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Mortality of wildlife in Nairobi National Park, during the drought of 1973-1974

JESSE C. HILLMAN *and* ALISON K. K. HILLMAN *Zoology Department, University of Nairobi, P.O. Box* 30197, *Nairobi, Kenya*

Summary

(1) The mortality of wildlife in Nairobi National Park during the drought period of 1973/74 was monitored by monthly ground counts. (2) Highest mortality rate was recorded for kongoni at 27%, followed by wildebeest at 10% and zebra at 7% of the live populations present in the Park. (3) The dry period was marked by a massive influx into the Park of the three species most affected. Eland also moved in, and subsequently left the Athi–Kapiti ecosystem entirely, while populations of the other species in the Park remained relatively static. (4) Proportionally the highest mortality was recorded in the driest part of the Park and in the forest. (5) Immature and female animals died earliest, but the overall sex and age ratios reflected those reported for live populations, except that a greater proportion of female wildebeest died than expected. (6) Mortality was suspected to result from poor physical condition and lowered disease resistance caused by malnutrition. This occurred during the latter half of 16 consecutive months of below-average rainfall, which considerably reduced vegetation growth. (7) The results are discussed in relation to those found elsewhere in this ecosystem, and in relation to domestic stock, human development and the future of Nairobi National Park.

Introduction

Since February 1972, regular total ground counts of eland (*Taurotragus oryx* Pallas) have been carried out by the authors at the end of each month in Nairobi National Park, in connection with a study of this species. In October 1973 it was noticed that there were more dead animals of various species of large ungulates than had been noted previously. This was preceded by a prolonged period of below-average rainfall, during which several species of plains ungulates visibly lost condition. In August, Kongoni (*Alcelaphus buselaphus cokei* Günther) and Grant's gazelle (*Gazella granti* Brooke) were seen on the highland area of the Ngong hills in the north-west corner of the Athi–Kapiti plains. This area is not normally frequented by these species, and a number of Grant's gazelle died there, apparently from a deficiency paralysis, induced by drought.

The dry period continued until April of the following year and was marked by the deaths of many animals including domestic cattle (*Bos indicus* Linn.). The three species most affected were kongoni, wildebeest (*Connochaetes taurinus* Burchell) and zebra (*Equus burchelli* Gray). During this period a systematic count of all carcases was made by the authors, while conducting the eland count.

A collection of skulls and a count of the total number of carcases present at the end of February 1974 was carried out by the staff of Nairobi National Park (Nairobi National Park, 1974; Norris, 1974). The Kenya Wildlife Management Project conducted three sample counts of carcases in the area south of Nairobi National Park, and one sample count in the Park after the rains had set in (Casebeer & Mbai, 1974). However, as far as we know, the data presented below are the result of the only regular, systematic monitoring of the mortality carried out over the whole Park for the duration of the drought.

Methods

Area description

Nairobi National Park covers an area of approximately 112 km^2 to the south-east of the city of Nairobi in Kenya, and is fenced on the north, east and west, with the long southern boundary open to the Athi–Kapiti plains. The plains and the Park are essentially part of the same ecosystem and there is considerable movement between them of several of the larger ungulate species. The Kitengela is an administrative sub-division of the Athi–Kapiti plains, of approximately 400 km^2 immediately south of the Park.

The area of the Park is topographically divisible into three zones by overlying rock layers (Saggerson, in press). These are defined by two escarpments and range in altitude from 1500 m above sea level in the east to 1800 m in the west (Fig. 1.). The vegetation communities within these zones are distinct. The high zone to the west is covered by semi-evergreen forest with open grass clearings; the lowest zone to the

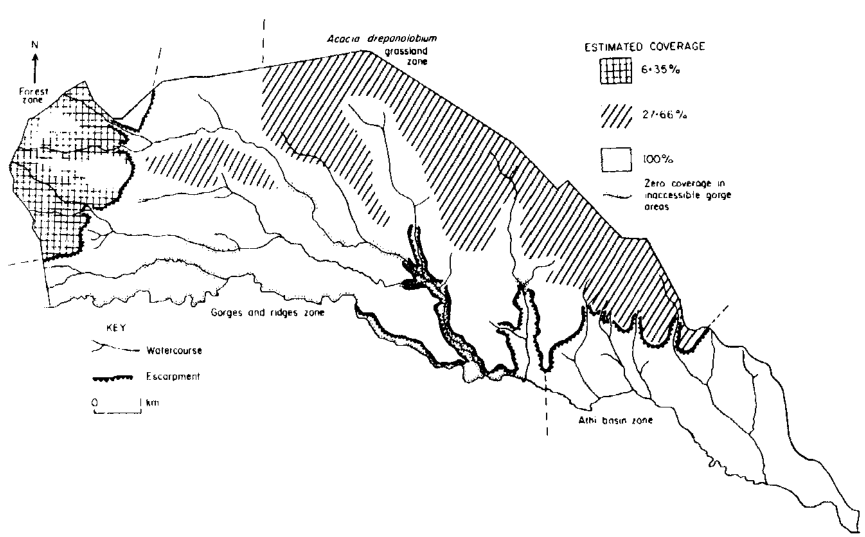

Fig. 1. Nairobi National Park: main topographical regions and vegetation/visibility zones used.

east, the Athi river basin, with open *Themeda triandra* Forsk./*Pennisetum mezzianum* Leeke grassland. The central zone consists of *Acacia drepanalobium* Sjöstedt ex Harms/*Themeda triandra* dwarf tree grassland in the north, and of open grass covered ridges, dissected by bushed river gorges in the southern part. The southern boundary is formed by the perennial Mbagathi river, and in addition, water is available in artificial dams and some persistent pools in the river gorges.

Counting procedure

The carcase count was carried out in conjunction with the routine procedure for counting live eland, which had been developed during the previous 20 months. The same two observers (the authors) were employed throughout. A short wheel base Toyota Land Cruiser was used to cover the entire Park area. Roads and tracks were used primarily, supplemented with off-the-road driving in areas of few or no tracks, or where the density of the vegetation within a zone necessitated greater coverage. The counts began between 06.00 and 07.00 hours and continued all day until the whole Park had been covered. If a count was incomplete by 19.00 hours when daylight ended, it was continued the following day.

Every carcase was recorded under the following categories:— species, location, age and sex. Only those carcases judged to have died within the previous month (see below 'Interval since death') were recorded. Location was recorded on a duplicated map of the Park. Age categories used for all species were adult, sub-adult and young-of-year. These correspond approximately with the ages 20 months and over, 12–20 months, and newborn to 12 months respectively (Peterson & Casebeer, 1972; Stanley Price, 1974; J. C. Hillman, unpublished data). Factors used in this classification included overall size, horn development and coat colour. Only carcases judged to be adult were sexed wherever possible. Sexual differences in horn structure were used, since these could be observed at a distance, and were not subject to damage by scavenging animals. No attempt was made to sex adult zebra, as this would have necessitated a time-consuming close inspection of every carcase which was not considered justifiable within the scale of the work. Carcases were observed from the vehicle using the naked eye and Leitz 12×60 binoculars. Driving off the road to each carcase was not considered justifiable in terms of habitat degradation and time.

Correction factors

For the purpose of this survey, the whole Park area was considered under four broad vegetation types, with distinct visibility characteristics. These were: (1) the forest; (2) the *Acacia drepanalobium* grassland; (3) the gorges and ridges area; and (4) the Athi Basin (Fig. 1). These roughly correspond with natural plant communities which are used differentially, both temporally and spatially, by the various ungulate species (Stanley Price, 1974). In each of these vegetation types, the mean of the maximum distances on both sides of the vehicle, at which the parameters of age, sex and time since death of a carcase could be discerned, was measured using a Wild rangefinder. The area sampled within each vegetation type was calculated from the product of the mean visibility distance calculated above, and the linear distance travelled. Correction factors were then derived from the proportion of the total area of each vegetation type covered. These were applied only to the totals of the three numerically major species (kongoni, wildebeest, zebra). Numbers of other species were not considered sufficiently high to warrant correction, nor was there any evidence for sex and/or age specific utilization of the different vegetation types to justify application of correction factors within sex and age categories. Correction factors for each vegetation type were as follows.

(1) *Forest* (10·08 km²). The forest was subdivided into two visibility and vegetation areas: (a) areas of open grassland (2·13 km²) where the carcase count was considered to be 100% coverage; (b) wooded areas (7·95 km²). where the mean of the maximum visibility distances under the relatively defoliated conditions of the drought was 30 m (n = 17). Coverage was calculated as 6·35% and a correction factor of × 15·74 was applied.

(2) *Acacia drepanalobium* grassland (30·87 km²). The mean visibility distance was 152 m ($n = 26$). The coverage was calculated as 27·66% and a correction factor of × 3·62 was therefore applied to this area.

(3) *Gorges and ridges* (53·57 km²). Coverage was calculated at 100% for most of this area, except for some stretches of gorge which could not be scanned with binoculars. These constituted 17% of the area, therefore a correction factor of × 1·2 was applied.

(4) *Athi Basin* (17·48 km²). Coverage was considered to be 100% and no correction factor was applied. The small area south of the main Athi river course was not included, since access is difficult and there is considerable human disturbance.

The mortality calculated, even after correction, is likely to be minimal. The actual numbers of animals that died were probably greater, and age categories may be biased towards adults, since carcases from young animals appeared to disintegrate relatively faster. In addition, the activity of scavengers may have broken and scattered remains in such a way that they were not counted. No account has been taken of animals killed by predators, rather than by drought conditions. Lion (*Panthera leo massaica* Neumann) are the main predators, and figures given by Rudnai (1974) indicate a mean of 8·5 animals of all species are killed each month by the lion population. However, it was not sufficiently known to what extent lion were killing their own prey, or feeding from animals that had died during the drought, and no allowance for this is made.

A source of bias may arise from an edge effect in the forest. The majority of ungulates dying in the forest region, kongoni and wildebeest, are not normally found there, but rather in the more open grassland areas. It is therefore possible, and from observation seems probable, that within the forest region, the density of live, and therefore probably of dead animals of these species was greatest in the open grass clearings and lightly bushed areas along the grassland–forest interfaces. However, it was known from direct observation of kongoni in open grass areas isolated within wooded regions, that the plains ungulates utilized the forest to some extent.

Interval since death

Since counts were done on a monthly basis, only those carcases which were estimated to have died within the preceding month were counted, thereby minimizing duplicate recording of the same carcase. Criteria used for estimating the approximate interval since death were based on previously recorded data, the state of the carcase and the state of the surrounding ground.

Each carcase was pinpointed on a map (scale 1 : 22 000) at the time of counting, thus the maps from previous counts gave an indication of the presence or absence of a carcase at the location in question. However, the scale of the maps and the density of the carcases limited the accuracy of this method. It was also known that in November 1973, Park staff had collected the skulls of some carcases. Thus headless carcases were known to be older than this date. In addition, subjective data were used where specific features of a carcase or location were recalled from the previous month.

Since changes in features indicating carcase degradation are gradual, carcases could be identified with relative certainty as being fresh, if death had occurred within a few days, but beyond that, a balance of all the factors had to be taken into account. Therefore the features used are described on an approximate time scale. It must be borne in mind that these are somewhat specific to the situation. For example, during the drought period, rainfall was extremely low, or non-existent, and clear skies led to a high evaporation rate. Thus carcases dried up very quickly, limiting the action of degrading agents including scavengers and microorganisms. Most carcases were evident throughout the drought period, but broke down very rapidly once the rains began. In a few cases the intervention of larger carnivores effected the dispersal of carcases within a few days introducing a possible error. The following factors, used to estimate the time since death, were obtained from repeated observations of known carcases during subsequent counts.

Factors indicating death within the previous few days. Smell, reddish colour of flesh, wet gut contents, liquid or moist appearance of drained body fluids, body hair lying flat, bloated body, attention by scavengers.

Changes in carcase features. Flesh rapidly dried to a black colour. Carcases more than a month old showed signs of fading due to bleaching and an increased air content in the tissue. Stomach contents dried into wads which were generally present for at least a month after death, and were later gradually dispersed by wind and insects. Body fluids showed as black residues on the ground in recent carcases, but began to disappear from carcases older than a month. Body hair developed a 'staring' appearance in older carcases and began to drop out. Where large patches of skin were visible, a carcase was generally considered to be more than a month old. Hair colour changed in zebra from black to brown, in wildebeest from black to grey and in kongoni from brown to yellow. The skin dried hard within a few days of death and could only be cut with a hacksaw. This was followed by crinkling and contraction, so that an increased prominence of the bones was noticeable in carcases that had been dead for some time. Bones showed a yellowish coloration due to fat content when fresh, but gradually whitened with drying. Evidence of scavengers having been on the carcase was gained by signs such as feathers, droppings and trampled grass which were considered to indicate that death had occurred within the previous month.

It is realized that these are only subjective criteria, but they were used consistently throughout the study, were tested on known carcases and were the result of specific environmental conditions.

Live count

Figures kindly furnished by the Warden, Nairobi National Park, show how many live animals of all species were present each month. The figures result from ground counts carried out monthly until February 1974 by staff of the Park and volunteers. The Park area is divided into fourteen count blocks, and it is common for a number of blocks to be uncounted each month due to lack of observers. Therefore correction factors had to be applied to the figures, to obtain estimates for total populations within the Park at the time. It is realized that the assumptions on which these had to be based allow for a considerable degree of error, but it was felt they would be nearer the actual situation than the uncorrected numbers. The blocks were grouped into the four main vegetation regions mentioned above, and the areas of both blocks and vegetation regions were calculated. The figures that were available for blocks within a vegetation region, were then expanded on a density basis to cover that region. The expansion was based on the assumption that the sample available for each vegetation type was representative of the animal density throughout the same vegetation type at the time of the count. This assumption was supported by the results of testing the method in cases where complete counts for vegetation regions were available. No more accurate correction factor could be derived from the data available.

Climatic factors

Data used are records of the East African Meteorological Department of the East African Community, for stations at Nairobi West, Embakasi airport and Athi River, which were the closest stations to the west, north and east of the Park respectively. Data for the Athi–Kapiti plains, which are the wet season dispersal area for many of the large ungulates, have been obtained from a network of storage raingauges set up by M. R. Stanley Price and continued by the authors.

Measures of potential evapotranspiration (E_o) for Nairobi West and Embakasi airport were taken from Woodhead (1968). Evapotranspiration (E_t) is obtained by multiplying E_o by a factor of 0·8 (Brown & Cocheme, 1964). The ratio of precipitation (P) to E_t was calculated to give effective rainfall on both monthly and cumulative bases, according to the method of Brown & Cocheme (1964). If this ratio, P/E_t, exceeds unity, the water requirements of the vegetation are met, and the soil profile is recharged with water. If P/E_t is less than unity, water stored earlier is used for transpiration by vegetation. Stanley Price (1974) has shown a correlation between P/E_t and grass moisture to be a useful indication of vegetation condition.

Results and discussion

Rainfall, vegetation condition and water availability

Fig. 2 shows rainfall from stations adjacent to the Park and in the Athi–Kapiti plains to the south of it. The records from Nairobi West, Embakasi and Athi River, situated around the Park, demonstrate the rainfall gradient which exists within it, and which is approximately aligned with the altitude gradient. The rainfall gradient is continued into the plains area in the south, with the highest annual totals being experienced in the north and west. The rainfall gradient is one of the main reasons why the Park forms a dry season concentration area for this ecosystem, a phenomenon which was accentuated during the drought as evidenced by the high numbers of large ungulates present for much of the time.

The 12-month period considered to be the most important in contributing to the drought, was that from March 1973 to February 1974 (Fig. 3). A comparison of the total rainfall during this time, with the mean annual total where available, or the previous 12 months total, demonstrates a considerable reduction, varying from 25 to 68% below the normal.

Rainfall is generally experienced in two periods, from March to May (the 'long' rains) and during October and November (the 'short' rains). Fig. 3 of cumulative

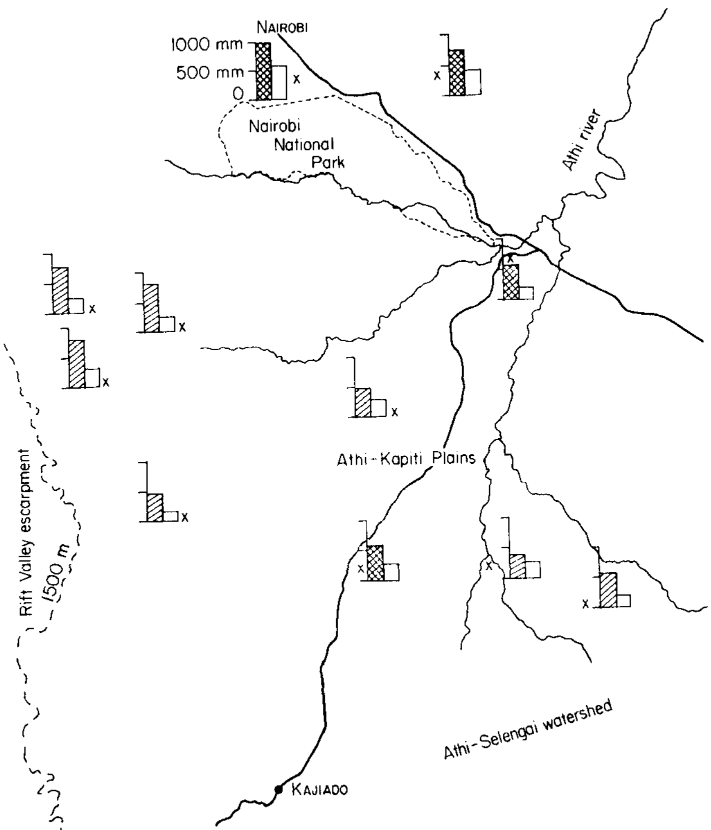

Fig. 2. Drought rainfall compared with normal rainfall (based on 10–year mean, where available, previous annual rainfall where not) for Nairobi National Park and the surrounding Athi–Kapiti plains. ×, Rain gauges; open columns, drought tainfall (3.73-2.74): cross-hatched columns, mean annual rainfall (based on preceding 10 years); hatched columns, annual rainfall for 12 months prior to drought period.

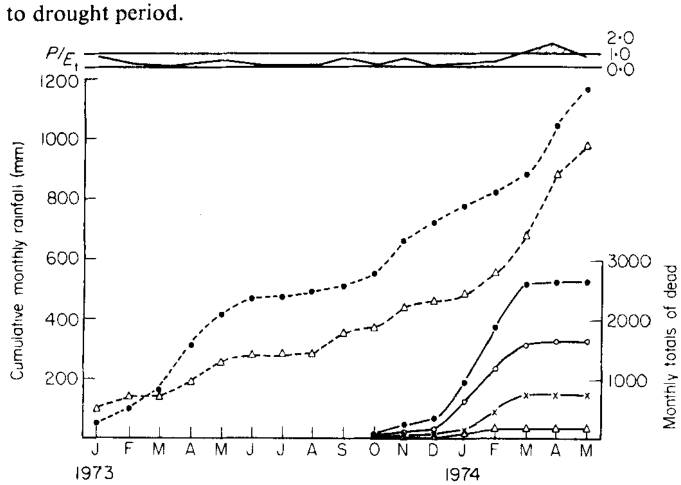

Fig. 3. Effective rainfall: P/E_t; together with cumulative monthly totals of rainfall at Embakasi; ●---●, cumulative monthly means for the 13–year period 1962–1974; △---△, cumulative monthly rainfall from January 1973 to May 1974; and the relative timing of deaths as expressed by corrected monthly totals: ●, total dead of all species; ○, kongoni; ×, wildebeest; △, zebra.

monthly rainfall at Embakasi around the drought period, compared with the monthly means for the period 1962–1972, shows that the reduced rainfall was due to a failure of both the long and the short rains in 1973. Added to this fact, sunlight figures for the same station, show a 20% increase in mean daily hours of sunlight for the months October and December, against the 8–9 year means for the same months. Cumulative totals of dead animals per month are superimposed on the graph to demonstrate the temporal relationships between the rainfall and animal deaths. It can be seen that no unusually high mortality was evident in the Park until 7 months of below-average rainfall had been experienced.

The cumulative effective rainfall for the months March 1973 through February 1974, at Nairobi West and Embakasi, were 0·34 and 0·28 respectively, indicating a considerable deficit in water requirements. The plot of monthly measurements of P/E_t for Embakasi on Fig. 3 shows that at no time during 1973 were the water requirements of the vegetation met. Prior to this, P/E_t was greater than unity in October 1972, and subsequently did not exceed unity until April 1974. The effective rainfall was only slightly higher at the western end of the Park where P/E_t exceeded unity at Nairobi West in January and April 1973, and subsequently in March 1974.

Although no actual monitoring of the vegetation was carried out, the reduction in vegetation biomass was evident in the very short, dry grass stubble and the defoliated bushes and trees. This was due, both to the lack of regeneration of the vegetation, and to a high biomass of herbivores feeding on it and mechanically breaking it down by trampling.

Towards the end of the drought period, a number of the permanent dams within the Park dried out completely and others had a greatly reduced area, and were effectively unavailable due to the expanses of mud exposed at their peripheries, in which many animals became mired. Stanley Price (1974) found previously that two almost rainless months coinciding with an unusually high biomass of ungulates significantly reduced the amount of free standing water, and numbers of animals involved were considerably lower than during this mortality period.

Total deaths

Table 1 gives the monthly totals of found carcases and corrected values for all species. The overall corrected total of 2623 carcases is considerably higher than, but of the same magnitude as the figure of 1527 carcases found by the Park staff by the end of February 1974. The totals of this survey until February are higher than those of the Park for kongoni, similar for wildebeest, but for zebra are slightly lower.

Kongoni, wildebeest and zebra together contributed 98% of the total number of dead animals, while kongoni alone comprised 62·7% of the total. It can be seen from both this Table and Fig. 3, that the initial death rate rose gradually in October, November and December, but in January escalated dramatically, and that the major die-off occurred during January, February and March. The first substantial rain fell in the last two days of March generally over the whole ecosystem. The vegetation responded rapidly and there was a considerable movement of the major herbivores out of the Park, although unfortunately no live counts are available to quantify this. Thus, although the figures for the April carcase count are considerably reduced, at least forty-eight animals were found to have died during that month. This could represent a fairly high percentage of the populations remaining in the Park, and is

Table 1. Monthly totals of dead animals (U—uncorrected, C—corrected)

	Oct. 1973		Nov.		Dec.		Jan. 1974		Feb.		Mar.		Apr.		May		Total	
Species	U	C	U	C	U	C	U	C	U	C	U	C	U	C	U	C	U	C
Kongoni (*Alcelaphus buselaphus/cokei*/Günther)	25	33	47	76	55	77	198	427	260	576	195	382	12	42	0	0	792	1613
Wildebeest (*Connochaetes taurinus*/Burchell)	22	26	24	37	14	21	58	102	177	278	190	300	3	3	0	0	488	767
Zebra (*Equus burchelli*/*Gray*)	7	11	12	22	13	22	29	54	21	41	13	22	0	0	0	0	95	172
Eland (*Taurotragus oryx*/Pallas)	2	2	4	5	6	22	6	7	1	1	3	3	1	1	0	0	23	41
Ostrich (*Struthio camelus*/Linn.)	5	6	0	0	0	0	0	0	0	0	1	1	0	0	0	0	6	7
Impala (*Aepyceros melampus*/Lichtenstein)	1	1	0	0	0	0	2	2	0	0	1	1	1	1	0	0	5	5
Reedbuck (*Redunca redunca*/Pallas)	1	1	0	0	1	1	0	0	1	4	2	2	0	0	0	0	5	8
Grant's gazelle (*Gazella granti*/Brooke)	1	1	0	0	1	1	1	1	1	1	0	0	0	0	0	0	4	4
Giraffe (*Giraffa camelopardis*/Linn.)	0	0	0	0	0	0	2	2	1	1	0	0	0	0	0	0	3	4
Warthog (*Phacochoerus aethiopicus*/Pallas)	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
Waterbuck (*Kobus ellipsiprymnus*/Ogilby)	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1
Buffalo (*Syncerus caffer*/Sparrman)	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1
Monthly total:	64	81	87	140	91	145	296	595	462	902	406	712	18	48	0	0	1424	2623

likely to have been a greater underestimate than usual, owing to the increased vegetation cover by the end of April, and the increased rate of carcase decomposition. It is known that the first rain after a dry period mechanically removes a considerable amount of the remaining standing grass crop (Cassady, 1973). Thus the effect of reduced food resources, and of cold, wet conditions on animals already in a weakened state could have increased the death rate for a short period, until the vegetation had responded sufficiently to be utilized. This was considered to be a major contributing factor to a population crash of nyala (*Tragelaphus angasi* Gray) in Natal (Keep, 1973).

Relationship of numbers of dead and live animals

(a) *Nairobi National Park*. Table 2 shows numbers of dead animals of each of the three main species, found per month as a percentage of the mean live counts for the same and the previous month for that species. This mean was taken as the most representative of the population during the month, allowing for movement in and out of the Park. Since the live counts ceased in February, carcase count figures for March were taken as precentages of February's count only, and those of April and May have had to be omitted.

Table 2. Dead animals as a percentage of total live each month. (Live and dead figures corrected. Live expressed as mean of same and previous month's totals in calculation of percentage dead. March dead expressed as precentage of previous month's live only)

	Kongoni			Wildebeest			Zebra		
Month	Live	Dead	%	Live	Dead	%	Live	Dead	%
Sept. 1973	5741	—	—	9428	—	—	2099	—	—
Oct.	7121	33	0·5	14936	26	0·2	6129	11	0·3
Nov.	3210	76	1·5	1647	37	0·4	1281	22	0·6
Dec.	5284	77	1·8	2066	21	1·1	1636	22	1·5
Jan. 1974	7307	427	6·8	10340	102	1·6	1565	54	3·4
Feb.	3725	576	10·4	10027	278	2·7	1752	41	2·5
Mar.	—	382	10·3	—	300	3·0	—	22	1·3
Apr	—	42	—	—	3	—	—	0	—
	Mean live		5898	Mean live		8074	Mean live		2410
	Total dead		1613	Total dead		767	Total dead		172
	% dead		27·3	% dead		9·5	% dead		7·1

For all the three main species the mortality rate was found to increase through the drought and was consistently highest in kongoni. The overall figure of approximately 27% of the kongoni, 10% of the wildebeest and 7% of the zebra present in the Park during the drought, does not necessarily represent the true figure for the whole population, since the Park is not a closed ecosystem. As a comparison, a figure of 3·2% of the population has been estimated as a natural adult mortality in wildebeest over a 7-month period, from data given by Peterson & Casebeer (1972). It must also be borne in mind that the effective mortality included a reduction in calf recruitment. For wildebeest, which normally have a birth peak in February and March, no calf production was noted in 1974 (C. E. Norris, personal communication; personal observations). Peterson & Casebeer (1972) estimate the yearly calf crop as 27·7% of the total population. Therefore, an effective loss of this percentage, plus the recorded mortality of 9·5% gives an overall effective mortality of 37·2% of the wildebeest population over the 7-month period. Peterson & Casebeer also estimate the normal calf mortality at 51·1% of the calves in the first year. Thus normal calf mortality is 14·2% of the population, which together with the normal adult mortality gives an expected natural mortality of 17·4% over a 7-month period. An estimate of kongoni calf production of 27·3% of the total population per year was made based on Gosling's (1974) figures for 1967 and 1968 for an apparently stabilized population. Although no kongoni calves were seen during the drought period, no observations on the kongoni population were made subsequent to the drought, so that the full magnitude of the loss through reduced calf production could not be estimated. Figures for loss of recruitment into the zebra population were not available, partly due to the lack of a birth peak, but a similar situation could be expected to occur.

It can be seen from Table 2, that the fall in numbers of dead wildebeest in December is related to an even greater fall in numbers of live present in the previous month. In response to the dry conditions in the early stages of the drought, wildebeest progressively concentrated in the Park, until the end of October when nearly 15 000 were recorded. This is an indication of unusually dry conditions, since it is considerably higher than the normal wildebeest dry season influx (Nairobi National Park count records 1961–1974; Stanley Price, 1974). It is also more than twice the peak of 6255 recorded in the 1960–1961 drought (Foster & Kearney, 1967). Large groups of wildebeest then moved out into the Kitengela during November in response to some rain in the plains south of the Park (personal observation). Although the figures show reductions in the numbers of live animals of other species, presumably largely through movement, that of the wildebeest was most marked, and this behaviour may have been one factor in their apparently higher survival rate than kongoni, as measured by their percentage dead in February and March when wildebeest again concentrated in the Park.

Fig. 4 shows the response of different species to the drought conditions. In the majority of years, wildebeest, kongoni, zebra and eland move into the Park in varying numbers, depending on the severity of the dry period between the long and the short rains (Nairobi National Park count records). The numbers of other species remain relatively constant between seasons. Movement into the Park by the four species

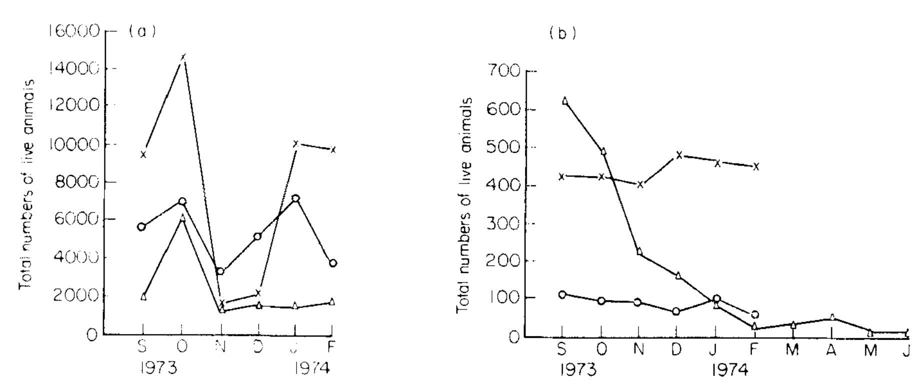

Fig. 4. Fluctuations in total numbers of live animals of some species in Nairobi National Park during the drought period. Sources: eland (J. C. Hillman); others (Park counts, corrected). (a) ×, Wildebeest; ○, kongoni; △, zebra. (b) ×, Grant's gazelle; ○, giraffe; △, eland.

mentioned above was greatly accentuated during the extreme conditions in 1973. Prior to the onset of mortality there was a peak of 714 eland in July which was the highest count recorded for the species over the 13-year period that counts have been carried out. In contrast to the other species, eland numbers subsequently declined, until by February 1974, there were only about twenty animals left in the Park. Re-sightings of known individual eland, and studies carried out in the Athi–Kapiti plains, showed that these animals left the plains ecosystem entirely. By May 1974, eland numbers in the neighbouring Selengai–Amboseli area had increased fourfold, from 1200 to 4900 animals, and by August had returned to normal (D. Western, pers. com.) Known eland were back in the Athi–Kapiti plains by June. The response of the eland was therefore to leave the plains area in favour of the perennial bush of the Selengai drainage area and probably that of the Rift Valley.

From the Figure, it can be seen that the three major species moved considerably between the Park and the outside area during the drought, As examples of other species, the total Park counts for giraffe and Grant's gazelle are shown on Fig. 4, and can be seen to vary very little over the period. Low total mortality percentages of 3·4% and 0·9% respectively were recorded for these two species.

(b) *Athi–Kapiti ecosystem.* Calculations made from the number of carcases counted in the ground mortality survey carried out by Casebeer & Mbai (1974) in the Kitengela area, and live population estimates for the same area for the nearest previous month (Savidge, 1973c, 1974a) result in the following precentage losses:

	Kongoni	Wildebeest	Zebra
January 1974	8·3%	1·8%	5·1%
February 1974	24·6%	4·1%	7·9%

These are similar to, though except for zebra, slightly lower than the estimates of 27%, 9·5% and 7·1% respectively obtained by us in the Park. The mortality rate for zebra would be expected to be higher due to the prevalence of poaching in the Kitengela (Casebeer & Mbai, 1974; personal observations).

However, Casebeer & Mbai (1974) postulate a total mortality for kongoni, wildebeest and zebra of 84%, 73% and 70% respectively on the basis of the difference in population estimates from two aerial counts made in November 1973 and July 1974 (kongoni 18 362 to 2890. wildebeest 42 237 to 11 606, and zebra 15 409 to 4667). Population estimates for this area for the three species, have been carried out since 1959 by various workers (Stewart & Zaphiro, 1963; Modha, 1969; Casebeer, 1970; Stanley Price, 1974; Savidge, 1973a, b, c, 1974a, b, c). Populations of all three species appeared to stabilize again by 1968, following the 1961 drought mortality and the means for population estimates for the period 1968 to 1972 are: kongoni 6713 (range 4845–9001, $n=15$), wildebeest 14 740 (range 10 008–24 252, $n=10$), zebra 12 018 (range 8439–16 376, $n=10$). It is known as is discussed earlier for the Park, that the Athi–Kapiti ecosystem is not a closed one for eland, and it is suspected that the same applies to wildebeest and zebra (local Maasai people, pers. com., personal observations). In the absence of more constant population estimates, it is felt that calculations of losses on this basis are not feasible. The percentage mortality found in the Park could be considered to be a sample, and that projections to the populations using the whole Athi–Kapiti ecosystem, of the mortality rate found in the Park would be reasonable for wildebeest and kongoni, while that for zebra should be somewhat higher.

A subsequent count carried out in January 1975 (Savidge, 1975) also supports the postulation that the extreme fall in numbers between November 1973 and July 1974 was due partly to emigration from the area. The count in 1975 gives mean population estimates for the Athi–Kapiti plains of 3568 for kongoni, 28 679 for wildebeest and 7751 for zebra. Compared with the count in November 1973, this then gives losses of 81%, 32% and 50% for the above three species respectively. These figures suggest that kongoni were hardest hit by the drought and that movement occurred in the other two species. The overall mortality for wildebeest also compares favourably with the potential mortality of 37·2% projected above on the basis of lack of calf recruitment.

Mortality distribution by area

Fig. 5 shows the death rate in each vegetation zone for kongoni, wildebeest and zebra. The corrected dead counts are taken as a percentage of the mean of the corrected live counts for the zone for the same and the preceding month, as in the previous section.

The highest mortality rates were recorded in the forest and Athi basin. The basin is normally the driest end of the Park, and in this year, received the greatest reduction of its normal precipitation (Fig. 2). Although kongoni and zebra were seen in thick forest, this is not considered normal habitat for these species in this area.

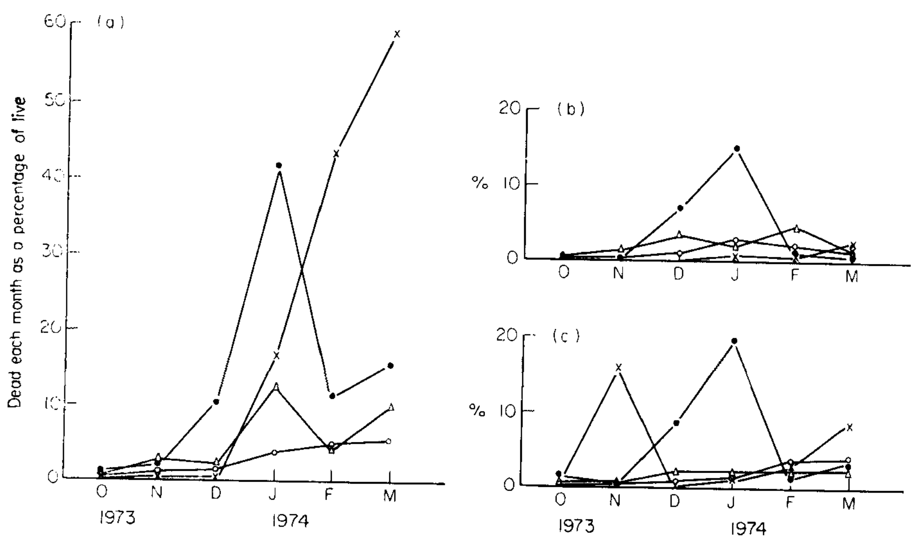

Fig. 5. Numbers of dead in each zone, each month, as a precentage of the mean of the same and previous month's corrected live count in each zone. (a) Kongoni; (b) zebra; (c) wildebeest. ×, Forest; △, *Acacia drenpanolobium*; ○, gorges and ridges; ●, Athi basin.

Distribution of mortality by sex and age

The numbers within different sex and age categories are expressed as a percentage of the total number of carcases of a species found each month, and are shown in Fig. 6. No correction was applied in the different vegetation zones since no evidence for differential sex and age distribution was found.

An interesting contrast exists between the death rates of male and female animals, in kongoni and wildebeest. For both species, the male death rate was very low to begin with, then increased toward the end of the drought period. The death rate for males

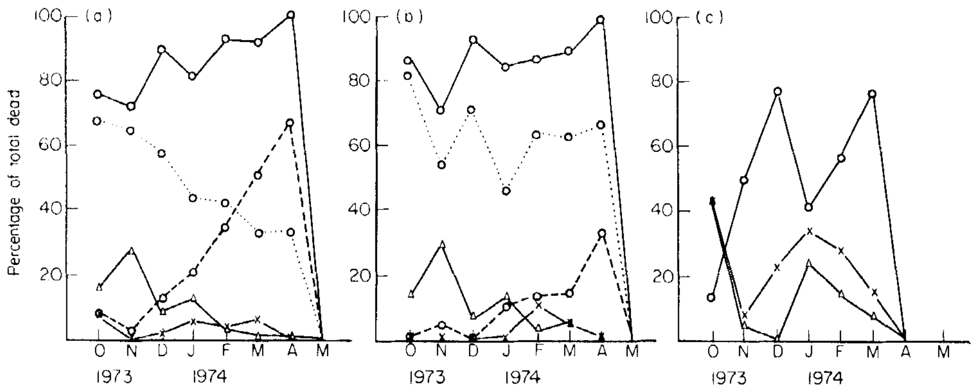

Fig. 6. Age categories of dead animals as a percentage of total dead. (a) Kongoni; (b) wildebeest; (c) zebra. ○—○, Total adult; ○---○, male adult; ○···○, female adult; ×—×, sub-adult; △, young of year.

overtook that for females in kongoni by the end of the drought, but this did not occur in wildebeest. Possibly the early susceptibility of the females was related to the greater physiological demands on them through pregnancy and lactation. The latter part of the drought coincided with the normal wildebeest calving season.

In all three species, the percentage of immature dead animals was lower than that of the adults, but in each case, the immature death rate was highest in the earlier stages of the drought. Table 4 of the actual numbers of dead found, by sex and age categories, for kongoni, wildebeest, zebra and eland, compares the sex and age ratios of dead found in this study, with ratios for live populations found in the same area, and of dead under normal circumstances. The ratios for live kongoni from Stanley Price (1974) are given separately for the Park and the plains area, and result from pooled data of three counts taken in both areas in the same months. Those for wildebeest and zebra from Peterson & Casebeer (1972) are representative of the total population occupying the plains area and the Park, but are calculated from the relevant months only (October, November, January–March) since the immature to adult ratios change throughout the year. However, for the above three species, the data are from years other than the drought period, and take no account of any differential movement which may have occurred at the time. The data from live eland are obtained from the animals present in the Park at the time of the drought, while the data for those dead found under normal circumstances apply to the Park area alone.

Following the early deaths of immatures in all species, few were seen during the drought, but it is not known whether this was due to death of newborn, loss or resorption of embryos, or a lowered conception rate. After the drought, some young wildebeest calves were seen in the Kitengela in June, and evidence from animals culled in areas of differing vegetation condition, indicates the possibility of a lack of conception in 1973 during times of stress (M. Woodford, pers. com.). Kongoni births show no peak season (Stanley Price, 1974), the birth peak of wildebeest normally occurs from February to March, but during the drought was not evident in the Park, while zebra foaling occurs throughout the year, with a slight peak from January to March (Foster & Kearney, 1967; Peterson & Casebeer, 1972). Eland produce young year round in this area, with a peak over the months August to January (J. C. Hillman, unpublished data).

Table 3. Age and sex categories of dead

Species	Age and sex categories						Ratio: adult/immature			Ratio: adult male/adult female		
	Ma	Fa	Ua	s	y	Total	Drought dead	Live popn	Normal dead	Drought dead	Live popn	Normal dead
Kongoni	250	347	97	38	60	792	N 1:0·1	N 1:0·5 K 1:0·3$_S$	—	N 1:1·4 K 1:0·9$_C$	N 1:1·4 K 1: 0·6$_S$	—
Wildebeest	60	302	63	29	34	488	N 1:0·1	NK 1:0·4$_P$	NK 1:0·6$_P$	N 1:1·5 K 1:0·6$_C$	NK 1:2·1$_P$	NK 1:1·1$_P$
Zebra	0	0	51	25	19	95	N 1:0·8	NK 1:0·5$_P$	NK 1:0·5$_P$	—	NK 1:1$_P$	NK 1:1·4$_P$
Eland	8	5	0	3	7	23	N 1:0·8	N 1:0·2$_H$	N 1:1·1$_H$	N 1:0·6	N 1:1·1$_H$	N 1:0·7$_H$

Sources other than this study: C, Casebeer & Mbai; 1974; H, Hillman J.C., unpublished data; P, Peterson & Casebeer 1972; S; Stanley-Price 1974.

Abbreviations: Ma, Male adult; Fa, female adult; Ua, unidentified (as to sex) adult; s, sub-adult; y, young of year.
Prefixes relate to data from: N, Nairobi National Park; K, Kitengela; NK, Nairobi National Park and Kitengela combined.

Cause of death

Many animals were in a visibly poor condition before any large number of deaths occurred in the Park. This was evidenced in kongoni in particular, by the prominence of ribs, vertebral column and pelvis beneath the skin, and a 'staring' pelage. Later in the drought the majority of kongoni were in this condition, most males in bachelor herds, however, appeared less afflicted until the end of the drought. Wildebeest also appeared to be in a poor condition, as did some eland and impala. Zebra showed very little evidence of a lowered condition. Animals in very poor condition were usually alone and not inclined to move, and finally lay down and were unable to rise again. It was noted that there were rarely any tick birds (*Buphagus erythrarhynchus* Stanley) on animals in poor condition. Several eland were seen with ears in a permanently drooping state, a condition caused by the brown ear tick (*Rhipicephalus apendiculatus*) and seen previously in an eland population in very poor condition (E. Elliot, pers. com.). Stomach contents obtained from eland that died in the drought contained very woody vegetation (M. D. Gwynne. pers. com.), suggesting a heavier than normal utilization of woody browse, and one animal was seen feeding off dead leaves on the ground, behaviour previously unobserved in this area.

Post mortem examinations carried out for the Park on animals dying in the drought, showed deaths to be due to malnutrition, and the *Babesia* parasite was found present at levels higher than normal (Norris, 1974). The amount of free standing water was considerably reduced, and since digestive efficiency of dry vegetation is dependent on available water (Stanley Price, in press), it is possible that during this drought, deaths resulted from poor physical condition and a lowered resistance to disease, caused by malnutrition.

Conclusions

The cumulative reduced rainfall over the period November 1972 through February 1974 led to a lowering of the vegetation condition and water availability generally in the Athi–Kapiti plains ecosystem, such that numbers of wildlife and domestic cattle died. Unusually large numbers of wildlife concentrated in the Park and the north-west corner of the Athi plains. At least 27% of the kongoni, 9% of the wildebeest and 7% of the zebra present in the Park died there during this period, and a low percentage of other species.

There was a marked contrast between nomadic grazing species, e.g. kongoni, wildebeest and zebra, and the relatively static mixed feeding and browsing species, e.g. impala, Grant's gazelle and giraffe, in this area. The former constitute the main biomass of mammalian herbivores in the Park and in the adjacent plains, along with domestic stock. The pattern of population numbers building up and then crashing at periodic droughts was reported previously, in 1953 and 1961, (Anon., 1961; Stewart & Zaphiro, 1963), for the same wildlife species and cattle. Thus it would appear that those species using movement as a means of maintaining a high biomass year round in a seasonally highly fluctuating environment, are using a different strategy for exploiting the available resources of this environment. The relatively static mixed feeders and browsers are exploiting a more constantly available part of the vegetation. They exist at a low biomass, necessitated by a low cover, dispersed food resource, which, however, is deeper rooting and exists near more constant water sources, both rainfall and water courses, in this ecosystem. These species appear to maintain relatively stable population levels even in the face of extreme climatic conditions. Waterbuck, although a grazing species (Kiley, 1966) in the latter category, were little affected by the drought. The eland are intermediate between the two general categories, being a nomadic browser on ephemeral herbs and perennial riverine bush, existing at an intermediate biomass (Stewart & Zaphiro, 1963). The species appeared to be affected by the drought to some extent, but by extreme movements was able to avoid the situation. Although no data are presented here on recruitment rates, the relative mortality patterns of these two basic types of environmental utilization in this area would appear to have characteristics conforming with those typical of *r*-selection in the case of the nomadic grazing species, and of *K*-selection in the case of the static browsers and mixed feeders (MacArthur & Wilson, 1967; Odum & Odum, 1959).

Stanley Price (1974) concluded that kongoni were the nearest equivalent of cattle in the Park and plains situation, and it would appear significant that both species were worst hit at this time. Some people in the area lost 90% of their cattle stock (J. K. ole Moiko, pers. com.), while others resorted to moving cattle out of the area, even to railing them 480 km to the coast when able to. In contrast very few sheep or goat losses occurred until the first rains fell. These last two are considered to be mixed feeders.

Ensuing development in the areas adjacent to the Park is likely to reduce the movement and acceptability of wildlife, with a more intensive human use of the area, necessitated by the rising population and land hunger. As pressure on wildlife resources increases, utilization of Nairobi National Park by wildlife could be expected to increase, and reductions of this nature to be more frequent. It is obvious that the Park is utilized when resources are scarce in the plains, and as long as human utilization of the resources continues, situations effectively similar to those of this drought could occur. Until utilization of the wildlife in the plains is both an economical and practical proposition, or until financial feedback occurs from the Park where this wildlife is exploited to the areas where the wildlife spends time, respect for wildlife and consideration for its requirements are unlikely to be forthcoming. The Park would thus have to depend on a considerably reduced wildlife resource with consequently reduced financial returns.

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