FEEDING STRATEGIES AND FORAGING IMPACT OF NON-MIGRATORY AFRICAN ANTELOPE

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FEEDING STRATEGIES AND FORAGING IMPACT OF NON-MIGRATORY AFRICAN ANTELOPE

By

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ABSTRACT

FEEDING STRATEGIES AND FORAGING IMPACT OF
NON-MIGRATORY AFRICAN ANTELOPE

By

Michael Joseph Kutilek

The feeding strategies of non-migratory antelope and their impact upon the forage were studied at Lake Nakuru National Park, Kenya, from late 1972 to mid 1974. The main large-mammal species in the park were defassa waterbuck, *Kobus defassa*, impala, *Aepyceros melampus*, bohor reedbuck, *Redunca redunca*, and Thomson's gazelle, *Gazella thomsonii*. These were found to practice a seasonal grazing rotation among six distinct forage habitats: marsh, moist-site grassland, alkaline grassland, dry-site grassland, grass-shrub and open woodland.

The dry-site grassland was heavily grazed by all four antelope species during the moist and wet periods. During the long dry period a divergence in habitat selection occurred as each of the antelope species showed preferences for two or more of the remaining five forage habitats. Each forage habitat had alternate periods of use and recovery which, under the existing circumstances, seemed beneficial to plants and herbivores alike. Non-migratory antelope evidently are successful because, on an annual basis, they find and utilize a wide range of food resources.

In the Lake Nakuru area, habitat diversity seems to be dependent upon alkalinity and moisture gradients in the soil resulting from

lacustrine influences. It is likely that the abundance of animals in this region is dependent on the presence of the lake as it affects and diversifies the vegetative habitat.

A comparison among four large-mammal ecosystems showed no clear-cut relationship between the number of large-herbivore species present and the proportion of vegetation consumed. It seems that, in some cases at least, the foraging impact of a few generalists can be similar to that of many specialist species.

Plant-animal interactions are also important from the management standpoint, since the park is threatened with overpopulation and overgrazing by the antelope. The recent addition of land, however, has apparently been beneficial to large mammals by including more of the habitats they use within the park. A comprehensive monitoring program is needed to assess the continuing impact of the expanding large-mammal populations on their environment. The dry-season forage habitats, which are small in size, are particularly vulnerable and should be protected from unsound development, tourist misuse and excessive overgrazing. It is suggested that on small land areas where sufficient habitat diversity exists, non-migratory antelope may have value in meat production schemes.

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In Kenya, I thank the Trustees of National Parks and the Director, Dr. Perez Olindo, for allowing and encouraging the study. I am also grateful to the Warden of Lake Nakuru National Park, Mr. Joseph Mbrugu, to the Assistant Warden, Mr. Arthur Mahasi and to the rangers and staff all of whom went out of their way to help me on numerous occasions.

The identification of plant specimens was carried out quickly and efficiently by the East African Herbarium. Other logistical assistance in Kenya was provided by Mr. and Mrs. Wayne Jarvi, Mr. and Mrs. Ian Marshall, Mr. and Mrs. John Hopcraft, Mr. and Mrs. George Stevenson, Mr. Ellis Monks and Dr. E. Voreski. My thoughts concerning the Nakuru National Park ecosystem were broadened by stimulating discussions with David Western, Chris Griffin and Marvin Pistrang.

I am greatly indebted to the U. S. Peace Corps and to its former Kenya Director, Robert K. Poole, for providing my initial introduction to wildlife ecology and conservation in Kenya. My work as a Peace Corps biologist from 1969-1971 provided a background for the research reported here.

At Michigan State University, I was supported by a tuition scholarship and by assistantships through the Department of Fisheries and Wildlife and the Office of Academic and Student Affairs in the College of Agriculture and Natural Resources. Funds for the field work were furnished by the Foreign Area Fellowship Program of the Social Science Research Council. The opinions expressed in this thesis and the errors, however, are entirely my own.

Finally, I am especially indebted to my wife, Anne, who has given so much and given up so much, during the course of this work.

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INTRODUCTION

East Africa is noted for its diversity and abundance of large mammalian herbivores. Talbot (1963) divided these animals into two major categories: migratory, in which the home range is large, and non-migratory, in which the home range is small.

Both groups are subject to rainfall patterns which are highly variable and seasonal (Thompson, 1965; Griffiths, 1972). Under this regime, the nutritional quality of many forage species varies greatly with the precipitation (Dougall et al., 1964; Lawton, 1968; Field, 1971). Ungulate migrations seem to be a response to water availability and forage quality (Bourliere and Hadley, 1970; Pennycuick, 1975). Migratory animals, therefore, appear to satisfy their nutritional needs by moving over great distances to the best quality of food resources available at any given time of the year. Moreover, migratory species feed upon a narrow range of forage components, i.e. on only a few forage species (Talbot and Talbot, 1963) or on a specific growth stage or stratum of vegetation (Vesey-Fitzgerald, 1960; Gwyne and Bell, 1968; Bell, 1971).

But what of non-migratory antelope? Faced with fluctuating climatic conditions, how do they satisfy their nutritional needs while restricted to small home ranges? Talbot (1963) suggested that non-migratory antelope are mixed feeders, eating different food resources during different seasons. Supporting evidence for this, however, has been lacking. Furthermore, if non-migratory antelope are mixed feeders, would this be compatible with the viewpoint that a large number of herbivore species will consume more of the total vegetation than will a few species (Talbot and Talbot, 1963; De Vos, 1969)? Or, would several species of generalized feeders remove as much forage as many species of specialists?

This study, therefore, tested two hypotheses: (1) that non-migratory antelope are successful because they find and utilize a wide range of food resources; and (2) that a greater proportion of the vegetation is consumed where many species of large herbivores are present.

A research program was carried out from September, 1972 through May, 1974 in Lake Nakuru National Park, Kenya. This area had only a few antelope species present in abundance, and all of these were non-migratory. The hypotheses were tested by determining the daily and seasonal forage utilization patterns of the antelope and by estimating the primary and secondary production parameters which were compared with other published results.

Finally, there is a threat of overpopulation and overgrazing by antelope in this national park (Kutilek, 1974). From a pragmatic standpoint, this study provides a data base for future management decisions and an assessment of the impact of large herbivores on their environment.

STUDY AREA

Lake Nakuru National Park is located in the Rift Valley Province of Kenya, East Africa (Figure 1) between $0^{\circ}18'$ and $0^{\circ}29'$ south latitude and $36^{\circ}02'$ and $36^{\circ}08'$ east longitude. It was first proclaimed a national park in 1961 but did not receive protection until 1968 when a warden and ranger force established a permanent headquarters. At that time, the park consisted of the lake (42 km^2) and a narrow strip of land (21.5 km^2) surrounding it (Figure 2). In early 1970 the park took administrative possession of an additional 3.6 km^2 of land south of the lake. By 1973 the World Wildlife Fund had raised money to purchase 148.8 km^2, including the 1970 acquisition. Annexation of this land was underway but not finished during the time this research was in progress. When annexation has been completed, the land area will be 170.3 km^2 and the total Park area about 212.3 km^2.

The park is surrounded by agricultural and urban development and thus, exemplifies the "island" concept of modern national parks (Petrides, 1963). Cattle raising has been the predominant land-use activity to the east and south. The former sisal estate to the west was recently converted to small agricultural holdings of cultivated grains and livestock. The provincial capital of Nakuru, with an estimated population of 60,000, lies just to the north and northwest and the municipality and national park share a common boundary for more than four km.

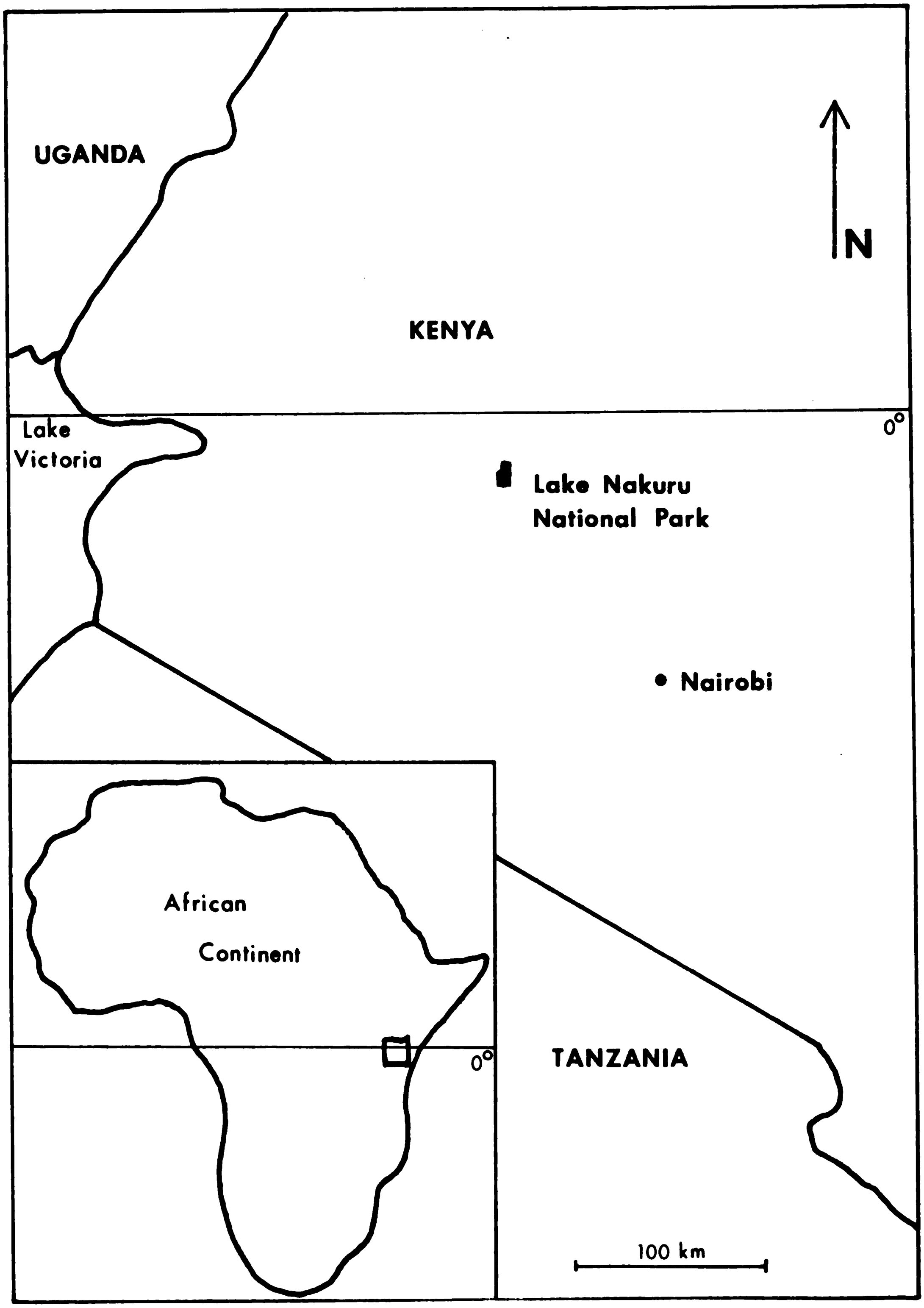


Figure 1. Location of Lake Nakuru National Park, Kenya.

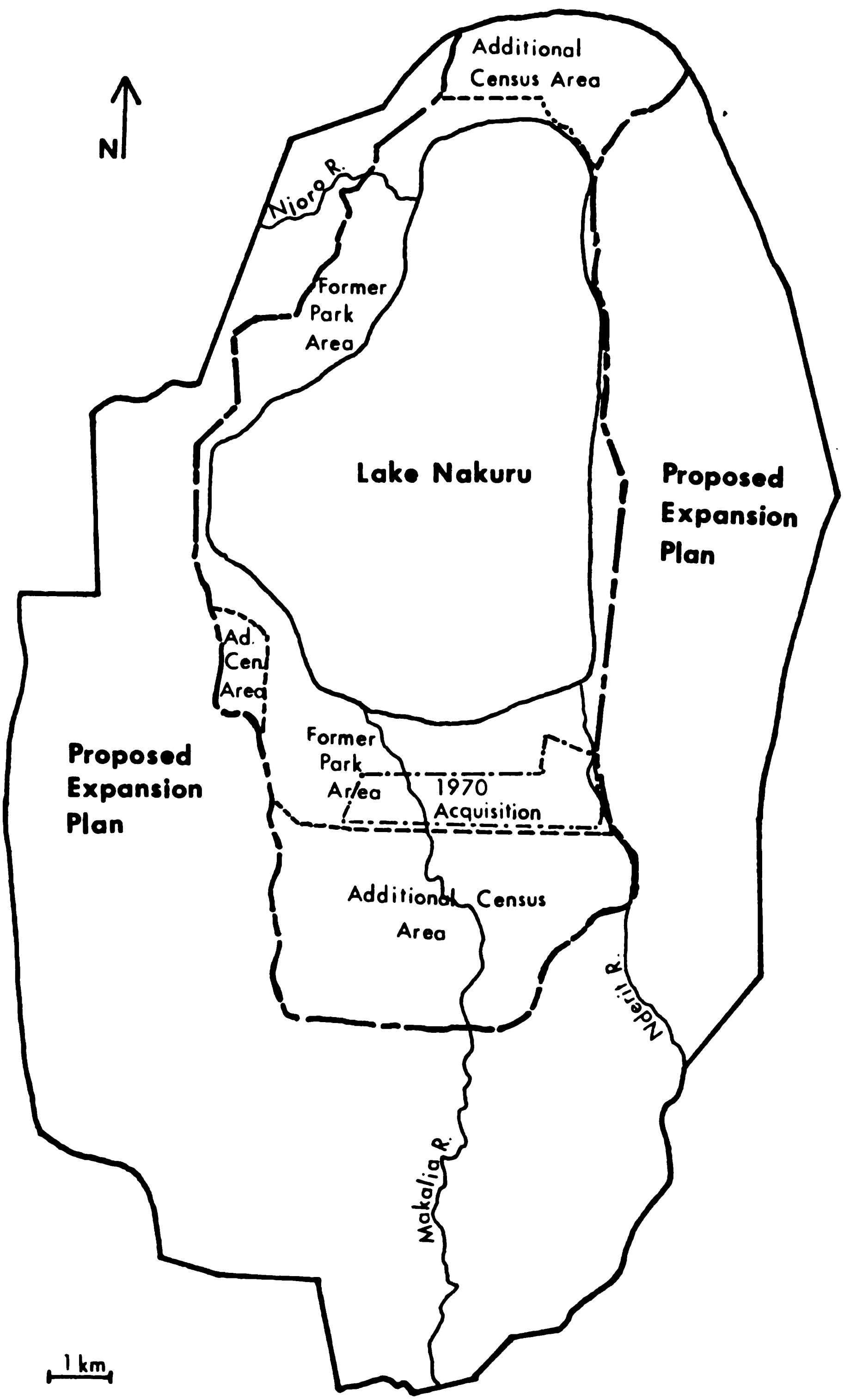


Figure 2. Lake Nakuru National Park, Kenya, showing the major boundaries as of December, 1973. The total census area was comprised of the former park area (including the 1970 acquisition) plus the additional census areas.

Lake Nakuru is one of a series of shallow alkaline lakes characteristic of the Rift Valley floor. It has no outlet and the accumulation of salts, mainly sodium bicarbonate ($NaHCO_3$), has given it a pH of 10.5. Throughout this study permanent fresh water sources were present at the Njoro and Nderit Rivers (Figure 2), at a series of springs along the northern and eastern shores, and at water troughs dispersed throughout the expansion area. Seasonally, fresh water was available at the Makalia River.

The lake has an elevation of 1765 m above sea level and is the lowest point within the park. The ground rises gently both north and south of the lake to an elevation at the park boundaries of 1820 m. Lion Hill along the eastern edge of the park has a maximum elevation of 2086 m. West of the lake are a series of escarpments forming the wall of the Rift Valley. The proposed park boundary lies among, and roughly parallel to, these escarpments at an elevation of about 2100 m.

A geological survey of the Nakuru region (McCall, 1967) indicated that the lake is bordered on the south and west by trona impregnated silts and on the north and east by alluvium of lake and swamp basins. Inland from the lake to the south and west are superficial and volcanic deposits which are interrupted by phonolitic outcrops forming the escarpments. Inland from the lake to the north are gravels, tuffs and diatomaceous silts. Lion Hill to the east is made up of phonolitic trachytes.

The soils are both volcanic and alluvial. The volcanic component was derived from recent unconsolidated ash while the lake deposits originated from a larger body of water which encompassed the Nakuru and Elmenteita basins several times in the geologic past (Washbourn-Kamau, 1971). Being of recent origin, the soils show no profile development other than a more humic surface horizon (Gethin-Jones and Scott, 1959).

METHODS

This study required data on: (1) climatic variability; (2) forage production, distribution and utilization; and (3) antelope distribution and density.

Climate

Two factors appear to be most important as climatic indicators in the dry tropics, rainfall and the potential evapotranspiration (Penman, 1948; Dagg *et al.*, 1970). Rainfall data were supplied by the East African Meteorological Department and the potential evaporation measurements were taken from Woodhead (1968). In warm dry tropical areas covered in vegetation the potential evapotranspiration (E_t) is equal to about 0.8 times the potential evaporation (Brown and Cocheme, 1969). The Thornthwaite (1948) classification, modified by Barry (1969), combines rainfall and potential evapotranspiration into a single value, the moisture index, by using two equations. The first computes the water balance (B_w),

$$B_w = P - E_t$$

where P is the rainfall and E_t the potential evapotranspiration. B_w is then standardized for any given time interval by calculating the moisture index (I_m),

$$I_m = \frac{100\ B_w}{E_t}$$

The moisture index has been further modified into the positive moisture index (I_m') using the formula,

$$I_m' = I_m + 101$$

This insures that all values are positive and thus, are amenable to statistical analysis. The positive moisture index is a measure of effective precipitation and is a reasonable indicator of both the month to month climatic variability and the amount of water available for plant production. By way of illustration, the positive moisture index has a value of one when there was no rainfall and a value of 101 when rainfall exactly balances the potential evapotranspiration.

Vegetation

More than 150 plant species were collected, pressed, dried, and sent to the East African Herbarium for identification (Appendix I). Duplicates were kept in a field reference collection.

A vegetation map was drawn from the most recent (1967) 1:50,000 aerial photographs from the Survey of Kenya by placing a clear plastic sheet over the photos and outlining the recognizable vegetation types. Those types undistinguished in the photos were delimited by ground studies (Poore, 1962) and fitted to the photomosaic by means of landmarks.

Eight animal exclosures, each measuring 10 x 16 m, were erected in the major vegetation types to measure primary production. National park authorities directed that the exclosures be inconspicuous and the minimum number required. With these criteria in mind, the sites were chosen to be as representative of each vegetation type as possible.

The exclosures were built with cedar posts and had five strands of barbed wire spaced closer together at ground level than at the top. The strands were held apart at constant distances from each other by cross wires and spacing sticks and formed a mesh with a minimum height of 1.5 m. The exclosures were known to prevent the entry of antelope and larger animals but rodents, lagomorphs, birds and insects passed through freely. Monthly counts of small mammal pellets were made to determine whether there was differential utilization of the fenced areas by these animals.

Within the marsh and grassland exclosures, eight 2.5 x 2 m plots were delimited. Each of these was further divided into five 2 x 0.5 m (1 m^2) subplots. For each time interval one of these fenced plots was clipped (as five individual subplots) and the results compared with those of a similarly handled unfenced plot located adjacent to the exclosure. Each plot was clipped only once. The samples were bagged, oven-dried at 100°C for a minimum of 24 hours and weighed. The net above-ground primary production for the interval was determined from the difference between earlier and current fenced clip-plots (Brown, 1954). The amount of forage consumed was determined from the differences in the weight of vegetation between fenced and unfenced clip-plots for the same sampling period (Milner and Hughes, 1968).

Plots were cut six times during a one year period. The clipping dates were made roughly to coincide with periods of increasing and decreasing rainfall. Clipping was carried out in late April, early June, early August, and early October, 1973, and in mid-March and late April, 1974. At least one plot in each exclosure was left unclipped throughout the study and, each month, measurements of height and estimations of the percentage crown cover for each species were made.

Browse production was estimated by clipping all new growth at the end of each wet period (Whitaker, 1961, 1963; Newbould, 1967). Browse clippings were made in early June and early October, 1973, and in late April, 1974. A minimum of 20 stratified random plots (2 x 0.5 m) were clipped to a maximum browsing height of 1.9 m. These samples were oven-dried, weighed and recorded. Browse clippings were not taken at the end of the dry periods but the amount of growth was assessed then. Within exclosures located in grass-shrub and open woodland areas, branches of representative shrubs were tagged and the twigs clipped. At the end of the interval these were examined for regrowth.

Crown cover, utilization and trend were determined by monthly surveys. In grasslands and marsh, the surveys employed 0.25 m^2 quadrats placed at 10 m intervals along stratified random survey lines. For each quadrat the percentage cover of each species and of litter and bare ground was estimated. To measure the intensity of utilization, a usage index was based upon the difference between the mean heights of fenced vegetation protected from grazing and trampling, and that of unfenced vegetation. The fenced plots excluded large mammals but foraging by smaller animals and the natural decomposition of vegetation was allowed to continue. A difference in height between fenced and unfenced vegetation, therefore, was assumed to be due to the effects of large mammals.

In grass-shrub and open woodland zones, 0.5 x 10 m random plots were employed to determine cover, utilization and trend. The percentage of crown cover for each plant species was determined within each plot. Forage utilization was measured as the percentage of browsed twigs between ground level and 1.9 m. Range trend data were analyzed using 18 separate analyses of variance, one for the cover index and one for the height of each species. The percentage cover data were transformed for the analysis using arcsine when any of the data points were less than 30 or greater than 70 percent (Sokal and Rohlf, 1969). Significant differences were tested among years within the same seasons (wet or dry).

Mammals

Sixteen counts of large mammals were carried out during the study period. The total census area comprised all of the former park area including the 1970 acquisition, plus part of the expanded area (Figure 2). Outside of this area, large mammals appeared to be few in number due to the unfavorable terrain and to settlement by people.

Total-area counts were made similar to those reported previously, but with some modifications. It was determined from the 1970-71 counts (Kutilek, 1974) that a peak feeding period for large mammals was between 0600 and 1000 hours. Moreover, the vast majority of animals were found, during this time of the day, in open places (i.e., in grasslands, marshes, and along the edges of grass-shrub areas and open woodlands). All censuses were made by Land Rover in the early morning, therefore, by quartering the open areas and by skirting the edges of grass-shrub and open woodlands.

The large mammals observed were recorded, when possible, by sex and size. Waterbuck, reedbuck and impala were categorized as males or females and as adults, subadults, juveniles and calves (including newborns). Thomson's gazelles were recorded as males and females and as adults, subadults and calves. Juveniles and subadults were lumped together as subadults in this species since they were difficult to distinguish in the field. Buffalo and hippopotamus were categorized merely as adults or subadults because of difficulties in sexing and aging.

Counts were conducted usually with one assistant. The park was divided into three major areas, each encompassing a number of previously-established counting zones (Kutilek, 1974). The boundaries of the major areas followed barriers which the animals did not frequently cross. The total area was counted on three successive mornings with reasonable assurance that no animals had crossed between areas during the night.

Census data were recorded on the basis of the 10 zones previously described (Kutilek, 1974). This enabled comparisons to be made between the former park area and the total census area. On the first morning, for example, animals were counted in the first major area but were recorded as being in zones 1, 2 or 3. The second morning, animals were counted in the next major area but recorded as being in zones 4, 5, etc. The areas outside of the former park boundary were integrated into this counting scheme and recorded as separate zones.

The value used to indicate the degree of concentration of animals near the lake was the difference between the density of animals within the former park area and that of the more-widespread total census area. The average annual rates of increase (r') were calculated as a percentage using a formula from Bowen (1967)

$$N_t = N_o (1 + r')^t$$

where N_t is the number of antelope in the population at the end of the sampling period, N_o the number at the beginning, and t the time elapsed.

To determine the habitat preferences of the main antelope species, 0.5 km^2 study plots were delimited in each of the six major vegetation types. On two consecutive days of each month, the number of feeding antelope were counted (by species) within each study plot. Counts were made in the early morning and again in the late afternoon and means were calculated from the four consecutive counts.

RESULTS

Climate

Positive moisture indices, calculated on a monthly basis for the entire study period (Table 1), showed that the rainfall exceeded the evaporation three months out of the 21. The positive moisture index was found to be related to both antelope distribution and forage utilization (see beyond).

The potential evapotranspiration is known to vary little between years or within the same month among different years (Woodhead and Waweru, 1969) so that, in comparing climatic variability over many years, only rainfall was considered. The rainfall level affects plant production since less than "normal" rainfall will depress the growth of forage while greater than "normal" rainfall will speed up growth and cause the taller grasses to be unpalatable to antelope early in the season (Anderson and Talbot, 1965; Spedding, 1971).

One measure of annual variability is the probability, within a particular month, of receiving a certain amount of rainfall. Using the long-term rainfall data from the Nakuru Railway station, only 22.2 percent of the annual totals fell with ± 0.5 standard deviations of the mean (Table 2). The heaviest rainfall months of April, May and August showed percentages of 54.8, 29.0 and 40.0, respectively. These data indicated that both annual and monthly

Table 1. Effective precipitation at Lake Nakuru National Park, Kenya, during the study period. See text for sources of data and for formulas.

Month/year	Rainfall (P)	Potential Evaporation (E_o)	Potential Evapo-transpiration (E_t)	Water Balance (B_w)	Moisture Index (I_m)	Positive Moisture Index (I_m')
Sept. 1972	30.0	138	110.4	- 80.4	- 72.8	28.2
Oct.	58.9	163	130.4	- 71.5	- 54.8	46.2
Nov.	59.9	138	110.4	- 50.5	- 45.7	55.3
Dec.	10.3	138	110.4	-100.1	- 90.7	10.3
Jan. 1973	17.7	163	130.4	-112.7	- 86.4	14.6
Feb.	23.2	163	130.4	-107.2	- 82.2	18.8
March	0.0	163	130.4	-130.4	-100.0	1.0
April	59.5	138	110.4	- 50.9	- 46.1	54.9
May	103.8	138	110.4	- 6.6	- 6.0	95.0
June	39.2	138	110.4	- 71.2	- 64.5	36.5
July	66.8	138	110.4	- 43.6	- 39.5	61.5
Aug.	138.6	138	110.4	28.2	25.5	126.5
Sept.	110.9	138	110.4	0.5	0.5	101.5
Oct.	42.5	163	130.4	- 45.4	- 34.8	66.2
Nov.	30.5	138	110.4	- 79.9	- 72.4	28.6
Dec.	0.0	138	110.4	-110.4	-100.0	1.0
Jan. 1974	21.7	163	130.4	-108.7	- 83.4	17.6
Feb.	16.0	163	130.4	-114.4	- 87.5	13.5
March	99.6	163	130.4	- 30.8	- 23.6	77.4
April	169.2	138	110.4	58.8	53.3	154.3
May	51.7	138	110.4	- 58.7	- 53.2	47.8

Table 2. Long-term rainfall data (mm) and rainfall probabilities. Data from the Nakuru Railway Station, 3.5 km northwest of Lake Nakuru National Park, Kenya.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
Number of years (n)	29	29	30	31	31	31	30	30	30	29	29	29	27
Mean rainfall ($\bar{y}$)	24.1	29.3	56.8	136.0	118.9	74.6	92.0	102.3	66.1	54.1	63.2	39.6	840.5
Standard deviation (s)	28.4	40.7	47.3	103.7	58.9	45.5	46.8	42.7	40.0	27.7	48.8	44.9	158.6
0.5 s	14.2	20.4	23.7	51.9	29.5	22.8	23.4	21.4	20.0	13.9	24.4	22.5	79.3
$\bar{y}$ + .5 s	38.3	49.7	80.5	187.9	148.4	97.4	115.4	145.0	86.1	68.0	87.6	62.1	919.8
$\bar{y}$ - .5 s	9.9	8.9	33.1	84.1	89.4	51.8	68.6	80.9	46.1	40.2	38.8	17.1	761.2
Percentage of n between $\bar{y}$ ± .5 s	27.6	44.8	40.0	54.8	29.0	41.9	40.0	40.0	26.6	44.5	51.7	51.7	22.2

variability was great but that the highest rainfall month, April, showed the least variability. The rainfall pattern appears to have influenced the breeding strategies of antelope and will be examined later in this context.

Vegetative Zones

Eleven vegetative zones were categorized by species composition. Of these, six were important as forage habitats for the main antelope species. These were marsh, alkaline grassland, moist-site grassland, grass-shrub and open woodland. The zones little used by ungulates were alkaline flats, mixed grassland, escarpment and rocky slope, mixed bushland and dense woodland. The distribution of the 11 vegetative zones was mapped (Figure 3).

Alkaline flats: These were seasonally flooded areas with sparse and patchy cover. When vegetation was present, it was usually the grass *Sporobolus spicatus* or the sedge *Cyperus laevigatus*.

Marsh: Marsh vegetation was periodically flooded by the lake and consequently was strongly influenced by the prevailing alkaline conditions. The dominant plant species was the sedge *C. laevigatus* which frequently grew in pure stands up to 1 m in height. Most marshes were edged on the upland side by a narrow belt of the alkaline-tolerant shrub *Pluchea bequaertii*. In some places along the northern and eastern lakeshore, fresh water springs ameliorated the alkalinity. There, *Typha domingensis* and *Cyperus immensus* were present, along with *Hibiscus diversifolius* and *Sesbania sesban* at the drier edges.

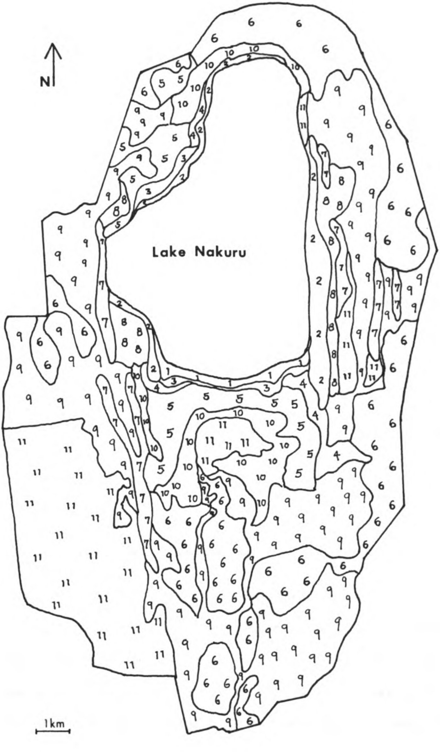


Figure 3. The vegetation types of Lake Nakuru National Park, Kenya, as of December, 1973. 1) alkaline flats, 2) marsh, 3) alkaline grassland, 4) moist-site grassland, 5) dry-site grassland, 6) mixed grassland, 7) escarpment and rocky slope, 8) grass-shrub, 9) mixed bushland, 10) open woodland, 11) dense woodland.

Alkaline grassland: The dominant vegetation of this zone was the alkaline-tolerant grass *S. spicatus*. This species grew in a thick mat, frequently as a pure stand, up to 1/2 m in height.

Moist-site grassland: This zone occurred as a buffer between the wetter more alkaline marshes and the less alkaline dry-site grassland further inland from the lake. It was covered by a nearly-pure mat of the grass *Cynodon nlemfuensis*, growing to 1/2 m in height.

Dry-site grassland: The medium-tall grasses *Chloris gayana* and *Hyparrhenia hirta* were dominant in this zone. When ungrazed, they grew to a height of 1 m or more. Scattered or clumped throughout this grassland type was the fever tree *Acacia xanthophloea*. During the wet season, the forbs *Indigofera circinella* and *Rhamphicarpa montana* increased in number. On compacted dry soils, such as those south of the lake, *H. hirta* became rare and *C. gayana* formed a mosaic with *Sporobolus ioclados* and, to a lesser extent, with *S. spicatus* and *Microchola kunthii*. Trees were mostly absent on these sites.

Mixed grassland: This type tended to be the furthest removed from lacustrine influences. Prior to park expansion, it was little grazed by wild ungulates since livestock raising was the prevalent activity. The mixed grassland may, in the future, become an important foraging area since a large portion has now come under national park control. The dominant grasses were *T. triandra, H. hirta, C. gayana* and *Aristida adoensis*. In some areas the shrubs *Lippia* sp. and *Psiadia arabica* were scattered throughout the grassland as were the trees *A. xanthophloea, A. gerrardii, A. seyal* and *Maerua triphylla*.

Escarpment and rocky slope: This zone comprised the moderate slopes and steep escarpments both east and west of the lake. The ground cover over most of the area consisted of the grasses *Pennisetum squamulatum*, *T. triandra*, *C. gayana*, *Setaria pallidefusca* and *Eragrostis cilianensis* interspersed with bare rock phonolites. On moderate slopes, *Aspilia mossambicensis* and *Acacia hockii* were the most common shrub and tree, respectively. On the dry moderate slopes, the small shrub *Aster muricatus* was also common. On the steep escarpments, the shrub and tree cover was mainly *Tarchonanthus camphoratus*, *Steganotaenia araliacea*, *Iboza multiflora*, *Plectranthus marrubioides* and *Cordia ovalis*.

Grass-shrub: The ground cover of this zone was largely *C. gayana* and the herbaceous shrubs, *Hypoestes verticillaris*, *Abutilon mauritianum* and *Kalanchoe densiflora*. The larger shrub cover consisted of *Rhus natalensis*, *T. camphoratus*, *P. bequaertii* and *Psiadia arabica*. Scattered *A. xanthophloea* provided some tree cover.

Mixed bushland: Included in this zone were a variety of woody plant associations, all of which were only marginally used by the major antelope species. Much of this zone was dominated by the "leleshwa" shrub, *T. camphoratus*. Ground cover consisted of the small shrubs, *Lippia* sp. and *Erlangea cordifolia* and the grasses *T. triandra*, *C. nlemfuensis*, *S. pallidefusca* and *Panicum atrosanguineum*.

Some areas were heavily wooded with the small-tree species *Acacia gerrardii* and *A. seyal*. At the extreme southeastern corner of the expanded park area, the above mentioned species were mixed with *Euphorbia candelabrum* and *Aloe graminicola*, a succulent tree and a shrub, respectively.

Where *A. xanthophloea* woodlands had been cut and burned to make charcoal, the shrubs *P. bequaertii, R. natalensis* and *K. densiflora* had taken over. The burning sites supported the shrubs *Solanum incanum* and *Tegetes minuta.* Where severe overgrazing by cattle had occurred, the dominant shrubs were *Chenopodium opulifolium, Aerva lanata, S. incanum, T. minuta* and *Withania somnifera.*

Open woodland: The tree cover of the open woodland which surrounded the lake comprised a nearly-pure stand of *A. xanthophloea* growing to a height of 30 m. *Acacia abyssinica*, when present, was scattered along the woodland edges. The undergrowth of the woodland at the north end of the lake consisted largely of the grass *Pennisetum clandestinum.* The northwestern woodland contained a mixed undergrowth of shrubs and herbs, mainly, *Achyranthes aspera, Justicia flava, Senecio petitianus* and *Galinsoga parviflora.* The dominant undergrowth species of the southern woodland was the herbaceous shrub *H. verticillaris* and to a lesser extent the grass *C. nlemfuensis.*

Dense woodland: The dense woodlands immediately northeast and south of the lake were comprised of nearly a pure stand of *A. xanthophloea.* Ground cover consisted of *H. verticillaris, S. petitianus, A. mauritianum, Capparis fasicularis* and *Urtica massaica.*

The southwestern sector of the park, on the Rift Valley escarpment, was covered by an oleaceous forest. The dominant tree species were *Olea africana, Euclea divenorum* and *Teclea simplicifolia* with scattered patches of *Cussonia holstii.* The understory consisted of *T. simplicifolia* saplings, the shrub *Gnidia subcordata* and the succulent *Aloe rabaiensis.* The ground cover was mainly comprised of *Sansevieria parva* and *Plectranthus assurgens.*

Immediately southeast of the lake on the southern slopes of Lion Hill was a dense stand of succulent woodland. The dominant tree there was *E. candelabrum* with *C. holstii* and *Obetia pinnatifida* scattered throughout the woodland edges. There was almost no shrub layer, however, the common plants of the woodland floor were the herb *Monothecium glandulosum* and the sedge *Mariscus impubes*.

Primary Productivity

Primary production was computed only with respect to the net annual above-ground primary production available for consumption by large mammals. As with numerous other studies (Braun, 1969; Harris, 1970; Western, 1973), production of forage beyond the reach of large mammals, i.e., tree canopies and that which occurred in habitats not utilized by the animals, was not measured. It was also infeasible, if not impossible, to exclude all herbivorous insects, birds and small mammals from the fenced plots. On East African ranges, however, the proportion of material eaten by these other herbivores is thought to be small as compared with the large herbivores (De Vos, 1969; Phillipson, 1973).

It was still necessary to determine whether differential foraging was taking place in the exclosures which would affect either production or standing crop. This was assessed for medium-small mammals by pellet counts on paired plots, one inside and one outside exclosures. The great majority of the fecal pellets counted were from the African hare, *Lepus capensis*, although some pellets of the springhare, *Pedetes capensis*, were also found. The pellet-count data were analyzed using a paired t-test and the differences found to be not significant at $P \leq 0.05$. This suggests that there was no differential foraging by these mammals within the exclosures.

The production data revealed that the moist zones were the most productive (Table 3). Marsh and moist-site grasslands had the highest production rate while dry-site grasslands, mixed grasslands, grass-shrub and open woodlands had the lowest. Alkaline grasslands were somewhat intermediate between wet and dry habitats.

During the year in which primary production was measured, the wet periods totaled 144 days and moist and dry periods totaled 221 days. The wet periods included the last half of March through May and most of August and September. The moist to dry periods included June-July and from October through the first half of March. In all habitats most plant growth occurred during the wet periods. During the drier months, however, the moist habitats produced a greater relative percentage of their growth than did the dry types. Browse plants which were marked and clipped inside exclosures at the beginning of October showed negligible growth by the middle of March, suggesting that there was little browse production during the dry periods.

The average annual primary production for both the former park area and the total census area were calculated by multiplying the mean annual primary production value for each vegetation type (Table 3) by the percentage of the area occupied by that type. For the former park area, 6 percent was not used by large mammals, 16 percent was marsh, 9 percent alkaline grassland, 6 percent moist-site grassland, 34 percent dry-site grassland, 6 percent grass-shrub and 23 percent open woodland. This yielded an average forage production

Table 3. Net above-ground primary production available to large mammals during the period April 1973-April 1974 in the main forage habitats of Lake Nakuru National Park, Kenya. Production values are given as means and standard deviations in grams/meter^2 oven-dry weight.

Forage Habitat	Production During Wetter Months (144 days)	Production During Drier Months (221 days)	Annual Production (365 days)
Marsh	597 ± 48	165 ± 14	762 ± 57
Moist-site grassland	435 ± 34	63 ± 5	498 ± 38
Dry-site grassland	422 ± 51	*	422 ± 51
Alkaline grassland	377 ± 39	38 ± 6	415 ± 43
Mixed grassland	401 ± 53	*	401 ± 53
Grass-shrub	356 ± 57	--	356 ± 57
Open woodland	321 ± 46	--	321 ± 46

*Values were slightly negative.

value for the former park area of 427 grams/meter^2/year. For the total census area, 7 percent was not used by large mammals, 15 percent was marsh, 7 percent alkaline grassland, 5 percent moist-site grassland, 22 percent dry-site grassland, 19 percent mixed grassland, 4 percent grass-shrub and 21 percent open woodland. This gave an average value for the total census area of 418 grams/meter^2/year. These two average values will be compared with other area of East Africa in a later section.

Can it be assumed that this single year of study yielded an "average" value for primary production? In the Serengeti Plains of Tanzania, Braun (1969) found a strong correlation between total annual rainfall and the net above-ground primary production. A similar relationship between the actual evapotranspiration and the net primary production has been demonstrated for a variety of habitats and latitudes but, in the dry tropics where the potential evapotranspiration exceeds the rainfall, the actual evapotranspiration is approximately equal to the rainfall (Rosenzweig, 1968). The evidence is that rainfall and primary production vary together. It follows, therefore, that an average season's rainfall would produce an average net primary production. The total rainfall recorded at the Nakuru Park gate from May 1, 1973 to April 30, 1974, was 838.8 mm and since this is very close to the 27-year mean of 840.5 mm, it may be taken that the annual primary production values observed (Table 3) represent close to average conditions.

<u>Range Condition and Trend</u>

Range analyses were carried out to determine whether there were significant trends in range condition. Changes in the percentage cover and in the height of grasses and sedges from year to year are two indicators of impending changes in range condition (Brown, 1954). A decline in the abundance of important forage species and/or a failure of these species to maintain height, would indicate range deterioration and a reduced herbivore carrying capacity (Nat. Acad. Sci., 1962).

The range data (Table 4) showed only two statistically significant differences among years within the same season. First, within the wet period *Cynodon nlemfuensis* showed a significant increase in height between September, 1972 and September, 1973. Second, there was a significant increase in the percentage cover for *Chloris gayana* between March, 1973 and March, 1974. The former may have been caused by heavy rainfall just prior to the 1973 survey, while the latter may reflect the severe drought conditions which prevailed in early 1973. In both cases, the significant differences were thought to be due to brief climatic fluctuations. These trends if persistant, however, would indicate range improvements.

No indications of overgrazing were detected in any vegetation type. Evidently, the standing crop of herbivores did not exceed the carrying capacity of the park during the study period.

History and Current Status of Large Mammal Populations

While more than 20 species of larger mammals occur in Lake Nakuru National Park (Appendix II), four of these account for more than 90% of all animals present (Kutilek, 1974). These are defassa waterbuck, *Kobus defassa*, impala, *Aepyceros malampus*, bohor reedbuck, *Redunca redunca*, and Thomson's gazelle, *Gazella thomsonii*.

Table 4. Range analyses of the important forage species in the six main habitats at Lake Nakuru National Park, Kenya.

Forage Habitats with Species, Litter and Bare Ground	End of Wet Period: Early October, 1971 Percentage Cover	Height	Mid-September 1972 Percentage Cover	Height	Mid-September 1973 Percentage Cover	Height	End of Dry Period: Mid-March 1973 Percentage Cover	Height	Mid-March 1974 Percentage Cover	Height
Marsh										
Cyperus laevigatus	--	--	92.0	83±	94.3	85.2	84.7	78.9	90.1	66±
litter and bare ground	--	--	1.6	--	1.0	--	4.4	--	1.2	--
Alkaline Grassland										
Sporobolus spicatus	--	--	88.6	44±	80.1	40.0	78.6	34.4	81.9	31.7
litter and bare ground	--	--	7.5	--	6.2	--	12.9	--	8.3	--
Moist-site Grassland										
Cynodon nlemfuensis	--	--	94.3	45.6*	99.0	53.1*	93.2	27.1	95.2	33.7
litter and bare ground	--	--	4.7	--	1.9	--	3.6	--	4.5	--
Dry-site Grassland										
Chloris gayana	47.6	71.9	40.9	68.2	43.2	78.9	23.7*	46.6	40.9*	54.8
Hyparrhenia hirta	29.8	77.6	19.1	89.4	30.4	70.5	21.6	61.6	23.0	57.2
litter and bare ground	6.4	--	13.0	--	9.3	--	20.9	--	13.8	--
Grass-Shrub										
Rhus natalensis	--	--	13.3	--	8.1	--	15.4	--	9.7	--
Hypoestes verticillaris	--	--	7.4	--	10.8	--	12.6	--	5.2	--
Open Woodland										
Achyranthus aspera	11.6	--	14.3	--	10.9	--	12.2	--	8.3	--
Justicia flava	4.4	--	5.7	--	8.4	--	7.6	--	6.3	--

*Denotes significant differences ($P \leq 0.05$) among years within the same season.

Why aren't there more species occurring in abundance? The number of species occurring at the turn of the century was greater than it is at present (Chapman, 1908; Meinertzhagen, 1957). For the most part, the reduction in the number of species or in the size of populations was a result of the land-use policies of the early European settlers, i.e., fencing, shooting and the belief that wild and domestic animals should not exist on the same ranges (Percival, 1924, 1928).

No quantitative data are available from the early 1900's but descriptions exist which leave impressions of relative species abundance. Comparing these early descriptions with data from current counts (Table 5) reveals that of the large herbivores, Coke's hartebeest, *Alcelaphus buselaphus cokii,* Jackson's hartebeest, *A. b. jacksoni,* bush pig, *Potamochoerus porcus,* eland, *Taurotragus oryx,* Masai giraffe, *Giraffa camelopardalis,* and elephant, *Loxodonta africana*, have all been locally exterminated in the Nakuru region. The hybrid Nakuru hartebeeste, *A. b. cokii* x *jacksonii* was hunted to extinction. The black rhinoceros, *Diceros bicornis,* was also thought to be locally extinct, but recently has been discovered in the oleaceous escarpment forests. Furthermore, Burchell's zebra, *Equus burchelli,* Grant's gazelle, *Gazella granti,* and Thomson's gazelle, *G. thomsonii*, now occur only as remnant populations. With protection of the area beginning in 1968, some herbivore populations (waterbuck, impala, reedbuck and Thomson's gazelle), reemerged and became dominants.

Of the carnivores (Table 5), the lion, *Panthera leo,* and cheetah, *Acinonyx jubatus,* have been locally exterminated while spotted hyaena,

Table 5. The status of some large-mammal populations presently and/or formerly located in the region of Lake Nakuru National Park, Kenya.

Species	Status c. 1900 Relative Abundance	Status c. 1900 References	1974 Status (this study)
Herbivores			
Burchell's zebra	A	1, 5	< 15
Thomson's gazelle	A	1, 5	> 400
Coke's hartebeest	C	1, 3	LE
Jackson's hartebeest	C	3	LE
Nakuru hartebeest	C	3, 5	E
Grant's gazelle	C	1, 3	< 10
Defassa waterbuck	C	6	>1200
Bohor reedbuck	C	5	> 300
Warthog	C	4	< 30
Impala	P	7	> 600
Bush pig	P	8	LE
Eland	P	1	LE
Masai giraffe	P	7	LE
Black rhinoceros	P	4	R
Elephant	P	4	LE
Carnivores			
Lion	C	1, 2	LE
Side-striped jackal	C	5	R
Cheetah	P	7	LE
Hunting dog	P	7	R
Spotted hyaena	P	1, 7	R
Leopard	P	7	R

Early status: A = abundant; C = common; P = present but relative abundance unknown.

Current status: E = extinct, LE = locally extinct, R = rare, numbers represent approximate population estimates for the total census area (45.8 km^2).

References: 1. Chapman (1902); 2. Jackson (1930); 3. Meinertzhagen (1957); 4. Percival (1924); 5. Percival (1928); 6. Simon (1962); 7. Williams (1967); 8. John Hopcraft (per. com.).

Crocuta crocuta and hunting dog, *Lycaon pictus*, are only occasional visitors to the park. The side-striped jackal, *Canis adustus*, and leopard, *Panthera pardus*, still maintain small populations within and around the park.

Density and Biomass of Large Mammals

Previous counts (Kutilek, 1974), showed that waterbuck, impala, reedbuck and gazelle made up 90 percent of all large mammals counted in the park. In addition, the hippopotamus, *Hippopotamus amphibius*, and the buffalo, *Syncerus caffer*, were important in biomass estimates since, though few in number, both species have large body weights. Estimates of the large-mammal density and biomass, therefore, were computed using data for these six species.

Data from three series of counts spanning 1970-74 (Table 6) revealed that the density of waterbuck was three to four times greater than that of any of the next most numerous species (impala, gazelle or reedbuck). Waterbuck, in fact, made up about 50 percent of the total density. Furthermore, Lake Nakuru National Park maintained the highest density for this species of any area on record (see Spinage, 1971 and Kutilek, 1974).

For waterbuck, impala and gazelle, the coefficients of variation in density for the former park area were nearly twice as large as those for the total census area (Table 6). The variability among counts, therefore, was less when a larger area of land was counted. This fact together with my observations of antelope movements made it clear that these populations ranged beyond the former park boundary even though this placed them in greater danger of poaching and other forms of human harrassment.

Table 6. Densities per km^2 of all large mammals and of the six main species in Lake Nakuru National Park, Kenya. The data are given as the means and coefficients of variation for groups of counts spanning 1970-74. The values in column A are for the former park area (28.4 km^2); those in column B are for the total census area (45.8 km^2).

Species	Apr 1970-Mar 1971 (n=8)* A	B	Nov 1972-Jun 1975 (n=6) A	B	Jul 1973-May 1974 (n=10) A	B
Total Combined (19 species)	64.20±13.80%	--	68.97±13.53%	46.18±9.92%	74.47±10.31%	54.38±6.16%
Defassa waterbuck	31.10±14.73%	--	35.69±10.84%	23.01±5.43%	38.00±7.08	26.30±4.37
Impala	9.01±20.39%	--	11.84±25.59%	9.26±17.80%	14.01±16.85%	12.01±8.08%
Thomson's gazelle	8.89±13.32%	--	10.78±7.70%	7.13±8.69%	10.65±11.46%	8.61±6.04%
Bohor reedbuck	8.76±30.85%	--	9.54±10.06%	6.09±10.51%	10.54±7.87%	6.65±7.22%
Buffalo	0.94±33.25%	--	0.65±76.92%	0.40±82.50%	0.83±53.01%	0.52±51.92%
Hippopotamus	0.41±44.97%	--	0.47±29.79%	0.29±31.03%	0.44±31.82%	0.29±31.03%

*Data from Kutilek (1974).

The distribution of animals in the park at any given time was related to climatic conditions. When the value for the difference in density of large mammals between the former park area and the total census area was regressed on the positive moisture index, two things became apparent (Figure 4): (1) the difference in density was always positive, *i.e.*, the density of animals within the former park area was always greater than that of the total census area; and (2) the animals concentrated near the lake when there was little effective precipitation (low I_m') and dispersed from the lake when there was greater effective precipitation (high I_m'). The animals did not drink the highly alkaline lake water so that shifts in their distribution are apparently related to their feeding strategies (see beyond).

The standing crop biomass of large mammals in Lake Nakuru National Park was calculated from census data using minimum weights for various sex and size catagories within each species (Appendix III). Waterbuck again proved to be the dominant large mammal species accounting for more than 75% of the calculated biomass (Table 7). The next most important large mammals with regard to biomass were impala, buffalo, reedbuck, hippopotamus and gazelle, respectively. Within the former park area of Nakuru, the standing-crop biomass is equal to or greater than that of most bush and savanna areas of East Africa (Kutilek, 1974) but not nearly so great as the grasslands of western Uganda and eastern Zaire (see Petrides, 1956; Petrides and Swank, 1965; Foster and Coe, 1968).

The Nakuru region is not a true savanna or bushland but a mixture of many vegetation types lying at the base of a catchment area.

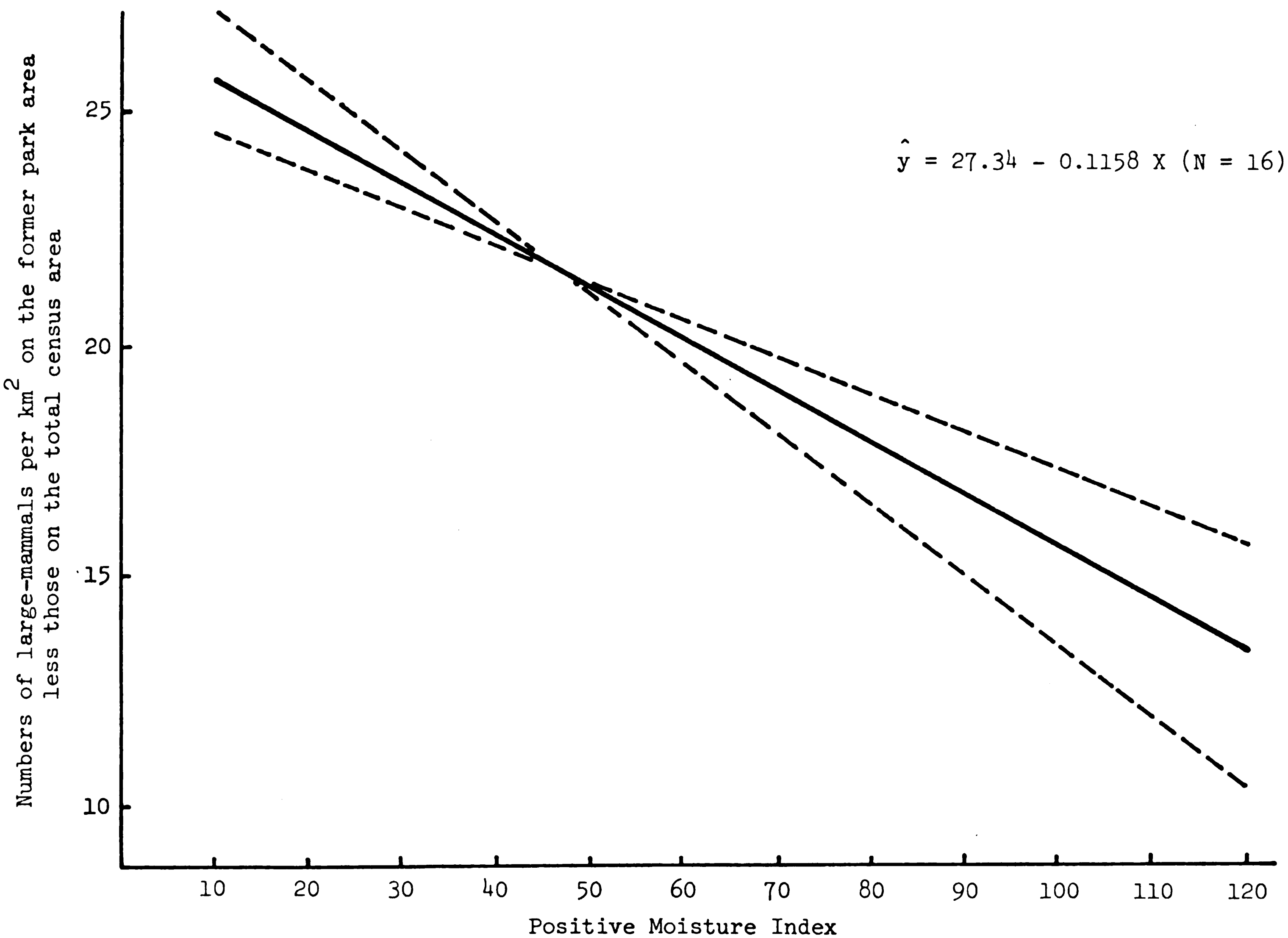


Figure 4. The regression of the difference in large-mammal density on the positive moisture index at Lake Nakuru National Park, Kenya, November 1972-May 1974. The dashed lines indicate 95% confidence limits on the slope.

Table 7. The standing crop biomass (kg/km^2) for the six main large mammal species in Lake Nakuru National Park, Kenya. The data are given as the means and standard deviations for groups of counts spanning 1970-74. The values in column A are for the former park area (28.4 km^2) and those in column B are for the total census area (45.8 km^2).

Species	Apr 1970-Mar 1971 (n=8)* A	B	Nov 1972-Jun 1973 (n=6) A	B	Jul 1973-May 1974 (n=10) A	B
Total of six main species	6298±801	--	6248±642	4068±155	6876±571	4766±268
Defassa waterbuck	4790±649	--	4788±548	3086±177	5248±366	3619±185
Impala	343±52	--	403±100	315±51	471±87	403±38
Buffalo	486±147	--	319±256	198±159	401±201	249±124
Bohor reedbuck	354±98	--	357±28	227±20	380±31	239±20
Hippopotamus	208±106	--	249±78	155±48	240±72	149±45
Thomson's gazelle	117±19	--	132±9	87±7	136±23	108±8

*Data from Kutilek (1974).

It annually receives a greater effective precipitation than many of the savannas to the south and may, therefore, have a greater carrying capacity than those areas. No attempt, however, has been made to estimate the carrying capacity since there are no signs of range deterioration (Table 4) and hence, no indication that animal numbers have exceeded the carrying capacity (De Vos, 1969).

Population Trends

When the mean numbers of animals in the former park area were plotted from the 1970-71, 1972-73, and 1973-74 counts, the four main antelope species appeared to be increasing (Figure 5). None of the differences among means were statistically significant at $p \leq .05$, but since all of the slopes trended upward, it is unlikely that the differences were due merely to random fluctuations.

The calculated mean annual rates of increase (Figure 5) were 6.52 percent for the combined populations, 6.94 percent for waterbuck, 16.0 percent for impala, 6.22 percent for Thomson's gazelle, and 6.29 percent for reedbuck. The calculated number of years for the populations to double were 10.0 for the combined populations and also for waterbuck, 10.1 for both reedbuck and Thomson's gazelle, and 4.5 for impala. While waterbuck is at present the dominant species in the park with regard to both density (Table 6) and biomass (Table 7), the current calculated rate of population growth for impala is more than twice that for waterbuck and the other species. If these rates continue unchanged, in 10 years time impala will surpass waterbuck in total numbers.

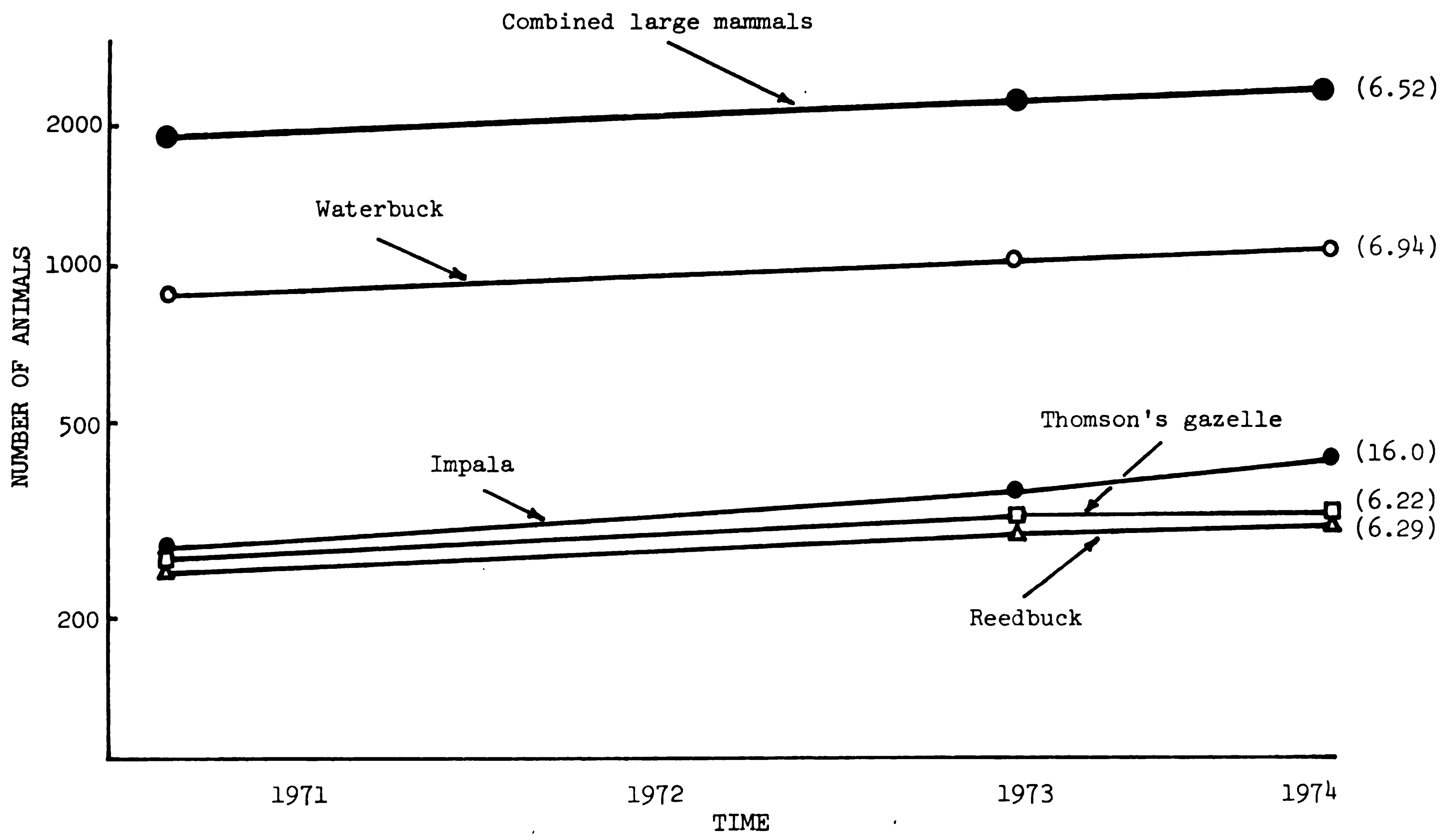


Figure 5. Population trends for large mammals in Lake Nakuru National Park, Kenya. Each slope was plotted by using the population means for three series of counts, 1970-71 (n=8), 1972-73 (n=6) and 1973-74 (n=10). None of the differences in means were statistically significant at $P \leq 0.05$ but all of the slopes increased with time. Values for the percentage mean annual rate of increase (r') are given in parentheses.

Breeding Strategies

Good nutrition is particularly important in late pregnancy and the early post-partum period to insure both proper fetal development and adequate milk production (Blaxter, 1967; Reid, 1968). Over much of East Africa, the forage is in its most nutritous and most palatable condition when the effective precipitation is greatest (Harker, 1961; Leuthold and Sale, 1973). Precipitation, however, is seasonal and highly variable and African ungulates display several evolutionary strategies to optimize calf production (Jungius, 1971; Sinclair, 1974). In the Nakuru region, one or more of three breeding strategies might have been expected to have evolved: (1) year-round calving; (2) synchronization of calving with the period of least variable but adequate rainfall; and (3) synchronization of calving with the end of a series of months in which one or more usually have adequate rainfall.

In order to determine which, if any, of these strategies had evolved, the percentage of calves in the population were plotted at each game count. Waterbuck, reedbuck, and Thomson's gazelle all hide their young during the first 3-4 weeks of life (De Vos and Dowsett, 1966; Estes, 1967; Hanks, *et al.*, 1969; Jungius, 1971). Therefore, the peaks of the graph for these three species occurred about a month after the actual calving peaks.

All four of these populations appeared to be using strategy (1) to some extent (Figure 6). Waterbuck combined strategy (1) with strategy (2) as shown by a plotted peak in May, which indicated an actual calving peak in April, the wettest and least variable month (Table 2). Reedbuck and impala combined strategies (1) and (3).

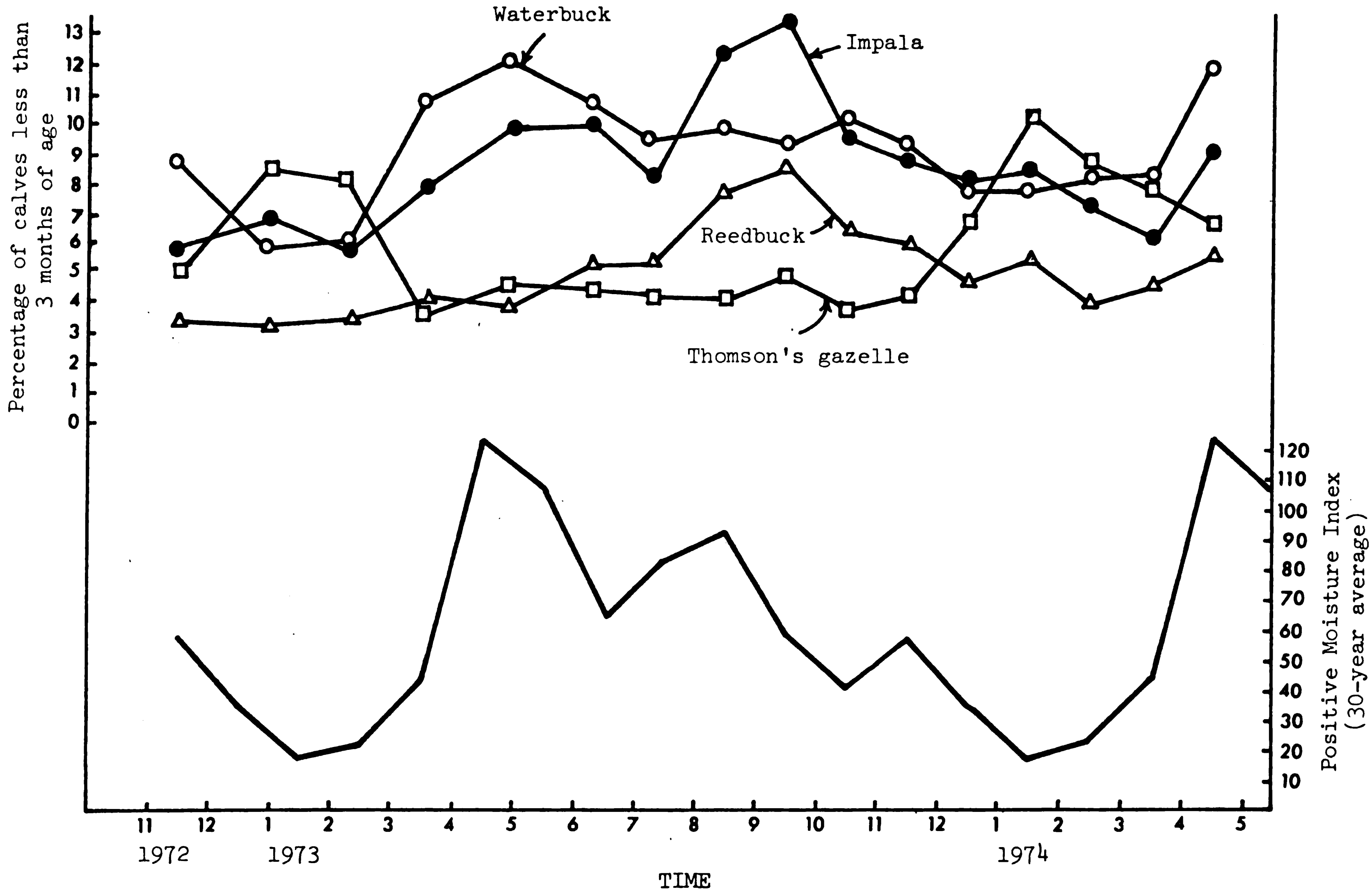


Figure 6. Monthly variation in the percentages of calves less than three months old in Lake Nakuru National Park, Kenya, 1972-74. The 30-year monthly averages for the positive moisture index are also plotted.

Those species had their actual calving peaks in August toward the end of a series of five moist to wet months. Thomson's gazelle produced young throughout the year, but showed a peak during the long dry period, the advantage of which is not understood and was not predicted. If, however, the Nakuru gazelle population is a remnant of the vast migratory herd which Percival (1924) described for this area, then perhaps an increase in calving during the dry season bestowed an advantage over the migratory range as a whole which is no longer evident when only the Nakuru data are considered.

Feeding Strategies

The feeding strategies of Nakuru antelope were closely tied both to daily and seasonal movement patterns. During any season, the movements and foraging patterns for each antelope species were similarly repeated every day. An example of this phenomenon was the daily pattern of waterbuck during the wet season in the southern part of the park. In the late afternoon (Figure 7), waterbuck emerged from the open woodland where they had spent the hot part of the day. They grazed, moving slowly toward the lake. As night approached, grazing subsided and the animals lay down in open areas near the lake. At dawn the animals arose and began grazing, moving away from the lake. By mid-morning they reached the open woodlands where they rested during the middle of the day prior to repeating this daily pattern.

Impala had a daily movement and feeding pattern similar to that of waterbuck. Reedbuck and Thomson's gazelle differed from the first two species by rarely moving through or foraging in open

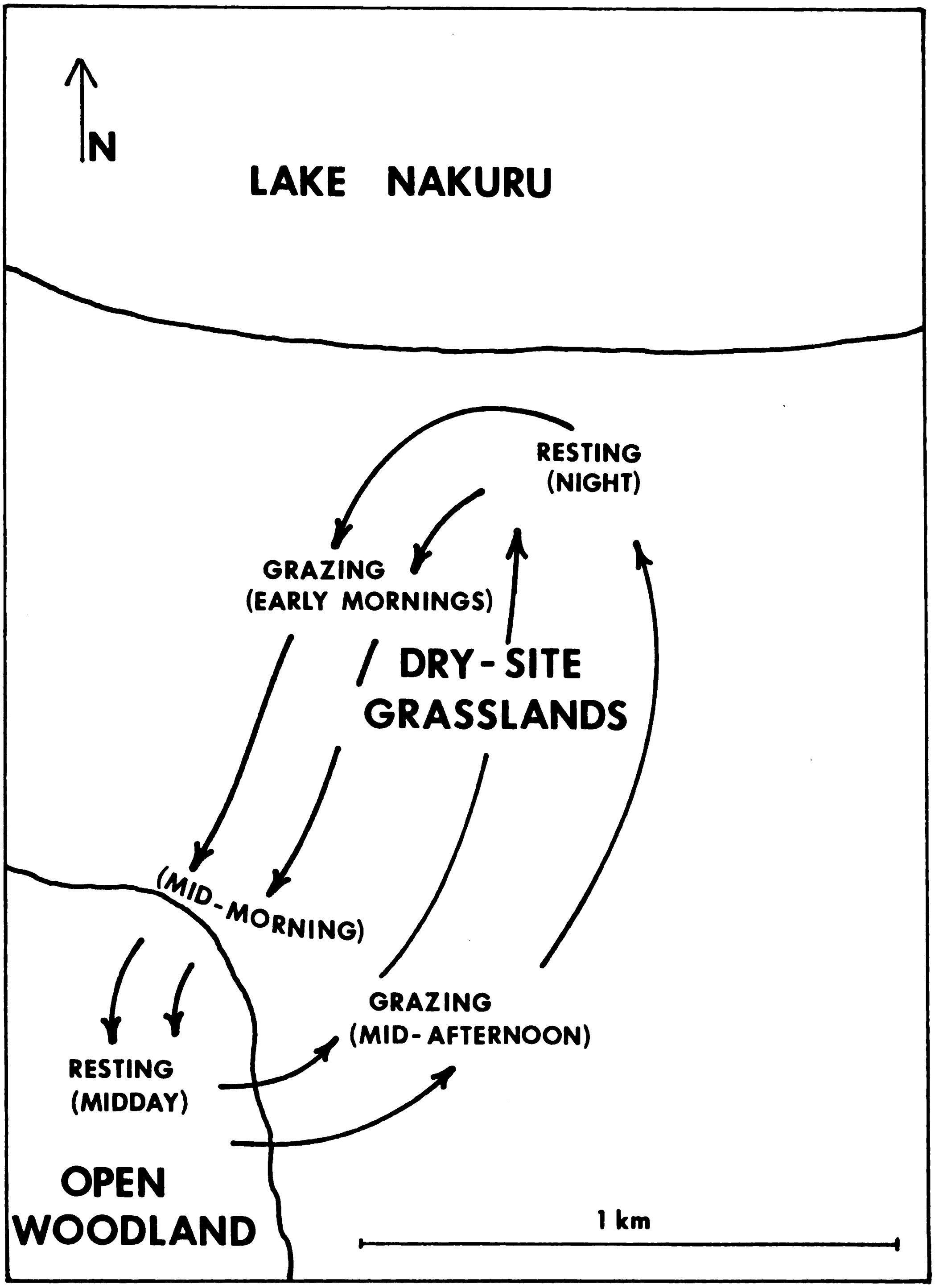


Figure 7. Wet season daily movement and foraging pattern of waterbuck in the southern part of Lake Nakuru National Park, Kenya, observed from 1972-74.

woodlands, but the former species occasionally used bushed areas for cover. More often during the midday heat, these two species chose the shade of scattered trees or of the taller grasses. Thomson's gazelle, in fact, rarely moved or foraged beyond the grassland habitats and spent the middle of the day lying in natural depressions with the taller grass providing some cover.

The daily movement and feeding patterns varied somewhat from species to species and from season to season but, in general, all four main antelope species, moved toward the lake in the afternoon and away from it in the morning. With waterbuck and impala, these movements might be explained by the geographical distribution of habitats. That is, the animals moved toward open woodlands, which are away from the lake, in the morning, and toward open areas, which are near the lake, in the afternoon. With reedbuck and Thomson's gazelle, directional movements also were oriented with respect to the lake even though these species did not move into woodland cover. The cause of these movement and foraging patterns was not clear but they seemed to result in a more uniform and consistent foraging effect than is likely to occur with migratory antelope which move through an area only once or twice per year. Continuous movements by the antelope over the same ranges would also enable more complete utilization of the edible forage.

Superimposed upon the daily movement cycles were seasonal foraging patterns involving six of the 11 distinct vegetation types. The dry-site grassland was the principal forage area for all four antelope species during the moist to wet period of the year (Figure 8). The long dry period, from mid-November to mid-March, had a potential

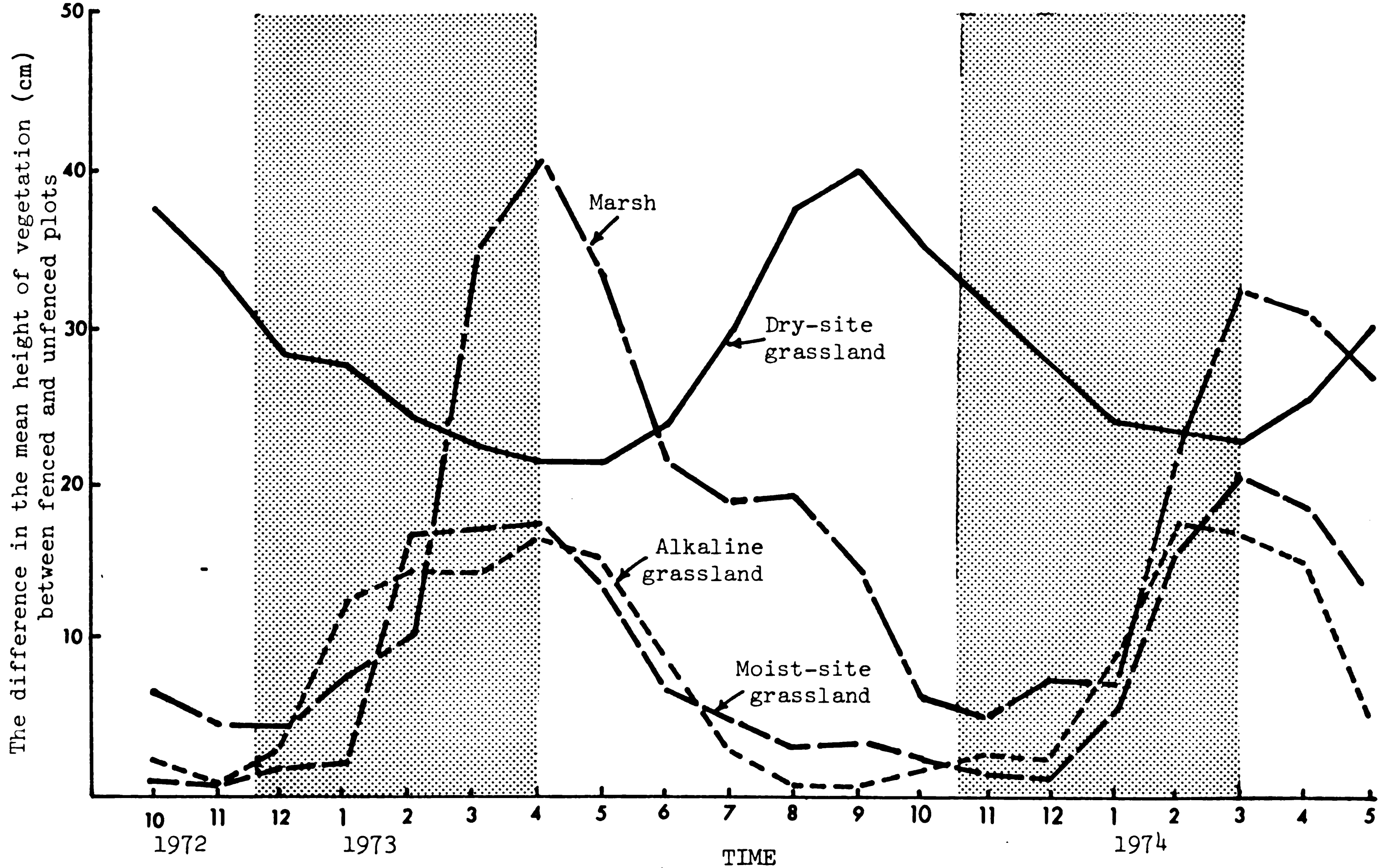


Figure 8. Monthly utilizations of several forage habitats in Lake Nakuru National Park, Kenya. The driest periods (stippled) had a potential evapotranspiration rate nearly three times greater than the rainfall. Graphic peaks indicate periods of greatest herbivore usage.

evapotranspiration rate nearly three times greater than the amount of rainfall ($I_m' \leq 35$). As the long dry period progressed the dry-site grassland was replaced as a foraging area by marsh, moist-site and alkaline grasslands. Foraging pressure (Figure 9) in the main browsing habitats (grass-shrub and open woodland) showed that these zones also were utilized mainly during the long dry period.

The densities of foraging antelope (by species) in each vegetation type (Figure 10a) also verified that the dry-site grassland was the main foraging area during the moist to wet period of the year. During the long dry period, however, the animals moved from this grassland to the other five vegetation types (Figure 10 b-f).

While the four antelope species all concentrated on the dry-site grassland during the wetter period, their habitat preferences tended to diverge during the long dry period (Table 8). Waterbuck fed in all five of the dry season forage habitats but impala largely became browsers using only grass-shrub and open woodland areas. During this same period, reedbuck and Thomson's gazelle moved to marsh and/or other grassland types.

Production Parameters

Petrusewicz and Macfayden (1970) stated that an area's herbivore consumption (c) divided by its primary production (p) is a good measure of the foraging impact within the ecosystem. In order for hypothesis (2) (see introduction) to be supported, the c/p ratio in ecosystems where many large herbivore species are present would have to be greater than where few species are present.

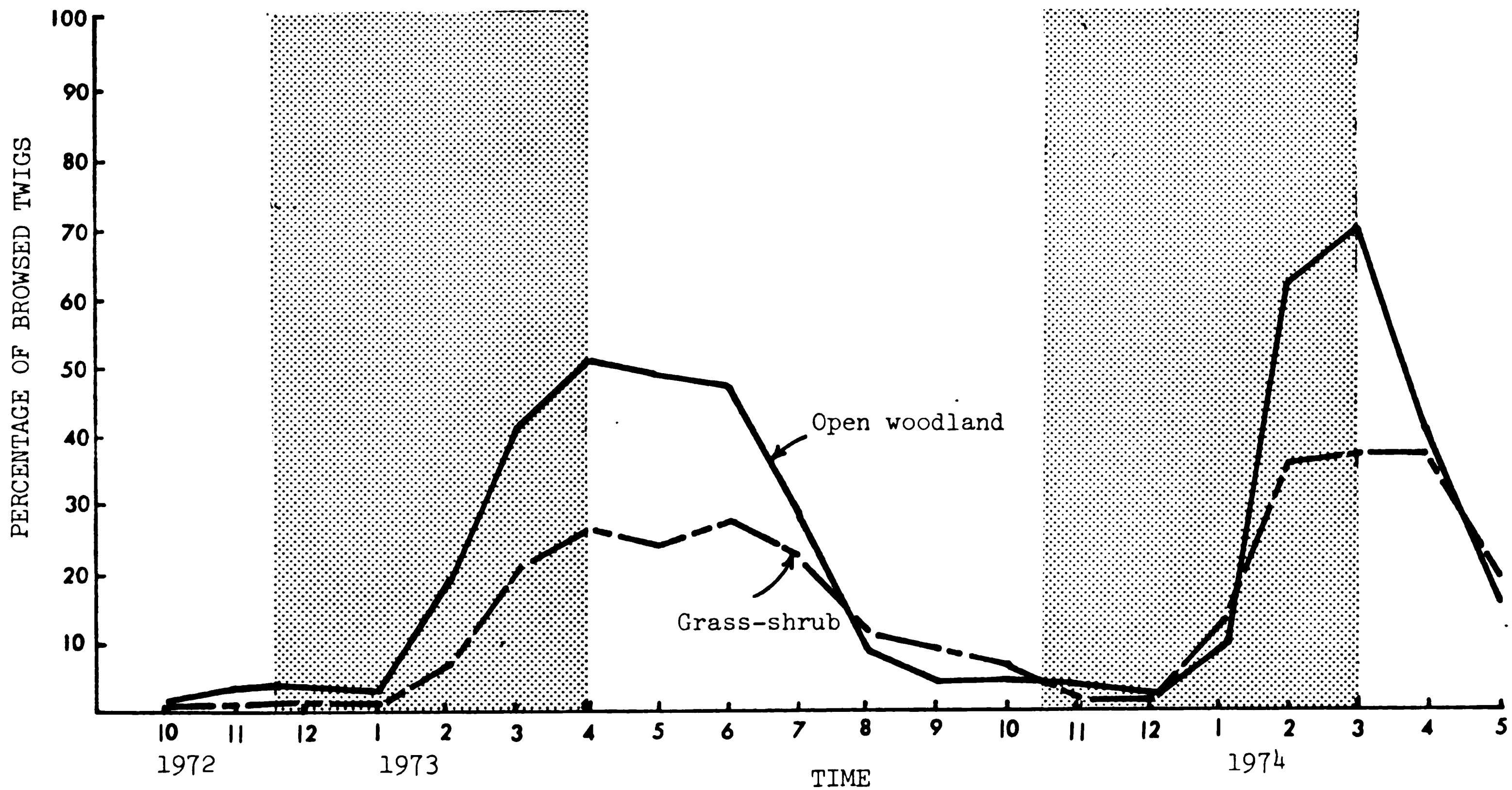
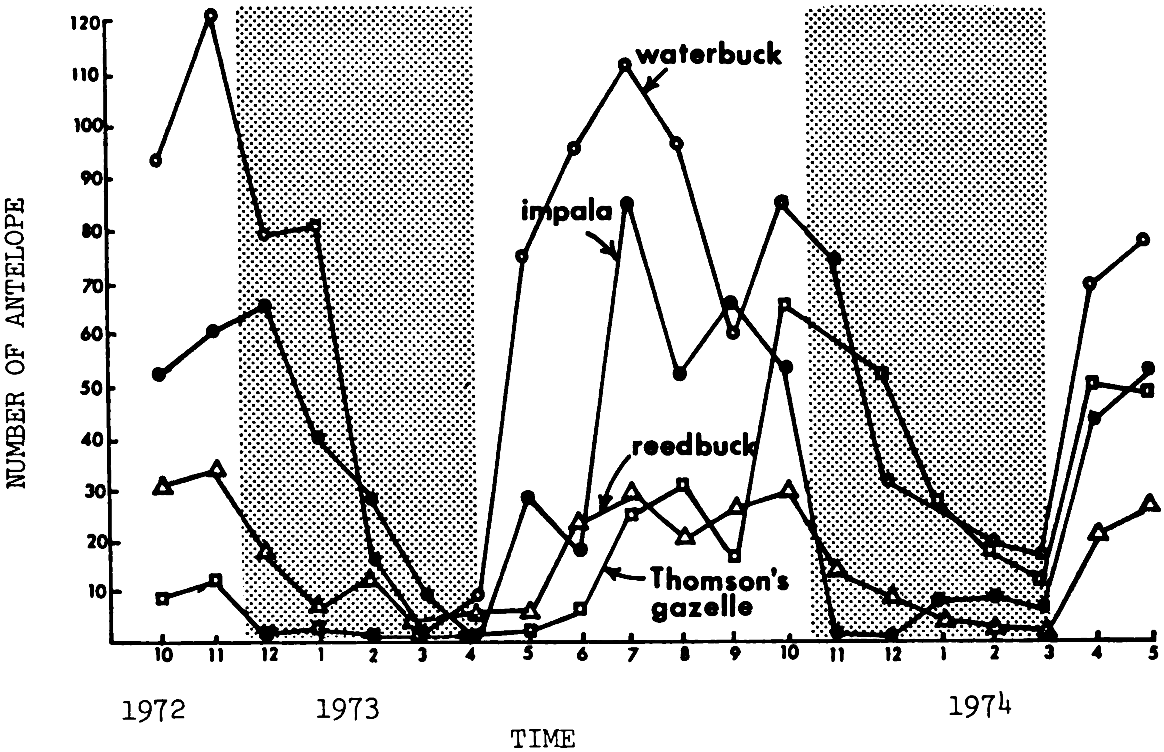


Figure 9. Monthly utilization of browse vegetation in Lake Nakuru National Park, Kenya. The driest periods (stippled) had a potential evapotranspiration nearly three times greater than the rainfall. Graphic peaks indicate periods of greatest herbivore usage.

Figure 10. Monthly changes in the densities of feeding antelope occupying the six forage habitats in Lake Nakuru National Park, Kenya. The driest periods (stippled) had a potential evapotranspiration rate nearly three times greater than the rainfall. The forage habitats are: a. dry-site grassland, b. marsh, c. alkaline grassland, d. moist-site grassland, e. grass-shrub, f. open woodland.

Figure 10 - Cont'd.

a.



b.

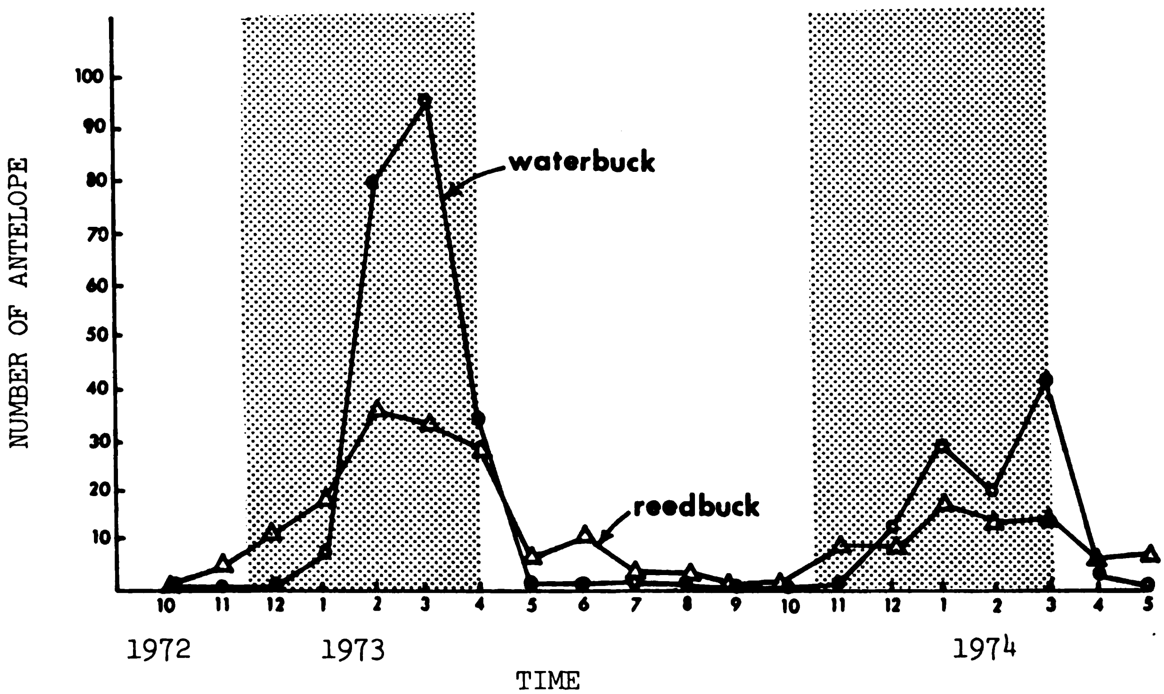
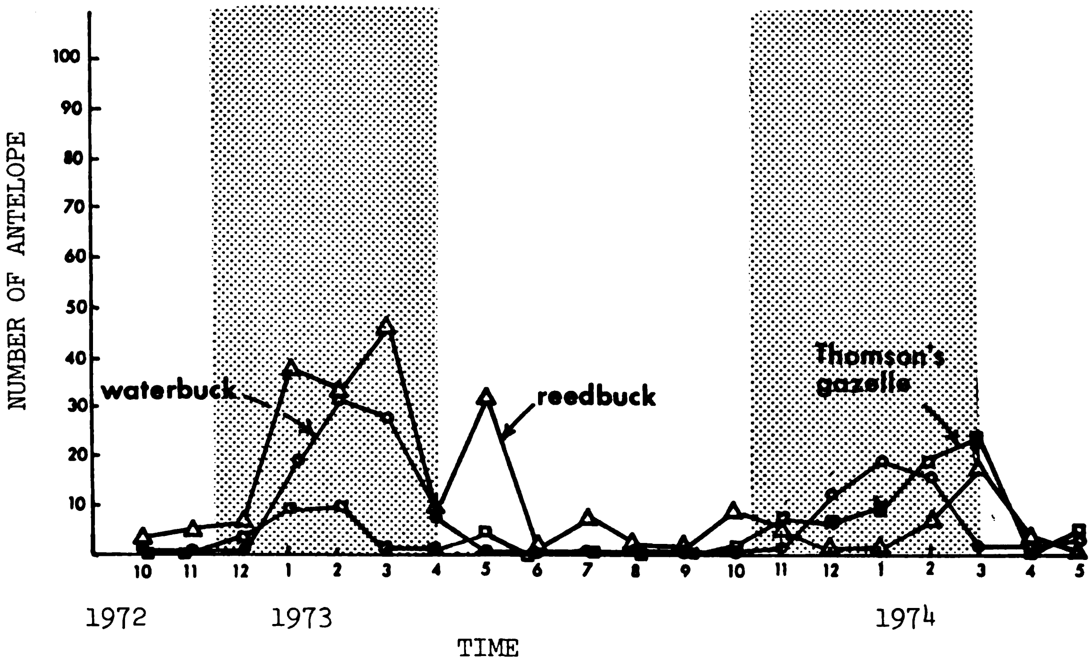
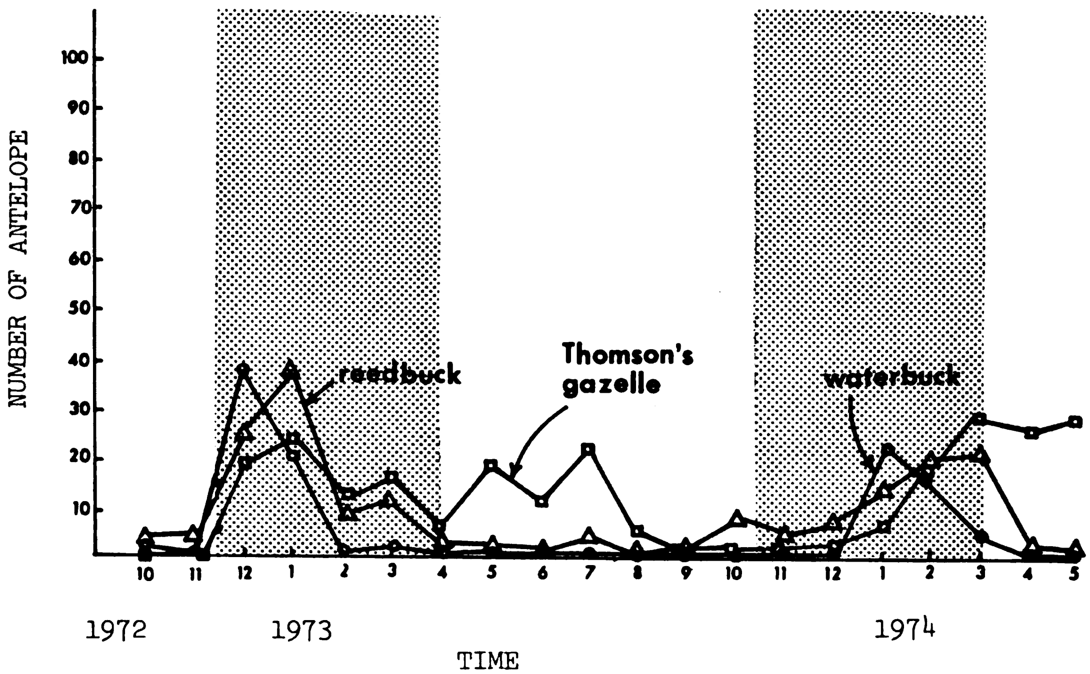


Figure 10 - Cont'd.

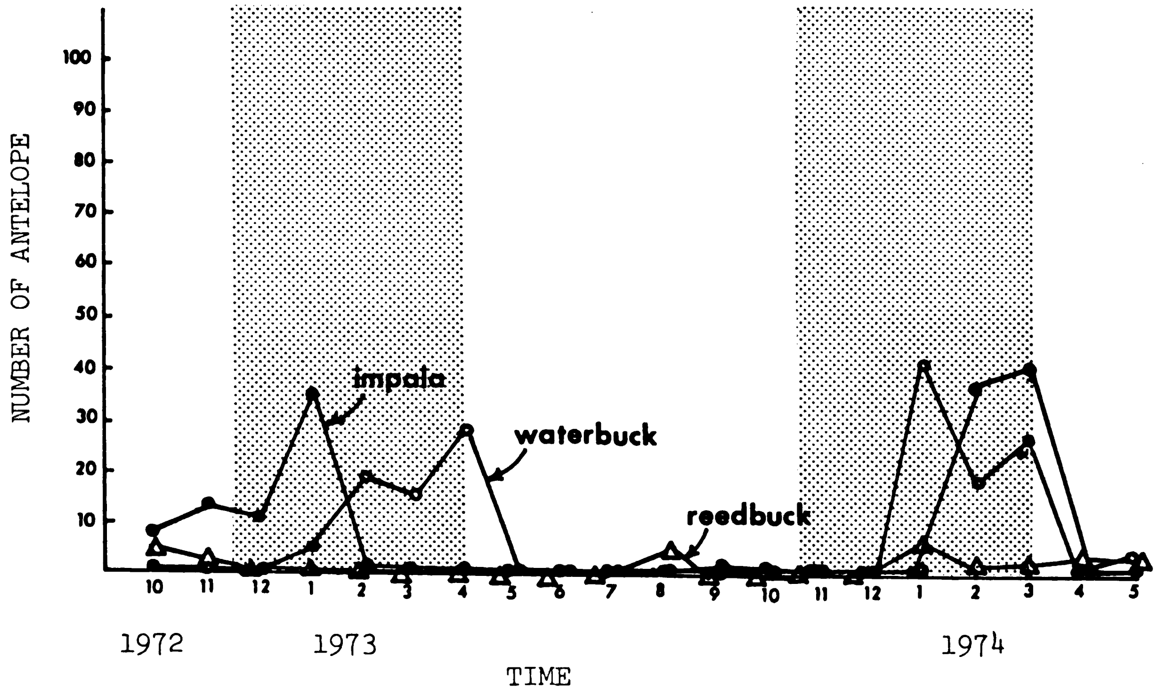
c.



d.

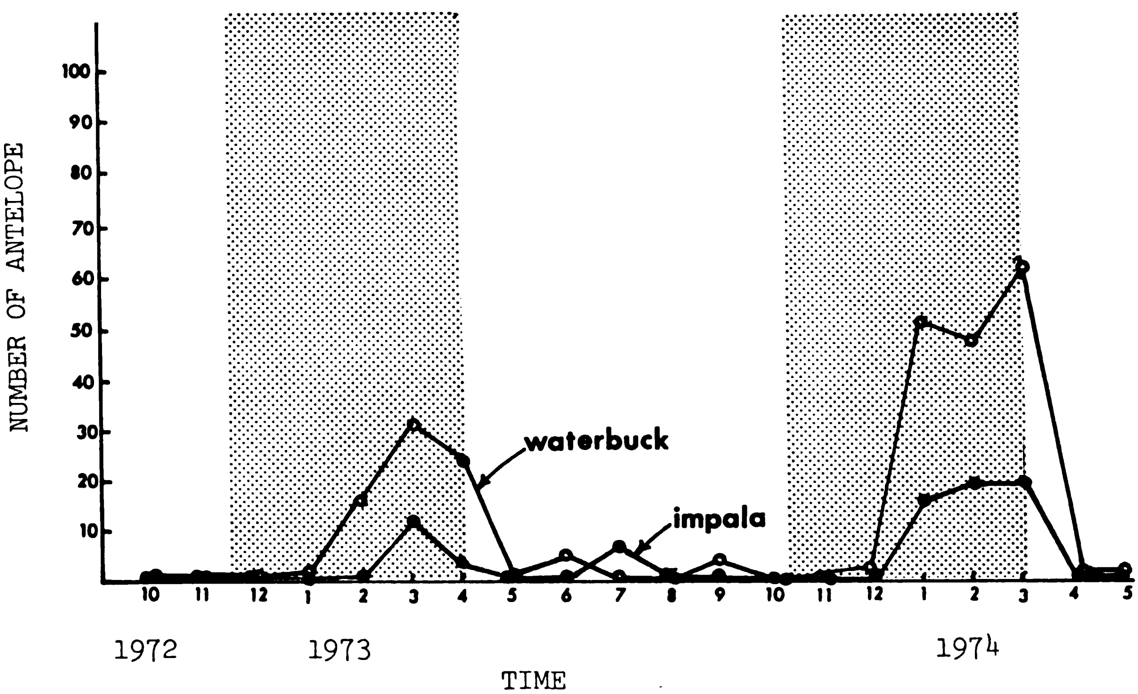


e.



NUMBER OF ANTELOPE
100
90
80
70
60
50
40
30
20
10
impala
waterbuck
reedbuck
10 11 12 1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5
1972 1973 1974
TIME

f.



NUMBER OF ANTELOPE
100
90
80
70
60
50
40
30
20
10
waterbuck
impala
10 11 12 1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5
1972 1973 1974
TIME

Table 8. Forage habitat preferences of the four common antelope species in Lake Nakuru National Park, Kenya, 1972-74. DSG = dry-site grassland; M = marsh; MSG = moist-site grassland; AG = alkaline grassland; GS = grass-shrub; OW = open woodland.

Species	Moist to Wet Period (April-October)	Long Dry Period (November-March)
Defassa waterbuck	DSG	M, MSG, AG, GS, OW
Bohor reedbuck	DSG, AG	M, MSG, AG
Impala	DSG	GS, OW
Thomson's gazelle	DSG, MSG	MSG, AG

Phillipson (1973) used the c/p ratio to examine the impact of foraging by large herbivores in the Serengeti ecosystem. His procedure which is used here, requires data for the annual primary production and for the standing crop biomass of large herbivores, from which their consumption rate is calculated using a series of assumptions.

In my study, a measured value for the consumption rate was also determined through clip-plots (Table 9) which was 14% greater than the calculated value. This error, however, is considered to be within reasonable limits for a gross estimate of this type.

Other studies which have simultaneously measured primary production and large mammal biomass include those of Western (1973) on the short-grass plains of the Amboseli Game Reserve in southern Kenya, Phillipson (1973) on the short to medium-grass plains of Serengeti National Park in northwestern Tanzania and, Harris (1970) from the bushland-grassland area of Mkomazi Game Reserve in north-eastern Tanzania. Amboseli and Serengeti maintain a large number of herbivore species while Nakuru and Mkomazi maintain only a few species in abundance.

The largest c/p ratio (Table 9) was found in Amboseli where 25 percent of the net available primary production was consumed by large herbivores. Serengeti, however, had a ratio less than half that of Amboseli (10.4 percent). The former park area of Nakuru was similar to Serengeti with a calculated value of 10.2 percent and a measured value of 11.9 percent. The total census area of Nakuru was somewhat less, with a value of 7.1 percent. Data from both the

Table 9. Estimates of primary and secondary production parameters for different regions of East Africa. Standing crop biomasses are given in grams/meter^2 dry weight; all other values given in grams/meter^2/year, except for the consumption/production ratio which is a percentage. The value for forage consumed in parenthesis was derived from clip-plots.

	Large Number of Herbivore Species		Small Number of Herbivore Species		
	Serengeti National Park, Tanzania	Amboseli Game Reserve, Kenya	Mkomazi Game Reserve, Tanzania	Lake Nakuru National Park, Kenya (Total Census Area)	Lake Nakuru National Park, Kenya (Former Park Area)
Net available above-ground primary production	300	200	250	418	427
Large-herbivore biomass[1] (standing crop)	1.0	1.6	0.25	0.95	1.38
Production by large herbivores[2]	0.2	0.32	0.05	0.19	0.28
Forage assimilated by large herbivores[3]	12.5	20.0	3.2	11.9	17.5
Forage consumed by large herbivores[4]	31.25	50.0	8.1	29.75	43.75 (50.96)
$\frac{\text{Herbivore consumption}}{\text{Primary production}} \times 100$	10.4	25.0	3.3	7.1	10.2 (11.9)

[1]Assuming water content of live weight = 80% (Phillipson, 1973).
[2]Assuming production/standing crop biomass = 20% (Wiegert and Evans, 1967).
[3]Assuming production = 1.6% of assimilation (McNeill and Lawton, 1970).
[4]Assuming assimilation efficiency = 40% (Hughes, Milner and Dale, 1964).

Sources of data: Serengeti (Phillipson, 1973); Amboseli (Western, 1973); Mkomazi (Harris, 1970); Nakuru, this study.

former park area and the total census area provide the probable maximum and minimum values for that park. Mkomazi had the lowest ratio of all (3.3 percent). These data show no clear-cut relationship between the number of herbivore species present in the ecosystem and the amount of vegetation consumed.

DISCUSSION

Riney (1964) hypothesized that, when an ungulate population is much smaller than could be supported by the available forage and it is suddenly freed of its limiting factors, it will undergo a single eruptive oscillation before attaining the range carrying capacity (Figure 11). The ungulate populations of Lake Nakuru National Park meet the criteria for such a situation. Beginning with the disturbances to the area caused by early European farmers and continuing until 1968, the wild ungulate populations were held at a low density apparently by competition from livestock and by heavy poaching. In 1968, all livestock was removed from the former park area and the incidence of poaching was greatly reduced by the installation of a ranger force. The four major antelope species, waterbuck, impala, reedbuck and Thomson's gazelle have apparently been increasing in number since that time (Figure 5).

Riney (1964) postulated that, with medium-sized antelope such as impala or reedbuck, the time involved between the initiation and peak of the irruptive oscillation would be 15-20 years. With smaller antelope (*e.g.*, gazelle), it would require a shorter interval and with larger antelope (*e.g.*, waterbuck), a longer one. Field studies (Klein, 1968; Caughley, 1970) have shown that Riney's model has validity. If so, the four main antelope populations at Nakuru

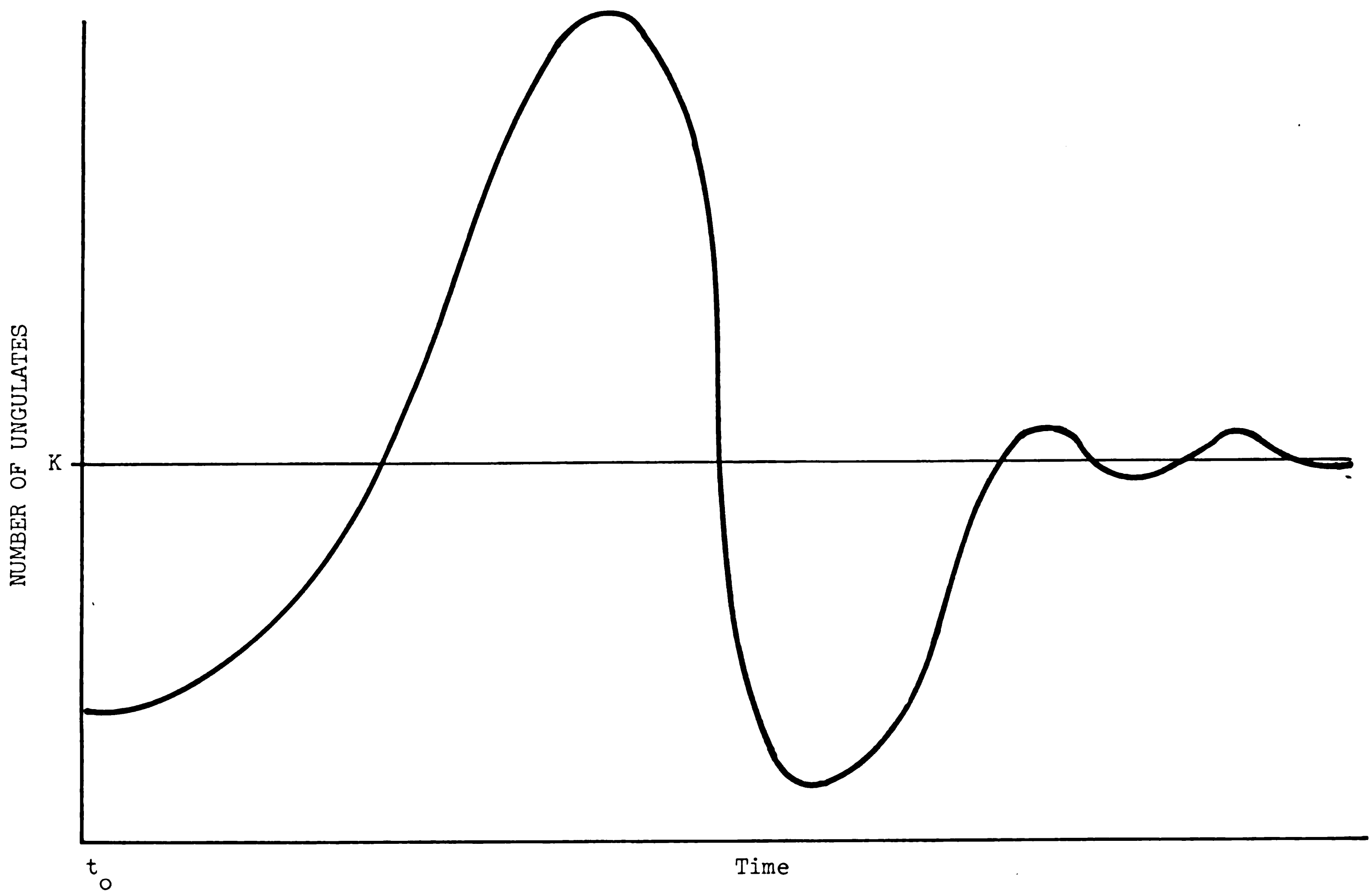


Figure 11. Model of a single eruptive oscillation expected to occur in ungulate populations when there is a large difference between the number of animals and the carrying capacity at time t_o (after Riney, 1964).

are in the initial stages of an eruption (Figure 11). Thus, these populations might be expected to exceed the range carrying capacity in the near future.

Recently, however, the park has been enlarged to about six times the land area it held in 1968. It is too early to tell what the ultimate effect of the land acquisition will be for the ungulate populations. It is likely, however, that if overgrazing develops, it would have the greatest effect on the dry-season forage habitats. These are relatively small in total land area but are heavily used during the long dry period of the year and thus, are critical to the maintenance of antelope.

The antelope of Nakuru were found to practice a natural grazing rotation among six distinct vegetation types. These data support the hypothesis that non-migratory antelope are successful because they find and utilize a wide range of food resources. Conversely, vegetative heterogeneity is essential in their habitat to provide a good quality of forage throughout the year. The grazing rotation practiced by the antelope allowed each vegetation type alternate periods of use and recovery and as long as no overgrazing occurs, is undoubtedly beneficial to plants and herbivores alike.

Within this rotational scheme, the antelope first selected the forage resources on the basis of the wet and dry seasons. The seasonal selection of forage may result from changes in forage palatability (nutritional quality). This factor has been suggested as the stimulus for movements of migratory antelope (Bourliere and Hadley, 1970; Western, 1973) as well as for the forage selectivity of livestock (Grunow and Van Ginkel, 1965). Palatability of forage is frequently measured by the crude fiber and crude protein contents.

It should be noted that, while ruminants can live without protein in their diets if they are provided with nitrogen in a simple organic form, in nature they receive most, if not all, of their nitrogen in the form of crude protein (McDonald et al., 1973). The main wet season forage habitat was the dry-site grassland. From previous studies (Dougall et al., 1964; Field, 1971), the grass species within this habitat showed a considerable loss in crude protein and an increase in crude fiber content during the dry season. If this same relationship holds true for Nakuru, then foraging by the antelope in the dry-site grassland subsided as palatability decreased. The antelope then shifted to the dry-season forage types, such as browse and the moist-site and alkaline grass species. These retain a high crude protein content during the dry season and hence, a high nutritional value (Harker, 1961; Lawton, 1968).

A second way in which the antelope selected forage resources was through the divergence of their habitat preferences during the dry season (Table 9). This separation is probably the result of the different abilities of each antelope species to digest either grass or browse while attempting to optimize the intake of high-protein forage (Hofmann, 1968; Stewart, 1971; Hofmann and Stewart, 1972). Thus, during the critical dry period, waterbuck became browsers as well as grazers, impala became browsers almost exclusively, and reedbuck and gazelle remained as grazers but shifted their feeding preferences more completely to the moist-site and alkaline grasslands.

The extent to which the divergence in habitat preferences acted to reduce interspecific competition is unknown. At the time of this study, however, there appeared to be an abundance of food resources and no competition was evident.

The concentration of antelope near the lake during the dry periods can be explained by the distribution of the dry-season forage habitats. Four out of five of these (marsh, alkaline grassland, moist-site grassland and grass-shrub) were located in close proximity to the lake. The diversity of habitats, in fact, is dependent upon the alkalinity and moisture gradients in the soil resulting from lacustrine influences. Since the antelope rely upon this diversity to provide their year-round food resources, it is likely that the abundance of animals is dependent upon the presence of the lake, as it affects and diversifies the vegetative habitat.

A comparison of consumption/production values from several East African ecosystems (Table 9) does not support the hypothesis that a greater proportion of the vegetation is consumed where many species of large herbivores are present. For example, Amboseli and Serengeti have equally large numbers of herbivore species, but show considerably different c/p values. Conversely, Serengeti has a larger number of species than the former park area of Nakuru, yet their c/p values are similar. The reason for the similarity in the latter case may lie in the feeding specificity of the herbivores themselves. Serengeti has many species each with specific feeding preferences (Bell, 1969) while Nakuru has a few species of generalized feeders.

MANAGEMENT IMPLICATIONS

Lake Nakuru National Park consists of two major ecosystems, the lake and the surrounding land. With its reputation as a sanctuary for the lesser flamingo (*Phoeniconaias minor*) the lake has attracted the interests of researchers, conservationists, park administrators and, of course, tourists. The problems and potential of the land component have been largely ignored. For example, the recent expansion of the park was carried out, not for the ecological value of the land and its plant and animal inhabitants per se, but, to provide a large buffer zone for the lake.

This study was one of the first attempts to examine some of the ecological interactions within the terrestrial ecosystem. It is hoped that it will form part of the data base for the formulation of management decisions and policies for this national park. A number of management implications have resulted from the study and five major ones will be discussed here.

The first of these involves the effect of the park expansion on large mammal populations. At the time the park was established, the antelope populations were apparently small and reclusive. No attempt was made to evaluate what the antelopes' habitat requirements were, or might become, when protection from disturbance was provided. During the wet season in particular, waterbuck, impala and gazelle frequently moved outside of the former boundary (Figure 4) apparently to take advantage of the new grass growth which occurred there. This suggests that the former park area was simply too small even for these non-migratory species.

Although it was not the original intention of the expansion plan, land acquisition has placed a larger part of the antelopes' habitat under park protection. It seems, therefore, that the ecological viability of the park with regard to large mammals has been substantially increased by the addition of this land.

A second management implication involves the need for a comprehensive monitoring program for the park. If indeed the antelope populations are increasing, then overpopulation and overgrazing could become a future reality. During the past 15 years, a heated controversy has developed over whether or not to cull populations which have apparently exceeded the carrying capacity in some of Kenya's national parks (Lamprey, 1974; Olindo, 1974). This argument has spread to the international arena dividing conservationists into two principal camps. One group states that the environment must be protected from gross and rapid changes which are brought about through over-foraging by large mammals, and that systematic culling should be instituted where it is deemed necessary, as part of a comprehensive management policy (Laws and Parker, 1968; Goddard, 1970; Parker, 1972). The opposing segment believes that overpopulations, with subsequent habitat changes, are part of the natural cycle of events. They claim that habitat changes are not necessarily synonymous with deterioration and that nature should be left to take its course (Glover, 1972). They further argue that if a species changes its habitat to where it suffers losses, other species better suited to the changed environment will move in and utilize the habitat until it gradually changes back once again.

A major problem with this argument is that the Africa of today is not the Africa of a hundred years ago. National parks and game reserves are fast becoming the last reservoirs of indigenous big game. Surrounding lands have been taken for other purposes and the wildlife there has been driven out or destroyed. If a wild population caused its habitat to be altered to where it could no longer provide for that population, where could it go? Where would other populations come from which could now live in that habitat? For many national parks in East Africa and particularly for Nakuru, the answer is that there is nowhere either for animals to emigrate or from which to immigrate.

An assessment must be made of the continuing impact of wild herbivore populations on the environment. The present study indicates that there are 4-6 important large mammal species in residence in Nakuru National Park and that these have their major impact on six main forage habitats. The effect of herbivores would be greatest during years when rainfall is below average so that a monitoring program for Nakuru Park should include the daily collection of rainfall data. Rainfall patterns are somewhat local and more recording stations are needed in the park, particularly at the southern end of the lake where antelope concentrations are greatest.

Gross changes in vegetation could be examined through aerial photos taken at 1-2 year intervals. The entire park area can be covered by eight overlapping 1:50,000 aerial photos. Ground surveys of the type used in this study should be undertaken at least twice a year to follow vegetation trends, preferably with one survey in September at the end of the wet period and one in March at the end of the long dry period. Particular attention should be paid to the dry-season forage habitats since several of these are most heavily used and will probably show the first signs of overgrazing. Total-area counts of large mammals (or, at least, the four main species) should be continued so as to record trends in density and biomass. A monitoring program, as outlined, will allow for the continuing evaluation of range trend with respect to both the effective precipitation and the density of large herbivores.

According to Riney's model, when a population exceeds the range carrying capacity, changes in the habitat brought about by overgrazing precipitate a population crash and subsequent natural regulation near the carrying capacity. The degree of habitat change needed to cause the crash may be great or slight and seems to depend upon the type of habitat and the species of herbivores involved (Glover, 1963; Harper, 1969; Caughley, 1970). A cropping program should be undertaken by Kenya National Parks if overgrazing begins to create unacceptable, long-term changes in the habitat. An invasion into grasslands of unpalatable shrubs such as *Tegetes minuta, Chenopodium opulifolium, Aerva lanata,* and *Withania somnifera* should be watched for and should not be allowed to occur.

In theory, a cropping program would maintain a high fecundity rate for the population since the necessary population regulator (habitat change) would be prevented from occurring. The National Parks administration, therefore, must be willing to carry out the program on a regular and sustained basis. If, on the other hand, habitat change due to overgrazing was minor and short-term, a population should be left to regulate itself. This latter course of action follows the current hands-off policy of Kenya National Parks. In my opinion, however, a flexible policy on the cropping issue should be outlined to deal with any contingency.

A third management implication of this study is that the stability of the lake and of the large-mammal populations surrounding it are closely related. Moisture and alkalinity gradients radiating from the lake create the vegetative diversity upon which the antelope depend and, therefore, destruction or deterioration of the lake would not only threaten the bird-life, but might have serious repercussions on vegetative patterns and thus, on the antelope as well.

A fourth management implication is that care must be taken in the movement of tourists through the park and in the placement of tourist developments such as roads, trails, picnic sites and camp sites. While this is true for all national parks, at Nakuru the most serious threat is to the dry-season forage habitats which are concentrated near the lake (Figure 3). Since the lake constitutes the major tourist attraction, these forage habitats are under continuous visitor pressure. Although they are very important for the maintenance of large mammals, they make up only a small percentage of the total park area. Any unnecessary or unplanned development which destroys or damages these habitats could have profound effects on large herbivore populations.

The road building of 1973 within Nakuru Park provides an example of the need to consider the ecological ramifications of all development projects. This road was constructed closer to the lake than the previous one and, as a result, cut through four dry-season forage habitats. These were marsh, moist-site grassland, alkaline grassland and grass-shrub habitats -- areas which were largely avoided by the old road. In the future it is hoped that development of this type will not be allowed and that the dry-season forage habitats will be given the utmost protection.

Habitat destruction has also been caused by the movement of tourists through the park (Kutilek, 1971). It is gratifying to see that Kenya National Parks have instituted a ban on all off-the-road driving. This rule has been strongly enforced since 1972 at Lake Nakuru and was instrumental in reducing unwarranted damage to the environment. Continued efforts must be made to monitor and reduce factors which could cause habitat deterioration and a lowered carrying capacity for large mammals. These particularly include unsound development, off-the-road driving and excessive overgrazing.

The fifth and final management implication involves the use of non-migratory antelope in game cropping and ranching schemes. With the human population growth rate at 3.3 percent per year (Kenya Population Census, 1969), land is at a premium in Kenya. Even the agriculturally marginal lands are much sought after (Capone, 1971). While research has shown that harvesting wild herbivores is a highly productive use of these lands (Petrides, 1956; Dasmann, 1962;

Talbot et al., 1965; Hopcraft, 1969), it is politically risky to put the vast acreages required by migratory antelope into game production schemes.

As this study has shown, non-migratory antelope species can maintain high population biomasses and, very likely, rapid turnover rates, provided that their habitats have adequate drinking water and sufficient vegetative heterogeneity. At the same time, they do not require the large tracts of land that migratory antelope do. These characteristics make some non-migratory antelope species likely candidates for small-scale meat production schemes.

Further research would be required to determine the best complement of herbivore species for the given area to be cropped or ranched. In particular, one would need to examine the amount of interspecific overlap in food preferences, and stock the area with antelope species which collectively would use a wide range of forage components. Nakuru could act as a model in this regard. It was with a certain amount of luck that the large-scale annilation of animals in the first few decades of this century left Nakuru with viable populations of waterbuck, reedbuck, impala and Thomson's gazelle. These species apparently practice complementary foraging while utilizing many habitat types. Where a diversity of habitats exist, a system like that at Lake Nakuru National Park could be established and have great value as a meat production scheme.

SUMMARY

From September, 1972 through May, 1974, a study was carried out at Lake Nakuru National Park, Kenya, which tested two hypotheses: (1) that non-migratory antelope are successful because they find and utilize a wide range of food resources; and (2) that a greater proportion of the vegetation is consumed where many species of large herbivores are present. The data collected were also important as baseline information for management purposes.

Only a few species of large mammals were present in abundance at Nakuru. This appeared to be a result of the settlement activities of early European farmers. Since the turn of the century, 17 species of large herbivores and carnivores have either been exterminated or have undergone severe reductions of their populations. Certain non-migratory large mammals, particularly, defassa waterbuck, *Kobus defassa*, impala, *Aepyceros melampus*, and bohor reedbuck, *Redunca redunca*, have recently increased in number. These species, together with Thomson's gazelle, *Gazella thomsonii*, hippopotamus, *Hippopotamus amphibius*, and buffalo, *Syncerus caffer*, were the park's dominant large mammals with respect to numbers and/or biomass.

The density for all large mammals in the former park area was $74.47 \pm 7.68/km^2$. The coefficients of variation for the density of waterbuck, impala and gazelle were all substantially reduced when censuses were carried out on a larger area of land. This suggested

that the former park area was of inadequate size to completely provide for these populations. The standing crop biomass for the former park area was 6876 ± 571 kg/km^2 which is higher than most savanna and bushland areas of East Africa. The biomass of waterbuck accounted for more than 75 percent of this total.

A comparison of population trends over a three year period revealed apparent increases in the number of waterbuck, impala, reedbuck and gazelle. While none of the difference among means were statistically significant, the trends were consistant and seemed to reflect real increases. The calculated annual rate of increase was 6.52 percent for all populations combined, 16.0 percent for impala, 6.94 percent for waterbuck, 6.29 percent for reedbuck, and 6.22 percent for gazelle. These antelope populations may all be in the early stages of an eruptive oscillation.

The vegetation was classified into 11 types, six of which were important foraging habitats for antelope: marsh, moist-site grassland, alkaline grassland, dry-site grassland, grass-shrub and open woodland. The annual net above-ground primary production was found to vary from 762 ± 57 (grams/meter^2/year, oven-dry weight) in the wetter marsh habitat to 321 ± 46 in the drier open woodland habitat with a mean value of 427 grams/meter^2/year for the former park area. Range analysis, by season, showed that few significant changes were discernable in either the percentage cover or in the height of plants. It appeared, therefore, that the antelope populations remained within the carrying capacity during the study period.

The four main antelope species were found to practice a seasonal grazing rotation among six distinct vegetation types, a finding which supports the first hypothesis. The dry-site grassland was the preferred habitat for all species during wet periods. During the long dry period, each antelope species used two or more of the remaining habitats. While some overlap in habitat preferences occurred, there appeared to be an abundance of food and no interspecific competition was evident. Resource selection of this type may be the result of seasonal changes in forage palatability coupled with ungulate nutritional adaptations. The overall foraging system resulted in each habitat having alternate periods of use and recovery, yielding benefits to plants and herbivores alike.

A comparison of primary and secondary production parameters from different large-mammal ecosystems in East Africa showed no clear-cut relationship between the number of large herbivore species present and the amount of vegetation consumed by them. The second hypothesis was, therefore, not supported.

The management implications of this study are: (1) the recent land acquisition has apparently been beneficial to large mammals in Nakuru National Park since it brought under national parks control more of the habitats which they used; (2) a comprehensive program should begin immediately to monitor rainfall, vegetation trends and the density of antelope, and a cropping operation should be initiated if unacceptable habitat changes result from overgrazing; (3) the diversity of forage habitats which the antelope rely upon for their year-round food resources is apparently the result of lacustrine influences and, therefore, deterioration of the lake may adversely affect the ungulate populations; (4) tourist developments and activities which are detrimental to the forage habitats should be avoided since they might lower the carrying capacity for antelope; and, (5) where limited lands are available and sufficient habitat diversity exists, non-migratory antelope might well be employed in game cropping and ranching schemes.

APPENDICES

Appendix I. A list of plant species collected in Lake Nakuru National Park, Kenya, from 1970-74. The families are arranged according to a modified Bentham and Hooker system used by the Kew Herbarium.

Menispermaceae

Stephania abyssinica (Dillon & A. Rich.) Walp var. *abyssinica*

Cruciferae

Farsetia stenoptera Hohst.

Capparaceae

Capparis fascicularis DC.

Maerua triphylla A. Rich. var. *johannis* (V. & G.) De Wolf

Malvaceae

Abutilon longicuspe A. Rich.

Abutilon mauritianum (Jacq.) Medic.

Hibiscus aponeurus Sprague & Hutch.

Hibiscus diversifolius Jacq.

Hibiscus flavifolius Ulbr.

Sida cuneifolia Roxb.

Sterculiaceae

Dombeya burgesiae Gerrard

Tiliaceae

Grewia similis K. Schum.

Rutaceae

Teclea simplicifolia (Engl.) Verdoorn

Toddalia asiatica (L.) Lam.

Celastraceae

Maytenus sp.

Rhamnaceae

Rhamnus staddo A. Rich.

Vitaceae

Cyphostemma orondo (Gilg & Bened.) Descoings

Sapindaceae

Dodonaea viscosa (L.) Jacq.

Anacardiaceae

Rhus natalensis Bernh.

Mimosaceae

Acacia abyssinica Benth. subsp. *calophylla* Brenan
Acacia albida Del.
Acacia gerrardii Benth.
Acacia hockii De Wild.
Acacia seyal Del. var. *seyal*
Acacia xanthophloea Benth.

Caesalpiniaceae

Cassia bicapsularis L.
Cassia didymobotrya Fres.

Papilionaceae

Crotalaria deserticola Bak.f. var. *deserticola*
Crotalaria vallicola Bak.f.
Indigofera circinella Bak.f.
Medicago laciniata (L.) Mill.
Rhynchosia sp.
Sesbania goetzei Harms
Sesbania sesban (L.) Merr. var. *nubica* Chiov.

Crassulaceae

Kalanchoe densiflora Rolfe

Cucurbitaceae

Peponium vogelii (Hook.f.) Engl.
Zehneria scabra (L.f.) Sond

Umbelliferae

Steganotaenia araliacea Hochst.

Araliaceae

<u>Cussonia</u> <u>holstii</u> Engl.

Rubiaceae

<u>Oldenlandia</u> <u>scopulorum</u> Bullock
<u>Pentanisia</u> <u>ouranogyne</u> S. Moore
<u>Tarenna</u> <u>graveolens</u> (S. Moore) Brem.

Compositae

<u>Aspilia</u> <u>mossambicensis</u> (Oliv.) Wild
<u>Aster</u> <u>muricatus</u> Less.
<u>Conyza</u> <u>floribunda</u> H.B.K.
<u>Conyza</u> <u>stricta</u> Willd.
<u>Crassocephalum</u> <u>mannii</u> (Hook.f.) Milne-Redh.
<u>Crassocephalum</u> <u>vitellinum</u> (Benth.) S. Moore
<u>Erlangea</u> <u>cordifolia</u> (Oliv.) S. Moore
<u>Galinsoga</u> <u>parviflora</u> Cav.
<u>Melanthera</u> <u>scandens</u> (Schumach. & Thonn.) Roberty
<u>Pluchea</u> <u>bequaertii</u> Robyns
<u>Psiadia</u> <u>arabica</u> Jaub. & Spach
<u>Senecio</u> <u>petitianus</u> A. Rich.
<u>Spilanthes</u> <u>mauritianum</u> (A. Rich.) DC.
<u>Tagetes</u> <u>minuta</u> L.
<u>Tarchonanthus</u> <u>camphoratus</u> L.
<u>Vernonia</u> <u>auriculifera</u> Hiern
<u>Vernonia</u> <u>brachycalyx</u> O. Hoffm.
<u>Vernonia</u> <u>pauciflora</u> Less.

Ebenaceae

<u>Euclea</u> <u>divinorum</u> Hiern

Oleaceae

<u>Olea</u> <u>africana</u> Mill.

Asclepiadaceae

<u>Cynanchum</u> <u>tetrapterum</u> (Turcz) R.A. Dyer
<u>Periploca</u> <u>linearifolia</u>

Boraginaceae

Cordia ovalis DC.
Cynoglossum coeruleum DC.

Convolvulaceae

Cuscuta campestris Yuncker
Ipomeae cairica (L.) Sweet

Solanaceae

Datura stramonium L.
Solanum incanum L.
Withania somnifera (L.) Dunal

Scrophulariaceae

Rhamphicarpa montana N.E. Br.

Acanthaceae

Dicliptera sp.
Hypoestes verticillaris (L.f.) Roem. & Schultes
Justicia flava Vahl
Justicia whytei S. Moore
Justicia sp.
Monothecium glandulosum Hochst.

Verbenaceae

Lippia sp.
Verbena bonariensis L.

Labiatae

Iboza multiflora (Benth.) E.A. Bruce
Lantana camera L.
Leonotis nepetifolia R. Br.
Leucas martinicensis R. Br.
Ocimum suave Willd.
Plectranthus assurgens (Bak.) J.K. Morton
Plectranthus kilimandschari (Guerke) Agnew
Plectranthus marrubioides Benth.
Satureja punctata (Benth.) Briq.
Tinnea aethiopica Kotschy & Peyr.

Nyctaginaceae

Commicarpus plumbagineus (Cav.) Standl.

Amaranthaceae

Achyranthes aspera L.

Aerva lanata Juss.

Celosia anthelmintica Aschers

Cyathula uncinulata (Schrad.) Schinz

Chenopodiaceae

Chenopodium opulifolium Koch & Ziz

Phytolaccaceae

Phytolacca dodecandra L'Herit

Thymelaeaceae

Gnidia subcordata Meissn.

Euphorbiaceae

Clutia abyssinica Jaub. & Spach

Croton macrostachys Hochst.

Croton megalocarpus Hutch.

Euphorbia candelabrum Kotschy

Euphorbia gossypina Pax var. coccinea Pax

Ricinus communis

Moraceae

Ficus capensis Thunb.

Ficus salicifolia Vahl

Urticaceae

Girardinia condensata Wedd.

Obitia pinnatifida Bak.

Urtica massaica Mildbr.

Agavaceae

Sansevieria parva N.E. Br.

Liliaceae

Aloe graminicola Reynolds

Aloe rabaiensis Rendle

Commelinaceae

Commelina benghalensis L.

Typhaceae

Typha domingensis Pers.

Cyperaceae

Cyperus immensus C.B. Cl.

Cyperus laevigatus L.

Cyperus obtusiflorus Vahl

Cyperus rigidifolius Stend.

Cyperus stuhlmanii C.B. Cl.

Cyperus teneriffae Poir.

Mariscus impubes (Stend.) Napper

Gramineae

Aristida adoensis Hochst.

Aristida kenyensis Henr.

Beckeropsis procera Stapf.

Brachiaria semiundulata (A.Rich.) Stapf

Chloris gayana Kunth

Chloris pycnothrix Trin.

Cymbopogon afronardus Stapf

Cynodon nlemfuensis Vanderyst var. *nlemfuensis*

Dactyloctenium aegyptium (L.) P. Beauv.

Digitaria scalarum (Schweinf.) Chiov.

Digitaria ternata (Stead.) Stapf

Ehrharta erecta Lam. var. *abyssinica* (Hochst.) Pilg.

Eragrostis cilianensis (All.) Lutati

Eragrostis superba Peyr.

Eragrostis tenuifolia (A.Rich.) Steud.

Harpachne schimperi A. Rich.

Hyparrhenia hirta (L.) Stapf

Microchloa kunthii Desv.

Panicum atrosanguineum A. Rich.

Pennisetum catabasis Stapf & C.E. Hubb.

Pennisetum clandestinum Hochst. ex Chiov.

Pennisetum purpureum Schumach.

Pennisetum squamulatum Fresen.

Rhynchelytrum repens (Willd.) C.E. Hubb.

Setaria orthosticha Harrm.

Setaria pallidefusca (Schumach.) Stapf & Hubbard

Setaria verticillata (L.) Beauv.

Sporobolus africanus (Poir.) Robyns & Tournay

Sporobolus consimilis Fresen.

Sporobolus filipes Napper

Sporobolus ioclados (Trin.) Nees

Sporobolus pryamidalis Beauv.

Sporobolus spicatus (Vahl) Kunth

Stipa dregeana Steud. var. elongata (Nees) Stapf

Themeda triandra Forsk.

Appendix II. A list of larger mammals recorded within the expanded area of Lake Nakuru National Park, Kenya from 1972-74 and their relative abundance.*

Primates		
Papio anubis (Fischer)	olive baboon	O
Cercopithecus aethiops (Linnaeus)	vervet monkey	O
Colobus polykomos (Oken)	colobus monkey	R
Carnivora		
Canis adustus Sundervall	side-striped jackal	R
Canis mesomelas Schreber	silver-backed jackal	R
Lycaon pictus (Temminck)	hunting dog	R
Crocuta crocuta (Erxlaben)	spotted hyaena	R
Panthera pardus (Linnaeus)	leopard	R
Tubulidentata		
Orycteropus afer (Pallas)	antbear	R
Perissodactyla		
Equus burchelli (Grey)	Burchell's zebra	R
Diceros bicornis (Linnaeus)	black rhinoceros	R
Artiodactyla		
Hippopotamus amphibius (Linnaeus)	hippopotamus	O
Phacochoerus aethiopicus (Pallas)	warthog	O
Tragelaphus scriptus (Pallas)	bushbuck	O
Kobus defassa (Ruppell)	defassa waterbuck	C
Redunca redunca (Pallas)	bohor reedbuck	C
Redunca fulvorufula chanleri (W. Rothschild)	Chanler's mountain reedbuck	R
Aepyceros melampus (Lichtenstein)	impala	C
Gazella granti Brooke	Grant's gazelle	R
Gazella thomsonii Gunther	Thomson's gazelle	C
Sylvicapra grimmia (Linnaeus)	bush duiker	R
Oreotragus oreotragus (Zimmerman)	klipspringer	R
Raphicerus campestris (Thunberg)	steinbok	R
Rhynchotragus kirkii (Gunther)	Kirk's dik-dik	O
Syncerus caffer (Sparrman)	African buffalo	O

*C = common, O = occasional, R = rare.

Appendix III. Minimum weights in kilograms used to calculate standing crop biomass estimates for Lake Nakuru National Park, Kenya (based on Ledger, 1964 and Sachs, 1967).

Species	Adult Male	Adult Female	Adult Unidentified	Subadult Male	Subadult Female	Subadult Unidentified	Juvenile or Calve
Hippopotamus			581			349	
Buffalo			544			326	
Defassa waterbuck	192	160		134	112		70
Impala	46	39		32	27		17
Bohor reedbuck	46	39		32	27		17
Thomson's gazelle	18	12				8	

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