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The enclosed papers were presented at the Conference on Land Use Problems in Areas Containing Game, February 20-23, 1961, held at Lake Manyara, Tanganyika, under the auspices of the East African Agriculture and Forestry Research Organization. They present some of the preliminary results of the Wildlife Research Project.

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Preliminary Findings on the Population
Dynamics of the Wildebeest in Narok District, Kenya

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Assisted by Martha H. Talbot; Project financed jointly by the
United States National Academy of Sciences - National Research Council,
the Government of Kenya, and the New York Zoological Society.

Effective wildlife management must be based on knowledge of the population dynamics of the species involved. The type of information needed by the wildlife manager is not essentially different from that required by a cattle rancher. Both must know, for example, the size of their animal population, the ratio of males to females, young to adults, age of reproduction, rate of reproduction, rates of mortality, and causes of mortality. Knowledge of food habits is also essential, but it does not come under the heading of population dynamics. The food habit findings of this study are the subject of a separate paper (Talbot, 1961).

In recent months much official consideration has been given to wildlife management in the Mara region of Kenya. From the standpoints of contact with domestic livestock, migrations, and game cropping, the wildebeest is probably the most important single herbivore involved. This paper presents a brief outline of our preliminary findings on the population dynamics of wildebeest in Narok District. The basic principles should apply equally to wildebeest in adjoining areas.

We wish to express our appreciation to the Kenya Game Department and the Kenya Veterinary Department, with whom we have worked closely throughout this project and whose friendly cooperation and aid have made this work possible; and to the East African Agricultural and Forestry Research Organization and the East African Veterinary Research Organization for facilities, equipment, and other forms of aid.

Methods

The present, long-term, ecological studies of plainsland and plains wildlife were initiated by the author on the Serengeti Plains in January, 1956, and the current field work began in July, 1959. Although attention is given to all species of wild animals in the study area, primary concentration is given the wildebeest, as it is considered to be the key species involved.

Study area: The area involved is the total area over which the wildebeest pass during their yearlong movements. In Tanganyika it includes the area bounded on the east by the Rift wall, the south by the southern

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end of the Serengeti Plains above Lake Eyasi, and on the west by Lake Victoria. In Kenya, the Rift wall is again the eastern boundary, the Mau escarpment is the northern edge, and the Siria Escarpment the western boundary of wildebeest movement. This paper is concerned primarily with the Kenya region.

Field Techniques: The two primary sources of data have been systematic observation and animal collections. Much valuable data has been collected from detailed, prolonged observation of individuals and herds while the observer remained in one spot. However, since the study area is very large, much use has been made of strip sample counts and observations, reconnaissances, and surveys made both by vehicle and by aircraft. The results of these have been checked by total counts and surveys.

Collections have been made of wildebeest throughout the year. The animals collected have provided a variety of data including information on weights, growth rates, condition, parasites, diseases, food, and reproduction. Most of the animals have been collected at random, to provide a random sample of ages and sexes. Some individuals have been picked for collection, for example, young animals at monthly intervals to provide a series of known-aged skulls from which ageing criteria has been determined.

Most animals have been collected by the writer with a shot in the neck vertebrae which drops the animal instantly. The rifle used is a telescope sighted .308, a high velocity, flat trajectory rifle which allows precision shooting at considerable ranges, to avoid undue disturbance of other animals. Usually during each collection a team of specialists from the Kenya Veterinary Department, East African Veterinary Research Organization, or East African Agricultural and Forestry Research Organization, has joined the Wildlife Research Project. Therefore, each animal collected has been subjected to exhaustive examination and analysis.

A further series of animals have been examined while immobilized. These drugged animals have then been marked and released, and their movements subsequently followed. The marked animals have provided particularly valuable data.

Results

Age: By examination of teeth, horns, and body structure criteria have been established which allow age determination to within about one month from one month to four years of age. Beyond four years of age, three stages are recognized: mature, old, and very old. The maximum longevity of the wildebeest in zoological gardens is 16 years (Bourlière,

F, 1955). Maximum longevity is rarely achieved in a wild animal, and we have assumed that although an occasional individual may live to an age of 16 years, 14 years is probably nearer the maximum practical age. We have divided the ages from five to 14 years into the three age stages recognizable from examination of the animal. Thus a mature animal is from five to eight years old, an old animal from nine through eleven, and a very old one over twelve years.

Weight: We have weighed 130 wildebeest of all ages. The weighed animals have been aged, and figure 1 gives the resultant age/weight chart. Growth is interrupted at about ten months by the "yearling disease" which strikes virtually all yearlings in the Narok District wildebeest population. The female growth rate follows a step-like pattern which appears to be correlated with periods of pregnancy. After the period of maximum growth is reached, at roughly five years, there is a slow but steady decline in weight through the rest of life.

Reproduction: Wildebeest young are born usually between late November and early April. The period when the majority of calves are dropped is January through March. The gestation period appears to be roughly nine months. Most (86 %) females are bred first when just over one year old, so that the first calf is dropped when they are about two years old. They normally have one calf a year after that until they reach old age (about eleven years old). A hundred percent of all cows examined between the ages of two and eleven were pregnant. In terms of the total female wildebeest population, over 95 % of the females over twenty months old have a calf each year. No definite evidence of twins has been noted.

The calf is nursed until next year's calf is born, and if the new calf is lost, the older one apparently resumes nursing until at least 16 months of age. The milk is only a supplement, however, for young wildebeest start eating grass when about ten days old, and grass makes up the bulk of their diet when about three months old.

Adult Mortality: The age/sex structure of the wildebeest population is shown in figure 2. Mortality among the adult males is evenly distributed throughout their lifespan, and a random sample of adult males shows virtually as many very old males as those in any other age class. Females, on the other hand, incur most of their mortality during their reproductive life. Only 2 % of the females who live past their first year survive beyond their eleventh. Reproduction is probably the reason for this disparity in mortality effects. Females which are heavily pregnant, are giving birth, or protecting their young are more vulnerable to predation and disease than males.

The primary known cause of adult mortality is predation. There are between two hundred and three hundred lions in the Narok District. In a study of predation in the Serengeti National Park and the Nairobi Park, Wright (1960) stated that the average annual kill per lion was 36.5 individuals of the major prey species. In Narok District the annual average prey kill per lion appears to be about 35 (this study). Wright (*ibid.*) found that wildebeest made up about half (49 %) of the lion kills, and this figure agrees with the present findings in Narok District. At this rate, between 3,500 and 5,250 wildebeest are lost yearly to lion alone. Added to this loss is predation by leopard, cheetah, hunting dogs, and hyaena, all of which prey to some extent on wildebeest (this study; Wright, 1960; Major Temple-Boreham, verbal). A conservative estimate of the yearly wildebeest predation loss, based on the above figures and observational evidence, is 4,000 animals. Of these, roughly 1500 are young animals and 2,500 adults. The adult wildebeest kill appears to be about 1100 females and 1400 males.

Calf Mortality: On the basis of the samples collected, there is no demonstrable mortality between conception and birth. During the first two weeks after birth a large percentage of calves die or are killed. This loss is due in part to predation, especially from hyaenas; and part to disturbance of the herds which results in the young animals becoming separated from their mothers. This latter factor is especially important in very large herds. The lost calves wander about from wildebeest to wildebeest, and are roughly shoved away by both bulls and cows, eventually to die of starvation or more likely, to be eaten by predators.

Following the first month of life, there is a steady loss of calves to predators, at a level much lower than that of the first month. During the past two growing seasons in Narok District, the annual predator kill of yearling wildebeest has amounted to about 45 % of the total calf crop.

The other principal known source of calf mortality is disease. Starting in October or November, usually following the short rains and a flush of green grass, numbers of seven to ten month old wildebeest calves are noted to be sick or dying. This condition continues in greater or lesser intensity through January, by which time about 40 % of the total initial calf crop has succumbed. Virtually all calves observed have been affected in some degree.

The E.A.V.R.O. personnel who have examined some of the sick animals believe that the disease is rinderpest (W. Plowright, verbal). It appears that the new born calves have a chloestorol immunity to this disease which they have received from their mothers. The initial

immunity presumably wears off after roughly six months, leaving the calves susceptible to rinderpest. Apparently, the animals are exposed to the disease about the time that their resistance is drastically lowered, through prolonged drought, extended migration, and/or the short-rain induced flush of green grass. The combination of these factors, probably plus others (including predation on the weakened animals), brings about a high mortality. Those animals which survive have presumably acquired an immunity to rinderpest.

During the past two years the combination of disease and predation during the first year appear to have reduced the annual calf population by 85 % (Figure 3).

Sex Ratio: The foetal sex ratio, which is apparently the sex ratio at birth, is 40 % females to 60 % males. After the first year of life, the sex ratio is 42 % females to 58 % males. The overall sex ratio of adult wildebeest is 45 % females to 55 % males. therefore, although there are more males than females in the total population, from birth to maturity there is a differential mortality in favor of female survival.

Size and Structure of Population: The present (January, 1961) wildebeest population in the Narok District is roughly 8,000 animals. The population structure is diagrammed in Figure 4.

The age and sex structure of the known annual mortality is diagrammed in Figure 5. It can be seen from a comparison of these two figures that with the wildebeest population at its present level, the population increase cannot balance its decrease due to mortality. If mortality factors remained constant, i.e. predation at the present level and disease taking 40 % of the annual calf crop, an adult population of about 16,220 would be required to balance the known mortality (Figure 6).

To check the accuracy of the above calculations, one can compare the present population with that counted in the course of Dr. Darling's ecological reconnaissance of the Mara in 1958. Darling (1960) records a total of 16,985 wildebeest from the Mara and the immediately adjoining plains in Tanganyika. He estimates (*ibid*) the total in the Mara area alone at 15,000. In the course of the present study at least part of the "Tanganyika wildebeest population" has been observed to enter Kenya and join the "Kenya population," and vice versa. Consequently, we have taken the effective Kenya population at that time to be between Darling's two figures, and to facilitate calculations called it 15,725.

If mortality and reproduction rates remained constant, and no other source of population loss existed, the wildebeest population should have decreased from 15,725 in October-November 1958 to 13,043

in October-November, 1960. This reduction would represent a loss of some 17 % of the initial total in two years. However, the actual census figures from this study show that the wildebeest population in October-November 1960 was roughly 7,000 (Figure 11), which represents a loss of ⁵⁵38 % in two years.

Mortality factors in addition to predation and disease include legal and illegal hunting, and accidents. The observed losses from these causes are not high enough to account for the figure of ⁵⁵38 %. The remaining known source of wildebeest population loss is emigration. From the preliminary analysis of the data it appears that most of the population loss, over and above the loss expected from predation and disease, is due to movement of the population out of the Narok District study area.

Population Movement: Although population movement or migration is not properly a part of population dynamics, in the present case it vitally affects the Narok District wildebeest population size and structure. Wildebeest migration is also of vital concern from the standpoint of wildlife management, both in Kenya and Tanganyika. Consequently a very brief outline of migration factors is included below.

In general pattern, the wildebeest herds spend the dry season near available water, usually in the south-west area of the Kenya Mara region, or across the border in the Tanganyika Mara or the northern extension of the Serengeti National Park. In the wet season they move north and east. There is no orderly or regular migration such as is observed in birds, but rather the picture is of an eddying and flowing, sometimes concentrated and sometimes dispersed. A detailed discussion of the factor involved in wildebeest migration will be the subject of a subsequent paper, but the two primary factors (as presented by the author at the Conference held in Arusha 11th and 12th May, 1960, on Research Problems in the Serengeti National Park) appear to be grass - species composition and stage of growth as determined by rainfall, fire, and grazing - and surface water.

The wildebeest display a marked preference for short ($\frac{1}{2}$ to 4 inch high) green grass (Talbot, 1961), and most of the observed "migratory" movements have been associated with a search for this type of feed in association with available drinking water. Herds travel long distances apparently following an observed rainstorm. Twice in the past year aggregations of up to 3,000 wildebeest have moved from the Mara River or Talek region of Narok District up across the Bardamit Plains to the Loita Plains, apparently following observed heavy rainstorms in that vicinity, only to discover that no green grass was available as the rain had actually fallen in the nearby hills. In both cases the animals

milled about on the dry plains for about two days then returned the way they had come. The total distance covered in these futile round trips was roughly 120 miles.

As long as short green grass is available the wildebeest will follow and feed on it. The habits and life cycle of the wildebeest appear to be strongly oriented around the availability and search for new green grass. For example, the location of calving appears to be determined primarily by grass growth and water. During the past two seasons nearly as many calves have been dropped in the other parts of the Narok District as on the Loita Plains, the traditional "wildebeest calving ground." From the results to date of the present study, there is no indication that access to the Loita Plains for calving is essential for the survival of the wildebeest. If the animals were denied access to that area for management reasons, for instance, by construction of a game fence, maintenance of the wildebeest population should be unaffected as long as sufficient, acceptable food and water were to be found in their remaining available range. It also appears that this principle should hold with the Serengeti wildebeest, if a game fence were to be constructed to keep the wildebeest within the park boundaries.

Local, small scale, herd movements appear associated with muddy ground and movements of other herds. The grazing patterns observed on various plains areas appear correlated initially not with the species of grass present, where this has been constant, but rather with the the available grasses that were growing on the driest footing. As postulated by Dr. H. Heady (Heady, 1959, verbal) and subsequently confirmed by the present study, wildebeest and many other wild species markedly avoid muddy "black cotton" soil wherever possible.

Movement and proximity of other wildebeest herds also appears to influence individual wildebeest movements. Individual animals or small herds have often been observed to leave an area occupied for some weeks, or to alter their own direction of movement, in order to join a larger "migrating" herd.

This follow-the-group behavior may explain the recent fluctuations in the numbers of Narok District wildebeest. During August and September, 1960, thousands of wildebeest^{and associated animals} from the Serengeti Plains migrated northward moving through the western edge of the northern extension of the Serengeti Park. These animals travelled from the Western Corridor section of the Park to the Talek Plains area in Kenya. The northern migration route of a part of the population, followed by land rover, covered 137 miles starting from the National Park boundary on the Western Corridor. The animals vacated the dry Central Plains and Corridor, and moved through the often-dense brush following the areas which had

been recently burned and rained upon, and which were carpeted with a flush growth of short green grass. For a period of four to six weeks these animals mingled with a part of the "Kenya wildebeest population," the wildebeest and associated species -- particularly zebra, thomson's gazelle, and topi -- concentrating on the Egolok and Talek Plains of Kenya and the plainsland near Kuka and the Bologonja River in Tanganyika, where grass fires followed by rain had produced a flush of grass. During late September and October the northern plains areas became dry and the bulk of these animals moved south, through the central and eastern portion of the northern extension of the Serengeti Park. Presumably these animals were accompanied by some of the animals "resident" in Kenya during the previous months. No marked wildebeest were observed in this movement south, but one topi marked in Kenya was subsequently observed in the Serengeti National Park. This specimen, a female, was marked near the Governor's Camp on the Mara River on July 17, 1960. She was sighted the following day, and was next observed with a young calf at heel at Seronera Camp in the first week of November (Matthews, 1961; G. Poolman, verbal), and was seen again near Seronera in early January 1961 (G. Poolman, verbal). Since the animal was marked one and $\frac{1}{2}$ months before the arrival in Kenya of the animals migrating north from the Serengeti, and was sighted at Seronera (roughly 120 miles south) after the return there of the "northern migration," it appears that this topi joined or followed the large herds from the Serengeti when they moved back south. From observation and counts, it appears that the same thing may have happened with a significant number of the wildebeest present in the Talek-Egolok area before the influx of the southern herds. This inter-territorial exchange of animals may be a frequent but irregular occurrence, with the direction and magnitude of movement determined by the patterns of rainfall, grazing and grass burning.

Conclusions

From the foregoing, brief outline of the preliminary findings on population dynamics of the wildebeest in Narok District, the following conclusions may be drawn:

1. The wildebeest have a very high reproductive rate. Over 95 % of all females of over one year of age produce one calf each year.
2. The mortality rate of wildebeest is extremely high. At the current rate, the combination of predation and disease annually remove such a large proportion of the wildebeest that a population level of over twice the present numbers would be required to achieve a high enough survival rate of young animals to maintain a population equilibrium. Therefore, before removal of any large numbers of animals is attempted, steps must be taken to reduce the mortality rate.

3. The population decline in the past two years (⁶⁵38 %) is too great to be accounted for purely by predation and disease. Much of the additional population loss appears to result from movement of animals south into Tanganyika.

4. The wildebeest population movements appear to be determined by grass growth, which is a function of burning, grazing and rainfall; and availability of water. The location of calving appears to be determined by these factors, and there is no indication that access to the Loita Plains is essential to wildebeest reproduction or survival, so long as adequate acceptable food and water exists elsewhere in their range.

5. Because of the interterritorial movements of the animals apparently following the changing distribution of their preferred grass foods, from the standpoint of population dynamics, ecological research and applied management, the region of the Serengeti National Park and the adjoining portion of the Narok District of Kenya are not separate entities and should be considered as a single ecological unit.

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