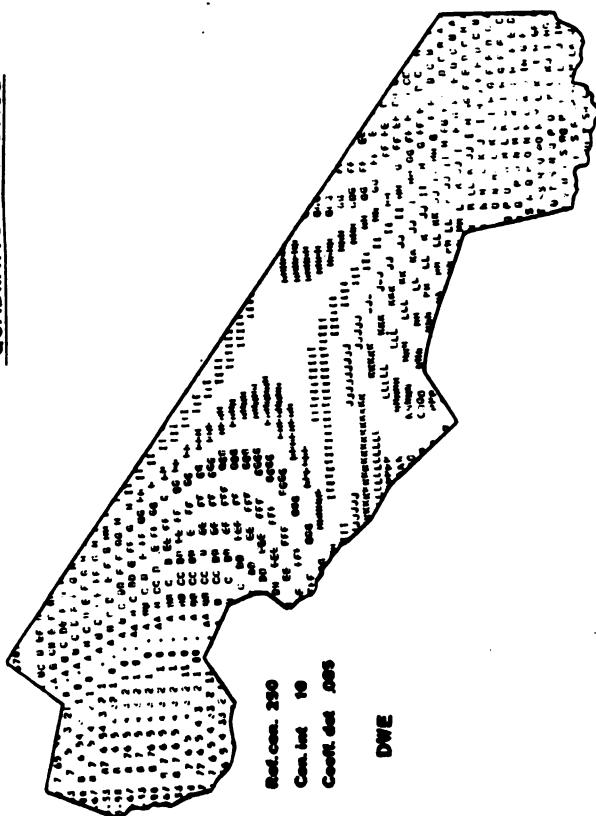


Figure 14. Cubic response surfaces derived from the 3rd order least-squares regression equation of biomass density on location. The data are the same as those used in Fig. 13, but the higher order equation allows a "better fit". Thus, here, 20% of the variation in wet season non-elephant biomass (W-E) is explainable by location.

CUBIC RESPONSE

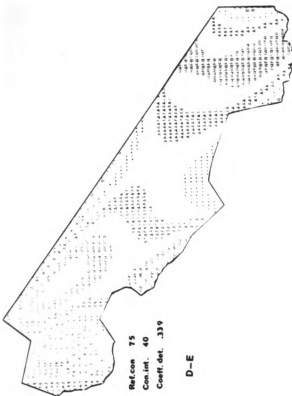
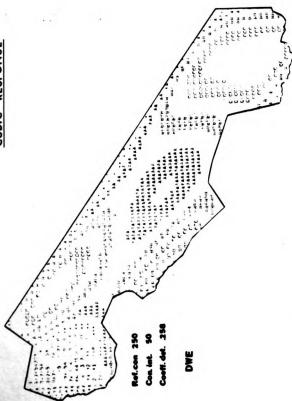
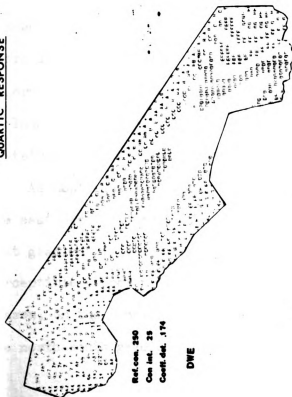
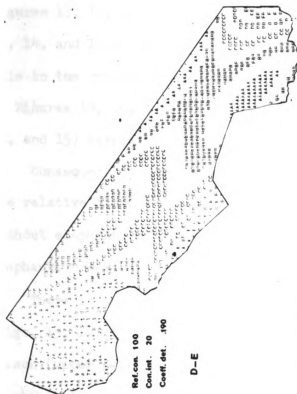


Figure 15. Fourth degree response surface resulting from the multiple regression analysis of large herbivore biomass density on the x, y location in the Mkomazi Reserve. The data are the same as those used for the quadratic and cubic responses. The least squares regression equation from which these results were obtained is of the form: $\hat{y} = \theta_0 x_0 + \theta_1 x_1 + \dots + \theta_n x_n + \epsilon$. 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.

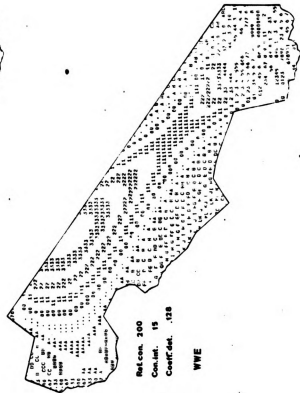
QUARTIC RESPONSE



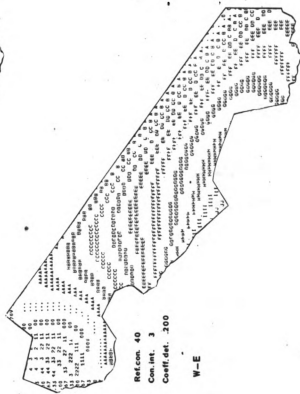
DWE



D-E



WWE



W-E

significant difference between the wet and dry season densities, two analyses were required. That is, a wet season plot (lower pair of Figures 13, 14, and 15), and a dry season plot (upper pair of Figures 13, 14, and 15). But since elephants were known to play an important role in the overall biomass pattern, analyses including (left-hand pair of Figures 13, 14, and 15) and excluding (right-hand pair of Figures 13, 14, and 15) 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).

There is indeed an east-west biomass gradient within the reserve (Figs. 13, 14, 15). 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 elephant biomass changes the picture completely. 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. 13, 14, 15). 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, Figs. 13,

14, 15). 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 the linear multiple correlations between density and location was not significant. In all cases, the multiple correlation ($\sqrt{\text{coeff. det.}}$) became highly significant at the 2nd (Fig. 13), 3rd (Fig. 14), and 4th (Fig. 15) 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 2nd order equation (quadratic response, Fig. 13) 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 3rd degree response (Fig. 14), between 12.8 and 20% of the variation is explainable by the x, y location. The percent variation explained by the 4th degree response (Fig. 15) is generally greater than 25, and about 34% of the variation in the dry season biomass of herbivores other than elephants is accounted for.

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/km² for the Dindira study area during the dry season (Table 5, P. 89), the mean annual biomass for the same area was 5548 kg/km². The mean annual standing crops for the Mbula (semi-permanent water) and the Mzara (seasonal water) study areas were 1934 and 707 kg/km² 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 2000 kg/km²; at 15 km from the permanent water the mean annual density fell to about 1000 kg/km².

The mean annual biomass over the entire area of the reserve was about 1200 kg/km². This amount is equivalent to 0.7 elephants/km², and in the eastern half of the reserve elephants make up over 90% of the total biomass. Therefore over a vast area (approximately 750 km²) all other herbivores combined sum to only about 150 kg/km². This is approximately equal to 1 oryx per km².

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 of animals 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. 16), a significantly nonrandom ($P < .05$) time trend was evident. These monthly totals are also significantly, but negatively, 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 of elephants were characterized by aggregates of many herds moving as a unit. An eastern population of about 1500 elephants migrates northward across the international boundary during the drier months (Harris 1968, Watson et al. 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 congregate in the mountain foothills within range of Dindira Dam. The migrants move into the Lake Jipe area of Tsavo

Figure 16. 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 two-month running mean. The correlation between the "unsmoothed" numbers and the aridity coefficient was highly significant ($P = .02$) and the monthly numbers of animals seen was significantly nonrandom ($P < .05$).



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 is 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 6-10 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.

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 the pooled wet and dry season means as well as 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 175-300 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 Kande 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-February 1965, 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 1200-1600; and, judging from their temporary absence elsewhere, they consisted of animals from both the

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. (* = Sig. at $P = .05$, *** = $P = .001$).

Dindira Dam Mbula Mzara
(Permanent H₂O) (Semi-permanent H₂O) (Seasonal H₂O)

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	<u>d.f.</u>	<u>M.S.E.</u>	<u>F</u>
Study area	2	553.4	10.8***
Seasons	1	223.2	4.4*
Interaction	2	921.0	18.1***
Error	33	51.0	

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 Figs. 13, 14, 15). 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 Figs. 13, 14, 15) and the mean biomass for the entire reserve rises to 1925 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, Figs. 13, 14, 15).

But of equal importance is the liberation of the other herbivores from the constraints of the dry season water source in the western end. The fact that this occurs was demonstrated by the highly significant interaction effect of areas x seasons (Table 7, P. 106) 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, Figs. 13, 14, 15). From this it is 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 it 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 wholly 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, P. 62; Figure 18b; Hemingway et al. 1966). At a recommended stocking rate of 6 ha per beast (McKay 1968, Hemingway et al. 1966) the southern border areas were estimated to be 15-20 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 et al. (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 elephant on the part of hunters and grazers in the eastern half of the reserve. Elephants have also shyed away from those areas of the Mkomazi in which substantial culling operations were undertaken in 1968 (Barry Turner, Pers. Comm.)

These observations are summed up as follows. Although zebra, oryx and gazelle co-inhabit 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 2-3 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 zero animals per km².

Elephants, on the other hand, do utilize the bushland along the Umba and since 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 (1963), Stewart and Zaphiro (1963), Talbot et al. (1965), and Pienaar 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 (C: 24,000 kg/km² 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 10-fold increase from only a few hundred kg/km² in the drier areas (Stewart and Zaphiro 1963) to several thousand under higher rainfall conditions (Potts and Jackson 1952, Talbot 1963). 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.

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 3000 during certain rainy seasons and even during the driest months they numbered in the hundreds.

Table 8. Comparative large herbivore densities (no./km²) and mean annual standing crop biomass (kg/km²) for different bushland areas of East Africa.

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

* The estimated weights used here are considerably less than those generally used elsewhere.

The mean annual number of cattle supported within the reserve was estimated to be $1500 \pm 10\%$. Using a mean population weight estimate of 225 kg (Deans et al. 1968), 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 per km² (1 per mi²) 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/km². 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.

C O M M U N I T Y S T R U C T U R E

Tropical ecosystems 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 commonly ascribed to the wet tropics, East African ecosystems reflect the same high species diversity; and because of the array of large animals, they have gained considerable notoriety.

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, Connell 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, Krauk and Turner 1969, Mitchell et al. 1965, Hirst 1969). Darling (1960) has described other aspects of the ecological separation of the large ungulates and the work of Lamprey (1963) provides still farther 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. 17). 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 constituency 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.

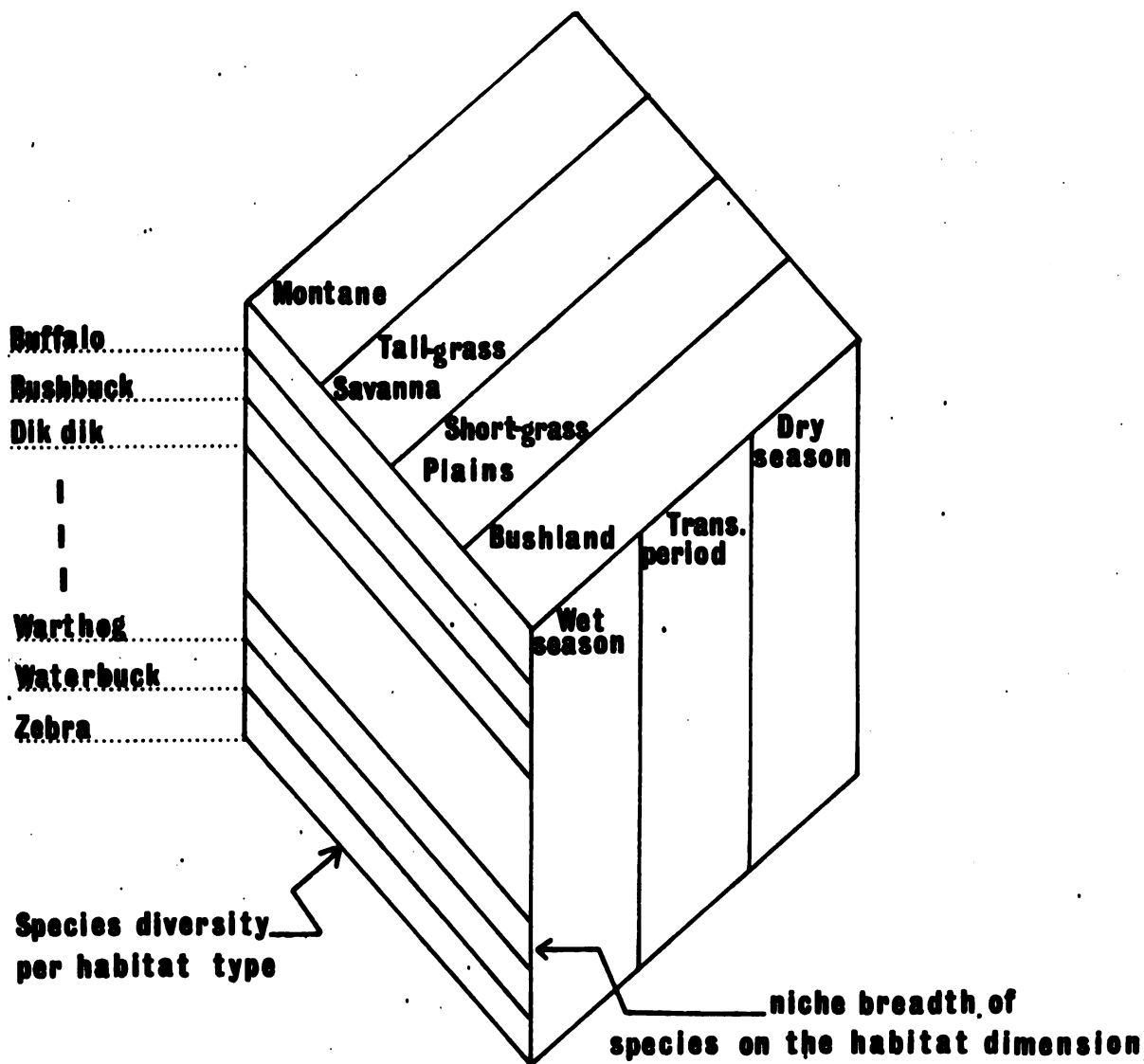
Clearly, the number of resources (dimensions) upon which a species' specificity could be evaluated is very large. This line of reasoning soon leads to the Hutchinsonian concept of each species occupying an n-dimensional hyperspace (Hutchinson 1957, 1965).

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

Figure 17. 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 $\log B' = -\sum P_i \log P_i$ (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).



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. 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 et al. 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:

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

Where P_i = the proportion of the total elements (individuals in this case) which occur in the i^{th} 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 $P_i = \bar{x}n_i / \sum \bar{x}n_i$ where N_i = the number of the i^{th} species occurring in each game count along a 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. 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). But theoretical consideration of the "clumped" distribution of biomass units and other aspects (Valiela, in prep.) may negate the validity of using biomass proportions in the standard information equations. Nonetheless, the mean individual biomass diversities for the various habitats were:

montane	$0.50 \pm .00$
bushland	$0.74 \pm .10$
open grassland	$1.18 \pm .22$
wooded grassland	$1.31 \pm .00$

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 greatly disparate distribution of the large species between the habitats, the difference between the numeric and biomass values would have been large.

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 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 tend to reflect the opposite response. The monthly values calculated for the entire reserve show a marked decrease during several rainy periods. Undoubtedly this was due to the ingress of large numbers of elephant and the consequent shift in biomass proportions.

NICHE BREADTH -- HABITATS

Whereas the concept of the ecological niche is old (Grinnell 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 organisms 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 $\bar{X}_i / \sum \bar{X}_i$ 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), wart hog (3.22), giraffe (3.11) and elephant (3.09) while the five most restricted species were bushbuck (1.22), duiker (1.63), buffalo (1.74), wildebeest (1.75) and reedbuck (1.97).

NICHE BREADTH -- TIME

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

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 $\log P_i = -\sum P_{ij} \log P_{ij}$ (see text for terminology).

niche breadth on four habitat types (1x4)		niche breadth on three seasons (1x3)	
rhinoceros	(3.42)	eland	(2.988)
eland	(3.31)	gerenuk	(2.975)
wart hog	(3.22)	reedbuck	(2.974)
giraffe	(3.11)	giraffe	(2.973)
elephant	(3.09)	wart hog	(2.953)
gerenuk	(2.92)	rhino	(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)

Only patterns applicable to the reserve as a whole can be described here. 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. 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 the various habitat types, the relative proportion of times a species was observed in the various habitats may be used as 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. 18). Since the observations are here categorized into four major habitat types, 25% of all observations would be expected for each habitat type if no affinities or preferences were operative. 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.

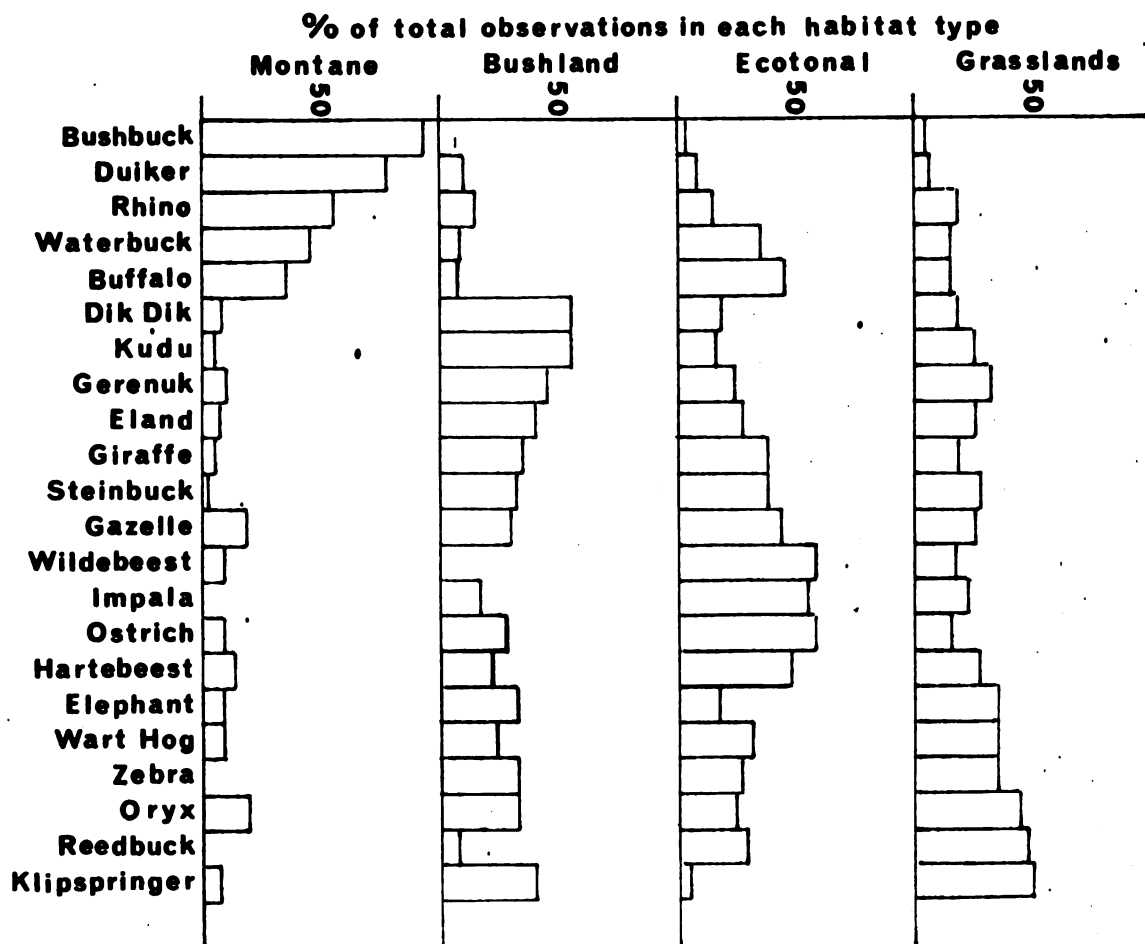
Five of the 22 species (bushbuck, duiker, rhinoceros, waterbuck and buffalo) were observed in montane or riparian forests greater than 25% of the time. Three of these species (bushbuck, duiker and rhino) occupied these environs the majority of the time.

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 ($\geq 40\%$) for bushland but were not recorded there a majority of the time.

Nine species; eland, elephant, gerenuk, hartebeest, kudu, oryx, reedbuck, wart hog 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,

Figure 18. 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 (lower left) to those which were observed most frequently in grasslands of varying types (upper right).



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 and the high incidence of tied observations, standard correlative techniques are 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). 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 $\sum x_i = X$.

Similarly, when the total observations of a second species are appropriately categorized, the number in each category is denoted y_i and

that total observations of species 2 is 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:

$$R_o = \frac{\sum (X_i + Y_i) \log (X_i + Y_i) - \sum X_i \log X_i - \sum Y_i \log Y_i}{(X + Y) \log (X + Y) - X \log X - Y \log Y}$$

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 x 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. 19).

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.

Figure 19. 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.

Species	Number
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

SPECIES

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1	1																									
2	.86	1																								
3	.84	.82	1																							
4	.80	.80	.72	1																						
5	.85	.81	.83	.72	1																					
6	.83	.77	.83	.75	.75	1																				
7	.76	.77	.68	.68	.76	.62	1																			
8	.72	.64	.67	.59	.74	.66	.61	1																		
9	.68	.69	.62	.51	.71	.68	.46	.54	1																	
10	.65	.59	.58	.50	.73	.63	.50	.56	.78	1																
11	.80	.60	.62	.59	.63	.63	.55	.66	.55	.57	1															
1	.72	.60	.62	.53	.69	.79	.52	.54	.69	.74	.50	1														
13	.61	.51	.61	.57	.67	.68	.61	.69	.57	.60	.58	.78	1													
14	.69	.63	.53	.29	.69	.50	.42	.62	.53	.61	.49	.43	.49	1												
15	.74	.66	.52	.41	.67	.53	.45	.35	.51	.69	.35	.50	.34	.40	1											
16	.77	.75	.54	.48	.66	.53	.46	.33	.39	.52	.34	.38	.26	.40	.71	1										
17	.70	.64	.44	.27	.53	.51	.20	.04	.47	.63	.05	.49	.12	.04	.46	.43	1									
18	.64	.57	.40	.29	.48	.39	.32	.34	.42	.66	.33	.48	.34	.34	.45	.34	.35	1								
19	.54	.48	.35	.29	.42	.35	.26	.23	.40	.52	.22	.44	.24	.27	.57	.51	.74	.44	1							
20	.53	.45	.38	.32	.46	.35	.37	.28	.36	.67	.27	.41	.34	.26	.46	.30	.20	.61	.38	1						
21	.60	.59	.07	.14	.31	.25	.22	.23	.28	.39	.24	.20	.41	.55	.14	.13	.04	.38	.19	.23	1					
22	.40	.23	.18	.12	.26	.12	.18	.10	.21	.51	.05	.24	.10	.15	.47	.25	.11	.54	.30	.67	.13	1				
23	.84	.82	.70	.60	.73	.76	.59	.43	.65	.68	.53	.74	.62	.29	.39	.29	.32	.51	.51	.40	.01	.01	1			
24	.78	.74	.53	.50	.56	.40	.44	.35	.53	.60	.41	.60	.49	.31	.36	.41	.40	.48	.53	.38	.39	.20	.66	1		
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	
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

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 0.861 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 Figure 19). Jackal manifested the highest degree of association between a carnivore and the herbivores mentioned 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 can not be definitely established 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 preceeding chapters emphasis has been placed on the description of abiotic and biotic components of the ecosystem. The purpose of the present chapter 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. When the observations can be more discretely classified into vegetation subtypes such as tallgrass, drainageway, bushed and wooded grass, and shortgrass; the description of habitat preferences and ecological separation will 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 roxberghiana 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 more 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 short grass plains and that the bushland is least productive of all (see Figure 8 p. 58). 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 cellulose and lignin. 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) 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 ECOSYSTEM AS A WHOLE

The onus of the ecologist is the integration of seemingly disjunct facts, figures and empirical knowledge into a coherent whole. This whole 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 autecologist or even 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 performs 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 9): Four species also accounted for between 44 and 96% of the total biomass.

Since maintenance and sustained work metabolism appear to be linear functions of the basal metabolic costs of homeothermic animals (Brody 1945, Kleiber 1961, Hemingsen 1960 in Lamprey 1963), an index to community metabolism is derivable from the mean weights of the species involved. Even though the standard metabolic function $70 \text{ kg}^{.75}$ (Maynard and Loosli 1956, National Academy of Sciences 1966) may underestimate the true fasting catabolism of indigenous East African ungulates

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). *, 2% contribution by zebra; **, 4% contribution by eland.

Species	% mean				% mean				% mean			
	annual number	Mzara	Mbula	entire res	annual biomass	Mzara	Mbula	entire res	annual metabolism	Mzara	Mbula	entire res
buffalo	45			12	48			9	49			10
elephant	9	8		25	38	61		72	32	50		67
gazelle		7	28								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		*			**			11	
total con- tribution of 4 spp. (%)	88	83	91	61	93	92	66	90	92	89	73	87

(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 9). This is further corroborated by the species-specific productivity estimates which are not finalized 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. 20).

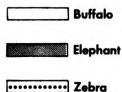
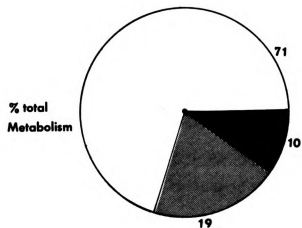
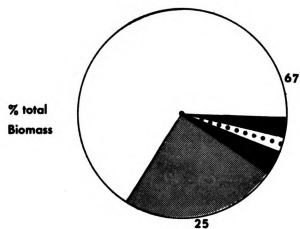
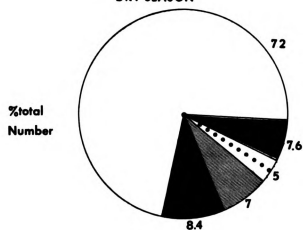
Buffalo completely abandon this area during the wet season and impala replace them as an integral species. Along with elephant and hartebeest they constitute approximately 90% of the total numbers and biomass while processing 93% of the energy flow.

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 must be that of signal processors or controllers for the system. Chew and Chew (1970)

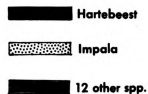
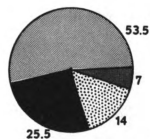
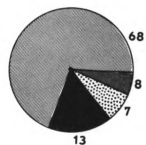
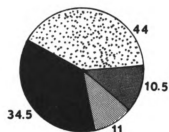
Figure 20. Mean seasonal species contribution to the numbers, biomass and large herbivore metabolism of the Dindira Study Area in the western end of the Mkomazi Reserve. Although the dry season biomass density of animals was approximately three times as great as the wet, the dry season biomass density was over six times that of the dry. 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.

DINDIRA STUDY AREA

DRY SEASON



WET SEASON



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 system'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 serves as the ultimate control on the herbivores (Errington 1963, Buckner 1966, Hirst 1969).

Ranging from nearly imperceptible homeostatic effects under "normal" conditions (Vesey-Fitzgerald 1960, 1963, Paine 1966, Paine and Vada 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 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 degradation) 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 experi-

mentation 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 $1/\text{km}^2/\text{yr}$ 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. 21a). 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 of the Mbaramu-Umba River; 15 km.) has been subjected to intense cattle grazing for over a decade. In the southern border areas, there is essentially no game ($<100 \text{ kg}/\text{km}^2$) 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, p. 62; Fig. 21b; Hemingway et al. 1966), while there has been no apparent degrading effect on the woody vegetation (Fig. 21b). It is therefore concluded that the "cattle-effect" is largely limited to the grass-forb component of the vegetation.

Figure 21a. 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 than 2 weeks time. In no area free from cattle grazing was there any substantial degradation of the grass-form component of the vegetation by elephants or other indigenous herbivores.

Figure 21b. 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 km² along the south-central and eastern boundaries of the reserve are overgrazed to the extent shown.



In the east-central section of the reserve (around Kamakota) the annual density of both cattle (1 cow/3-4 ha) and elephants (1.0/km²) 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. 21b).

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. 22a).

The combined effects of cattle, elephants and fire on the vegetative component of the system 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. 23). Matched photographs were taken in 1967 after 10 years of the combined effects of fire and elephant usage (right hand column, Fig. 23). 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 implication should be obvious; if the bushed and wooded grassland structure is to be maintained, fire, elephant, and possibly other herbivore management will be required.

Figure 22a. 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.

Figure 22b. 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.



Figure 23. 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.

**Vegetation changes surrounding an
artificial water supply from 1957 to 1967**



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, p 106). 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 (10-15 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

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year. The "coincidence" of these patterns seems almost teological and is deserving of further appraisal.

The alternative hypothesis of competitive exclusion in certain areas but not in others is only testable by evaluating the interspecific competition coefficients derived from a system of Lotka-Volterra equations. 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 herbivore component in most temperate regions (Odum et al. 1962, Golley 1960, Chew and Chew 1970, Slobodkin et al. 1967). Petrides and Swank (1966) estimated that 9.5% of the available net production in a small area of Queen Elizabeth Park, Uganda was consumed by elephant 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 crudely estimate the food intake per ruminant stock unit in the Mkomazi Reserve. The standard maintenance diet for range cattle is estimated to be about 20 lb. of air dry forage per day for a 1000 lb. range cow (Stoddart and Smith 1955). This makes no allowance for growth and reproduction, however, and therefore 25 lbs. (11.3 kg) per stock unit/per day is used here. From this it is estimated that the mean annual standing crop of herbivores on the Dindira Study area ($5,548 \text{ kg/km}^2$) would consume 50,447 kg of air dry forage per year. The estimated net annual production of this area is about $3 \times 10^5 \text{ kg/km}^2$ 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 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 herbivores is likely to raise the percentage utilization to at least 17.5%. This is a substantially greater amount than reported for temperate areas.

The idea that a greater percentage of the total energy 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 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 et al. 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 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 can not be overemphasized.

In conclusion, the interrelations of the various system components can not 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/m²/yr. 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 Mn is localized in the upper few cm of the soil profile and is likely to be deficient in several Na-saturated vertisolic soils. Mn 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 condition 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 time 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.

S U M M A R Y

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 55-60 cm in the northwest to only 35-40 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 gm/m² in the higher rainfall areas of the northwest to approximately 170 gm/m² 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/km² while that of the central and eastern sections drops to about 1000 kg/km². 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 five-fold, 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, wart hog, 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 wart hog 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 80-90% of the total numbers and biomass and 85-90% 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 16-18 "nondominant" large herbivores accounted for only 10-15% 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 ecological systems, 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 was 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.

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APPENDIX

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--June, 1967.

Station									Month
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	Jun 1
						.0	.0	.0	Jul 9
						1.0	1.5	1.3	Aug 6
		.0	.0	.0	.0	.0	.3	.3	Sept 5
		.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 1
.0	.0	5.1	6.3	5.1	1.0	2.8	.5	1.5	Jun 9
.8	.5	.0	.8	.0	.5	.0	.0	.0	Jul 6
.0	.5	.8	.0	.0	.0	.0	.0	1.0	Aug 6
.0	.0	.2	.0	.8	.0	.0	.0	.7	Sept
.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 1
.5	5.1	4.1	4.1	5.3	10.2	8.6	7.9	1.8	Mar 9
21.8	12.4	29.5	7.9	32.5	13.5	20.3	20.3	18.0	Apr 6
10.7	9.1	8.1	6.4	7.9	18.3	16.0	16.8	18.0	May 7
1.3	1.0	1.0	1.5	1.3	.0	.8	.5	.8	Jun
36.6	29.4	49.6	22.9	54.4	50.6	73.9	64.5	40.9	

APPENDIX I

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	1965	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
Jun.	26.58	25.36	18.75	15.65	22.69	20.53
Jul.	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

APPENDIX I

I. 4. Monthly absolute maxima, minima and the absolute temperature range recorded during 1965-66 at the Same Meteorological Station ($^{\circ}\text{C}$).

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
Jun.	29.30	28.30	12.21	13.59	17.1	15.3
Jul.	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 16:00 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
Jun.	63	96	33	44	46	58
Jul.					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

APPENDIX I

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. 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
KAMAKOTA	MAORI	MZARA	NDEA	MBULLA	TEBAYA	SAME	
					.75		Mar
					.88	.70	Apr
					.42	.66	May
					.83	1.0	Jun 1
					1.0		Jul 9
					.86	.88	Aug 6
		1.0	1.0	1.0	.97	.97	Sep 5
		1.0	1.0	1.0	.80	.71	Oct
		1.0	.78	1.0	.46	.21	Noc
		1.0	0.0	+ .05	.13	.41	Dec
1.0	.84	1.0	.76	.81	.77	.75	Jan
.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
1.0	1.0	1.0	.57	.91	.95	.86	Jun 9
.93	.95	.93	1.0	.95	1.0	1.0	Jul 6
1.0	.95	1.0	1.0	1.0	1.0	.91	Aug 6
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
1.0	1.0	1.0	.50	.34	+ .53	.81	Feb 1
.95	.65	.72	.62	.23	.41	.86	Mar 9
+ .56	.06	.40	+1.51	+ .08	+ .62	.45	Apr 6
.15	.27	.49	.35	+ .59	+ .42	.92	May 7
.89	.91	.87	.89	1.0	.95	.97	Jun

APPENDIX II

II. 1. A listing of the Mkomazi soils as classified by the American 7th approximation to a comprehensive soil classification system (U.S.D.A. 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

III. 1. 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 lommellii Mez
Bothriochloa glabra (Roxb.) A. Camus
Bothriochloa radicans (Lehm.) A. Camus
Brachiaria defloxa (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.) Schweick.
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 Leake
Rhynchelytrum repens (Willd.) C. E. Hubb.
Rhynchelytrum setifolium (Stapf) Chiov.
Rhynchelytrum villosus (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 bulbosus 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 aequinoctiale (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 sp.

Polygonaceae

Oxygonum sinuatum (Meisn.) Dammer

Amaranthaceae

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

Aizoaceae

Gisekia pharnaceoides L.

Portulacaceae

Calypotrothea taitensis (Pax & Vatke) Brennan
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 melanoxydon Guill. & Perr.
Erythrina sp.
Indigofera schimperi J. & S. var. *baukeana* (Vatke) Gillett
Indigofera spinosa Forsk.
Indigofera zenkeri Bak. f.
Indigofera sp.
Lonchocarpus ericalyx 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 ugwenensis 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.

Thymelaeaceae

Gnidia latifolius (Oliv.) Brenan

Rhizophoraceae

Cassipourea malosana (Bak.) Alston

Combretaceae

Combretum aculeatum Vent.
Combretum molle R. Br. ex G. Don.
Terminalia kilimandscharica 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

Verbenaceae

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. nr. *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

Aspilium 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.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 buck

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 owl
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 fly-
catcher
Puff-back flycatcher
Paradise flycatcher

Turdidae

Olive thrush
Red-tailed ant thrush
European rock thrush
European wheatear
Pied wheatear
Capped wheatear
Cliff chat
Stonechat
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
Pint-tailed whydah
Fischer's whydah
Paradise whydah
Broad-tailed whydah

Fringillidae

Brimstone canary

APPENDIX IV.2.

Recorded Mammal Species

for the Mkomazi Reserve

Insectivora

Macrosepididae

Elephantulus sp.

spectacled elephant shrew

Rhynchocyon 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

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
Hystriidae	
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
Lycan 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 margo colonus	East African banded mongoose
Ichneumia albicauda ibeana	East African white-tailed
	mongoose

Hyaenidae

Proteles cristatus termes
Crocuta crocuta
Hyaena hyaena dubbah

Masailand aard-wolf
spotted hyaena
striped hyaena

Pelidae

Felis lybica taitae
Caracal caracal nuficus
Leptailurus serval hindei
Panthera pardus fusca
Panthera leo massaicus
Acinonyx jubatus

Taita wild cat
caracal
Ukamba serval
Bengal leopard
Masai lion
cheetah

Tubulidentata

Orycteropodidae

Orycteropus oper

aard vark

Proboscidea

Elephantidae

Loxodonta africana
knochenhaueri

East African elephant

Hyracoidea

Procavidae

Procavia johnstoni

rock hyrax

Perissodactyla

Equidae

Equus asinus
Equus burchellii

domesticated ass
Burchell's zebra

Rhinocerotidae

Diceros bicornis

Cape black rhinoceros

Artiodactyla

Suidae

Potamochoerus porcus
Phacochoerus aethiopicus

bush-pig
warthog

Giraffidae

Giraffa camelopardalis

Tanganyika giraffe

Bovidae

Strepsiceros imberbis
Tragelaphus scriptus
Taurotragus oryx
Bos taurus
Syncerus caffer
Sylvicapra grimmia

lesser kudu
bushbuck
East African eland
domesticated cow
Cape buffalo
bush duiker

Kobus ellipsiprymnus
Redunca redunca
Oryx beisa
Alcelaphus busclaphus
Oreotragus oreotragus
Raphicerus campestris
Rhynchotragus kirkii
Aepyceros melampus
Litocranius walleri
Gazella granti
Capra hireus
Ovis aries

Swahili common waterbuck
Bohor reedbuck
fringe-eared oryx
Coke's hartebeest
klipspringer
Tanganyika steinbok
Taita dik dik
Tanganyika impala
Gereruk
Grant's gazelle
domesticated goat
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
wart hog	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

