

# Population trends of resident wildebeest [*Connochaetes taurinus hecki* (Neumann)] and factors influencing them in the Masai Mara ecosystem, Kenya

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## Abstract

Population trends of resident wildebeest (*Connochaetes taurinus hecki* (Neumann)) and factors influencing them in Masai Mara ecosystem between 1977 and 1997 were investigated. Population trends were analyzed using aerial census data collected through systematic reconnaissance flights. Aerial censuses pertaining to resident wildebeest populations (non-migratory) were identified from migratory populations through spatial analysis. Regression analysis was used for population trend analysis. The impact of land use changes on wildebeest population was analyzed by comparing changes in wildebeest densities in cropped and non-cropped areas. Relationship between population size and rainfall fluctuations was used to assess the influence of rainfall on trends. Comparison of cattle densities in cropped and non-cropped areas was used to get an insight into possible competition between cattle and wildebeest for food. The results show that resident wildebeest population in the Masai Mara ecosystem has declined from about 119,000 in 1977 to about 22,000 in 1997, an 81% decline. The decline is mainly attributed to loss of former resident wildebeest wet season grazing, calving and breeding ranges to agriculture. Rainfall fluctuations and possible competition between wildebeest and cattle during periods of limited food resources may have further contributed to the decline. © 2001 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

The Masai Mara National Reserve (MMNR) and adjoining group ranches (hereafter referred to as Masai Mara Ecosystem) in Kenya, form the northern portion of the Serengeti–Mara ecosystem to which wild animals (especially wildebeest and zebra) migrate annually. The ecosystem has the richest wildlife resources and offers the most spectacular wildlife watching in Kenya (Stelfox et al., 1986). These rich wildlife resources to a certain extent depend on the facilitation process maintained by annual migration of wildebeest and zebra. The wildebeest and zebra from Serengeti National Park migrate and stay in the Masai Mara ecosystem between June

and November (Maddock, 1979). They occupy mainly the reserve and the adjoining group ranches. The resident wildebeest population also migrate between the reserve and the adjoining dispersal areas (Fig. 1) within the ecosystem. These migrations clearly show that the protected area (the reserve) is not adequate for the protection and viability of migratory wildlife species in the ecosystem. Rarely can wildlife parks be established so as to encompass an entire ecosystem. For this reason the viability of wildlife inside most protected areas is frequently influenced by outside factors (Jansen, 1986).

Habitat fragmentation or complete habitat loss is thought to be responsible for many wildlife species becoming endemic or extinct (Caughley and Sinclair, 1994; Prins and Olff, 1998). Prins and Olff (1998) note that an ecosystem that becomes smaller due to areas being put under cultivation (where wild grazers cannot occur any more) will show a decrease in species packing. This is the result of increased competition, although local

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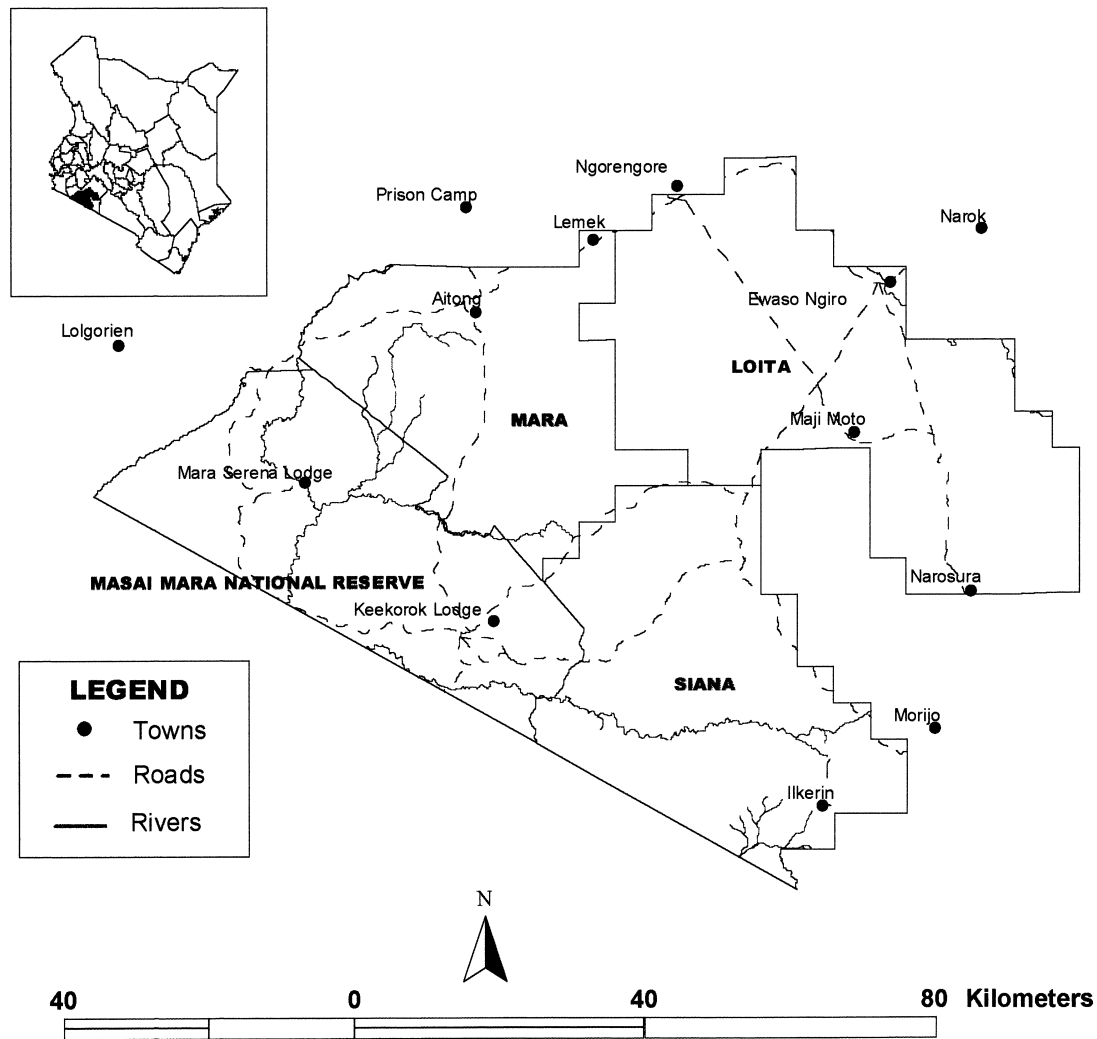


Fig. 1. Map showing (a) the four range units within the Masai Mara ecosystem and (b) the location of the study area in Kenya.

extinctions may play a role too. Norton-Griffiths (1995) also notes that wildlife managers are most concerned about the conversion of privately owned rangelands to agriculture and ranching. Lado (1996) observes that the most serious long-term threat to the future of wildlife populations in Kenya is the indirect effects on habitat resource destruction or alteration. In Africa, the increasing conversion of natural lands to agriculture and human settlements is mainly attributed to increasing human population and is thought to be responsible for the increasing decline in wildlife resources (Johan, 1995).

The wildebeest is a flagship or keystone species in the Masai Mara ecosystem because of its occurrence in large numbers and its annual migrations within and outside the ecosystem (Talbot and Talbot, 1963; Sinclair, 1995). Their migration generate, through their grazing activities, optimal conditions for other large mammals, a process generally referred to as facilitation

(Bell, 1970, 1971; Prins and Olff, 1998). This facilitation can only be sustained through regular migrations between protected and dispersal areas. However, the dispersal areas are increasingly being converted from pastoral grazing areas to agricultural and human settlement areas (Norton-Griffiths, 1995; Sinclair, 1995). For example, between 1975 and 1995, the area under wheat in the Masai Mara ecosystem has increased from 4875 ha in 1975 (Karime, 1990) to 11,000 ha in 1985 to 50,000 ha in 1995 (Serneels et al., in press). The long-term impact of these land use changes on the population of the wildlife species (especially the migrants) has not been studied. However, a number of studies undertaken in the ecosystem indicate that populations of most wildlife species are on the decline (Brotten and Said, 1995; Grunblatt et al., 1996; Sitati, 1997; De Leeuw et al., 1998; Ottichilo et al., in press).

In this study we analyze the trends of the resident wildebeest population in Masai Mara ecosystem over

the past 20 years (1977–1997). We further analyze the relationship between crop (wheat) expansion, rainfall fluctuations and cattle density and wildebeest population trends.

## 2. Study area

The current study was carried out in c. 6000 km<sup>2</sup> of the Masai Mara ecosystem, in the southern part of Narok district, Kenya. Following Stelfox et al. (1986) we distinguished four range management units in the study area (Fig. 1). The Masai Mara National Reserve (MMNR) and the Mara group ranches are mainly composed of *Themeda* grassland. Dwarf-shrubland and *Acacia drepanolobium* grassland characterize the Loita plains while Siana consists mainly of hills and plains supporting *Croton* shrubland and other woody species interspersed with grassland. More detailed descriptions of vegetation and land use are given by Ottichilo et al. (in press) and Stelfox et al. (1986).

## 3. Methods

### 3.1. Data collection

In the current study we used animal counts from 42 censuses conducted in the ecosystem between 1977 and 1997. The data was collected by the Department of Resource Surveys and Remote Sensing (DRSRS) using a systematic reconnaissance flight (Norton-Griffiths, 1978). The data and method appear reliable (De Leeuw et al., 1998; Ottichilo and Khaemba, in press). The ecosystem was surveyed along transects oriented in east-west direction and spaced at 5 km intervals. Flying heights were c. 90 m (1977–1985) and 120 m (1985–1997). Two experienced and well trained observers (Dirschl et al., 1981) occupied the rear seats of a high wing aircraft (Cessna 185 or Partinevia) and counted animals that appeared between two rods attached to the wing struts. The field of vision between these rods was calibrated by flying repeatedly across ground markers of known spacing (Ottichilo and Sinange, 1985). The numbers of animals falling within the survey strips on either side of the aircraft along each 5 km transect segment were counted and recorded into tape recorders by the two Rear Seat Observers (RSO). Groups of animals >10 in number were also photographed and later counted with the aid of a 10× binocular microscope and overhead projector. Population estimates (P.E.) for every species and every census were calculated using the Jolly 2 method (Jolly, 1969). Although the method gives too large standard deviations, the means are reliable (Khaemba and Stein, in press).

Lastly, information on the presence or absence of agriculture and the crop species present (mainly wheat) was recorded by a Front Seat Observer (FSO) on 5×5 km sub-unit basis.

### 3.2. Distinguishing migratory and non-migratory period

This study analyzed trends in the resident wildebeest population. This required identification of a sub-set of censuses conducted during the non-migratory period, from the larger set of 42 censuses conducted throughout the study period. Using fixed starting and end dates for the migration as reported by Maddock (1979) would have been a simpler method to allocate the censuses to either the migratory or the non-migratory period. However, we deemed this approach invalid because for the last 20 years the periodicity of the movements of migrants have not been fully described (Sinclair, 1995). Also experience gained by tour operators and reserve management show that the exact month and date of the onset and end of the migration varies considerably between years.

Instead, we developed a method which uses the observed spatial distribution pattern of wildebeest to decide whether there was migration or not. The rationale for this was based on Lamprey (1984) who reported that during migration, wildebeest concentrate in and around the MMNR and adjoining group ranches, while during non-migratory periods resident populations are concentrated in the Loita plains. We first analyzed and verified whether this pattern which was based on analysis of 12 censuses in 1978–1979, held for the period between 1977 and 1997, and then used the distribution pattern to differentiate between censuses pertaining to migratory and non-migratory periods.

We calculated the weighted mean centre (Walford, 1997) of the distribution of wildebeest for all 42 censuses according to:

$$X_w = \sum X_i W_i / \sum W_i \text{ and } Y_w = \sum Y_i W_i / \sum W_i$$

Where  $X_w$  and  $Y_w$  represented the weighted mean centre expressed in Universal Transverse Mercator projection (UTM),  $X_i$  and  $Y_i$  represent the UTM coordinates and  $W_i$  the weighting variable for observation point  $i$ , which corresponded to the number of animals, recorded by the RSO.

We then fitted a geometric mean regression (Sokal and Rohlf, 1995) through the 42 calculated weighted mean centres of the distribution of wildebeest. We subsequently projected the weighted mean centre of every census on the geometric mean regression line, and calculated the distance of these projections to the Tanzanian border. The location of these points along the geometric regression line was then used to analyze the displacement of the centre of the wildebeest population between

seasons. For this purpose we plotted the day number (Julian) of the year when each census was conducted against its respective distance from the Tanzanian border. The procedures described above resulted in the selection of 21 censuses pertaining to the non-migratory period. These were used for further analysis as described below.

#### 4. Analysis

##### 4.1. Populations trends

We first regressed the 21 wildebeest population estimates against time in order to determine whether there was evidence of trend in the resident wildebeest population. The factor time was expressed as year of observation, with decimals indicating the day number within the year. The dependent variable (wildebeest population estimate) was log transformed prior to analysis because exploratory data analysis revealed non-linearity in its relationship with time. The null hypothesis was: **H<sub>0</sub>**:  $\beta = 0$ , the alternative was two-sided (i.e. **H<sub>a</sub>**:  $\beta \neq 0$ ), where  $\beta$  is the slope for the population.

We next plotted maps in order to analyze whether there was evidence of change in the spatial distribution of the density of resident wildebeest population over the last 20 years. The recorded wildebeest density ( $n \text{ km}^{-2}$ ) for every  $5 \times 5 \text{ km}$  aerial survey sub-unit was averaged for the following four time periods: 1977–1979, 1982–1984, 1985–1989 and 1990–1997. Arc View GIS software was used for this and other spatial analysis throughout this study.

##### 4.2. Analysis of factors related to the observed population trends

Previous research (Douglas-Hamilton, 1988; Sitati, 1997) claimed that expansion of agriculture is the main factor influencing wildlife population trends in the Masai Mara ecosystem. However, a decline of resident wildebeest population may be a result of more than one single factor. Therefore, we analyzed the relation between size of the resident wildebeest population with rainfall and agricultural encroachment. We additionally investigated whether there was indirect evidence of increased competition between cattle and wildebeest.

We first plotted the extent of wheat farming as recorded by the front seat observers; using dots to indicate whether crop growing had been recorded (presence) or not (absence) during the four periods. We then addressed the question of whether a relation existed between encroachment of agriculture and average density of wildebeest prior to agricultural encroachment. The null hypothesis was that prior wildebeest density did not differ between areas encroached and not encroached by agriculture. A simple *t*-test was used to test this hypothesis.

We also addressed the question of how encroachment of arable farming has affected the density of resident wildebeest. If farming did not have an effect one would expect the same rate of decline for areas affected by farming and areas not encroached. We used FSO data to identify sub-units ever affected and those never affected by agriculture. Next, we calculated population densities for these two samples. We then separately regressed the logarithm of wildebeest population density against time for areas occupied and not occupied by crops. Prior to the analysis, we expected that the rate of decline would be higher in areas with agriculture compared to those without. This led us to the following null and one-sided alternative hypothesis: **H<sub>0</sub>**:  $\beta_+ = \beta_-$  and **H<sub>a</sub>**:  $\beta_+ > \beta_-$ , where  $\beta_+$  and  $\beta_-$  represent the slopes for the regressions in areas with and without crops respectively. We used a *t*-test to test for differences in slopes between these two samples.

Rainfall is one of the main factors that influence primary production in semi-arid areas (Phillipson, 1975). Its fluctuations in time and space influence the abundance and distribution of herbivores (Prins and Olff, 1998). In this analysis 20-year rainfall records from two meteorological stations were used to investigate whether rainfall fluctuations during the period had any influence on wildebeest population fluctuations and whether droughts occurred during the period. Rainfall data recorded at the meteorological station in Narok, located at 15 km from the centre of the Loita plains was used in the analysis. Norton-Griffiths et al. (1975) indicated that the rainfall year in the Serengeti-Mara ecosystem is considered to start in November. Therefore, to calculate annual rainfall totals, rain falling between 1 November of one year and 31 October of the following year should be used. This November–October period is more relevant ecologically than the period January–December for it represents one complete seasonal cycle (Norton-Griffiths et al., 1975; Prins and Loth, 1988).

The mean annual (November–October), mean wet season (November–May) and mean dry season (June–October) rainfall and respective variability were calculated. Determination of drought or wet year was done according to Prins (1996). The resident wildebeest population estimates were regressed against the annual total rainfall as well as wet and dry season rainfall in the year of census. Lastly, the residuals of regression analysis of the relation between wildebeest densities in cropped and non-cropped areas in Loita plains and time of observation were plotted against annual, wet season and dry season rainfall to determine any relationship between them.

Increase in competition with cattle could be another factor negatively affecting the resident wildebeest population since cattle and wildebeest are known to overlap by >60% in their forage requirements (Hansen et al., 1984). During the crop-growing season (November to

June), cattle are moved out of the crop fields to the adjacent non-cropped rangelands (Livestock Officer, pers. comm.). Hence, we expect an increased density of cattle on these non-cropped rangelands during this period. These rangelands are, at this period of the year, occupied by the resident wildebeest population (Lamprey, 1984). The expected increased density of cattle could lead to increased competition with wildebeest. Given that the range conditions of these areas have been generally reported to be poor (Mwichabe, 1988), increased competition with cattle in this particular period could in the long-term have a negative effect on the wildebeest population density.

We first analyzed the available 42 censuses, to verify whether there had been an increase in the density of cattle during the study period. Our null hypothesis was that the density had not increased:  $H_0: \beta = 0$  and the alternative was two sided:  $H_a: \beta \neq 0$ , where  $\beta$  is the slope of the regression line. Second, we tested the hypothesis that in the non-cropped area the difference in density of cattle between crop growing and non-growing period equaled zero. We compared censuses from the same year, one in the crop growing periods and the other in non-growing periods. We used a matched-paired test, since repeated records were made on the same sub-unit.

## 5. Results

### 5.1. Spatial distribution

Fig. 2, which shows the weighted mean centre of the distribution of wildebeest for the 42 censuses, reveals two distinct clusters. The southwesterly cluster, situated within and around the MMNR, is located at distances of < 40 km from the Tanzanian border. A second cluster in

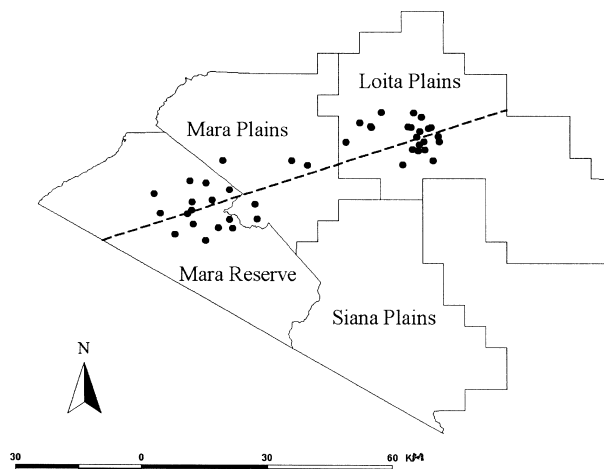


Fig. 2. Location of weighted centre mean of distribution of wildebeest recorded in 42 censuses, between 1977 and 1997. The line fitted through the data represents the geometric mean regression line:  $y = 555.3 + 0.338 * X$ .

the Loita plains is located at distances of > 60 km from the Tanzanian border. Two censuses are located somewhat in the middle of these two clusters.

Fig. 3A shows a relationship between the distance from the Tanzanian border and the day number, while Fig. 3B relates estimated population size and day number. Together the figures show that censuses taken between mid November (day number > 320) and late May (day number 150) correspond to wildebeest population sizes < 200,000 and occur at distances > 60 km from the Tanzanian boundary. We classified these 21 censuses as non-migratory censuses. Population estimates > 200,000

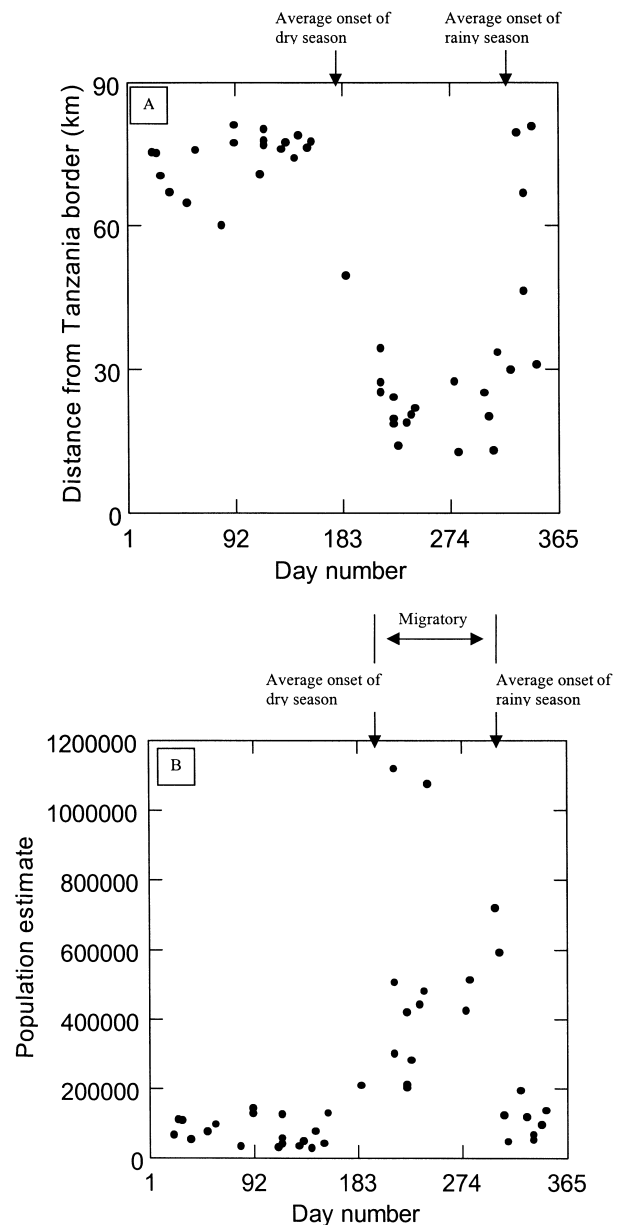


Fig. 3. Relation between time of the year (Julian day number) when the censuses were conducted and (A) the distance of the weighted mean centre of the distribution of wildebeest, from the Tanzania border, (B) the estimated size of respective wildebeest population.

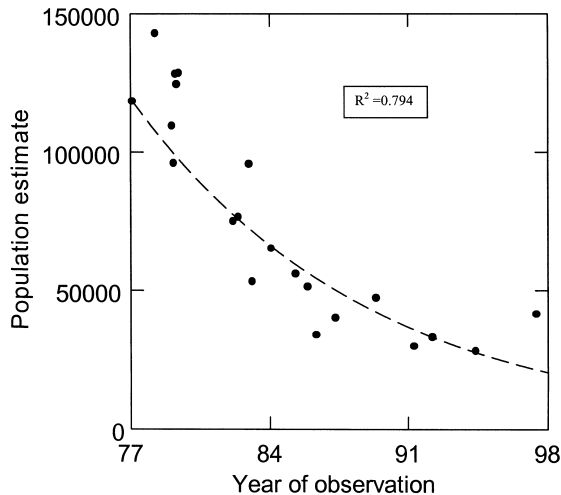


Fig. 4. Relation between year of observation and the size of the resident wildebeest population. The fitted regression line corresponds to:  $\text{Ln}(Y) = 18.158 - 0.084 * X$  ( $R^2 = 0.794$ ;  $n = 21$ ;  $P < 0.0001$ ).

animals, at distances  $< 30$  km from the boundary were recorded between mid June and November. Because of the period in the year, higher population sizes, and closer distance to the Tanzanian border, we classified these 19 censuses as migratory period censuses. Two censuses fell outside the two clusters mentioned above. These two censuses most likely represent transitional resident and migratory populations that have not fully dispersed. We therefore did not allocate these two censuses to the non-migratory period.

### 5.2. Population trends

Fig. 4 shows the relation between the size of the resident population and year of observation. The fitted regression model indicates that the resident wildebeest population declined ( $P < 0.001$ ) from 119,000 in 1977 to 22,000 in 1997 at an annual rate of 8.4%.

Fig. 5 shows change in wet season wildebeest density between 1977 and 1997. Initially in the late 1970s, highest densities occurred in the northern parts of the Masai

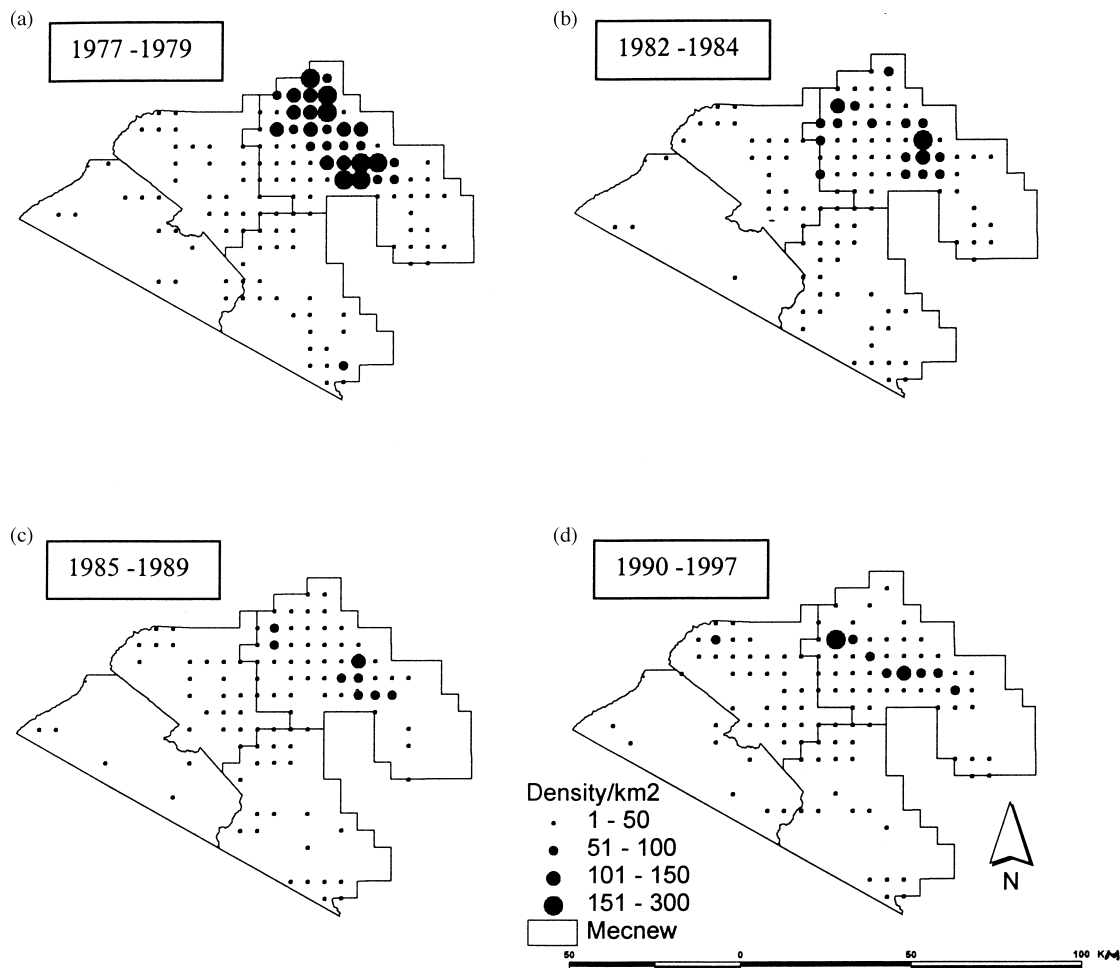


Fig. 5. Average density ( $n \text{ km}^{-2}$ ) of wildebeest recorded in the Masai Mara ecosystem for (a) 1977–1979, (b) 1982–1984, (c) 1985–1989 and (d) 1990–1997.

Mara ecosystem particularly in the central and north-western parts of the Loita plains. In the early 1980s (1982–1984) densities appear to have declined considerably in northern and central parts of the former 1970s high-density areas. During the late 1980s (1985–1989) densities further declined in these areas including eastern parts. By the 1990s the densities appear to have declined significantly in all these areas in comparison to the late 1970s densities. Hence, this decline in wildebeest densities started in the early 1980s and continued to 1997 (Fig. 5). It appears to be most pronounced in the Loita plains.

### 5.3. Factors related to observed population trends

Table 1 shows the wet and dry season and annual total rainfall for the 20 year period. It identifies two exceptionally wet years and five drought years. Regression models of estimated wildebeest populations against these annual rainfall figures reveal significant relationships ( $P < 0.05$ ) with annual total and wet season rainfall (Fig. 6). Plots of residuals of regression lines of wildebeest densities in agricultural and non-agricultural areas of Loita plains further showed that annual and wet season rainfall had relationship with wildebeest

Table 1

Yearly wet season, dry season and total rainfall for Narok meteorological station and the mean of the 21 years between 1977 and 1997 with overall year deviations from the respective 20-year means. Unusually wet or drought years are defined as years with more or less than 20 year mean plus or minus the standard deviation (S.D.) respectively)

Year	Wet season	Dry season	Total rain	Deviation	Wet or drought
1977	739	166	905	173	
1978	1024	66	1090	358	Wet
1979	808	89	897	165	
1980	635	169	804	73	
1981	546	55	601	−131	
1982	415	167	582	−150	
1983	567	192	759	28	
1984	298	108	406	−326	Drought
1985	759	97	856	125	
1986	459	40	499	−233	Drought
1987	769	153	922	191	Wet
1988	761	92	853	122	
1989	718	182	900	168	
1990	709	119	828	96	
1991	388	131	520	−212	Drought
1992	395	79	474	−257	Drought
1993	623	151	774	42	
1994	495	52	547	−185	Drought
1995	487	145	632	−99	
1996	523	273	796	64	
1997	599	120	719	−13	
Annual mean	606	126	732		
S.D. of mean	175	56	181		
variability (%)	30	45	25		

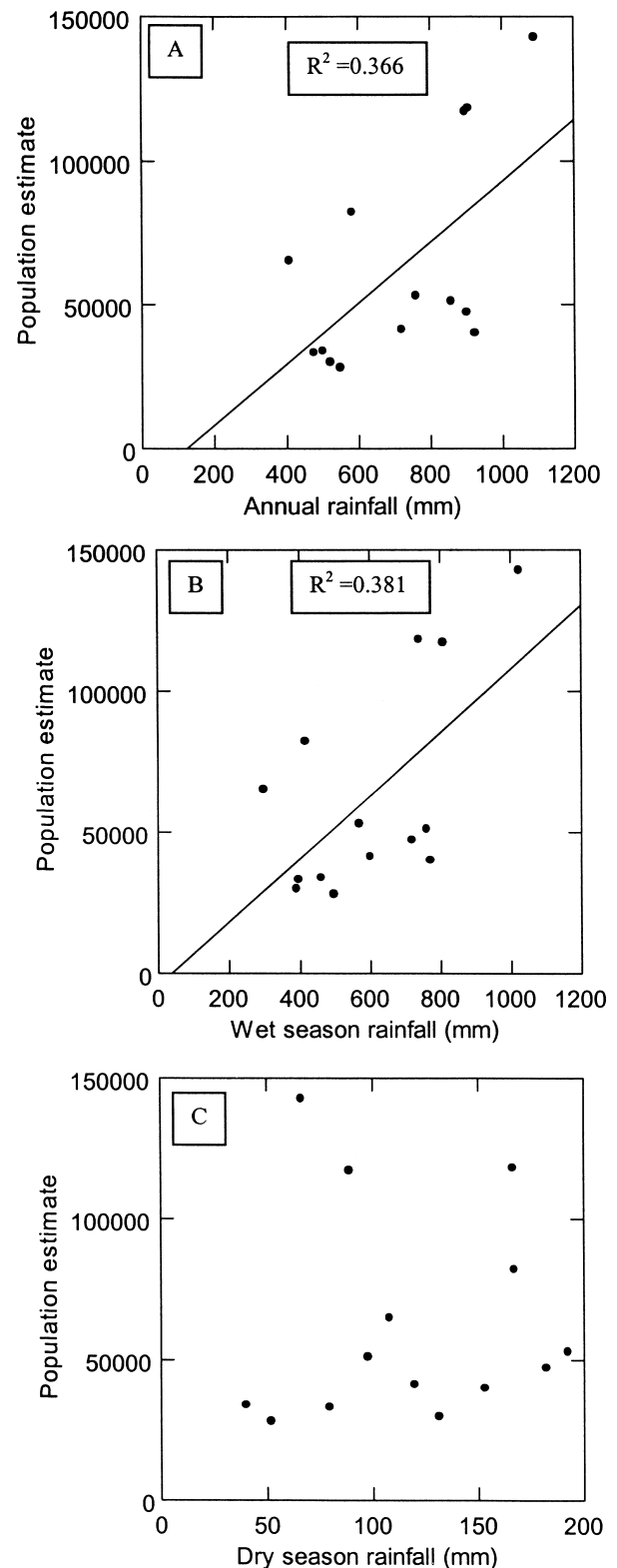


Fig. 6. Relation between wildebeest population estimate and (A) annual rainfall, (B) wet season rainfall, (C) dry season rainfall at Narok meteorological station. Lines correspond to regression equations for annual rainfall ( $y = -13169.12 + 106.15 \cdot X$ ;  $R = 0.366$ ;  $P = < 0.022$ ) and wet season rainfall ( $y = -4304.02 + 12.09 \cdot X$ ;  $R^2 = 0.381$ ;  $P = 0.019$ ).

density trends. There was no significant relationship with dry season rainfall.

Fig. 7 shows presence of large-scale wheat growing in the Loita plains from 1978 to 1997. The highest expansion occurred during the 1986–1989 and 1991–1997 periods. There appears to be a remarkable coincidence between the area where wheat growing has encroached upon the Masai Mara ecosystem and where wildebeest have declined (Fig. 5). This is further demonstrated by Fig. 8 which shows that wildebeest density in 1977 was much greater on average in the areas subsequently cultivated for agriculture ( $t = 1.67$ ,  $P < 0.0001$ ).

Fig. 9 shows relation of wildebeest population density in the Loita plains against year of observation for agricultural and non-agricultural areas. In both cases the log-linear regression models show significant downward trends in wildebeest densities. In areas encroached upon by agriculture the annual rate of decline was 9.8% compared with 7.1% in areas without agriculture. A test for differences in slopes of the two models was highly significant ( $P < 0.0005$ ).

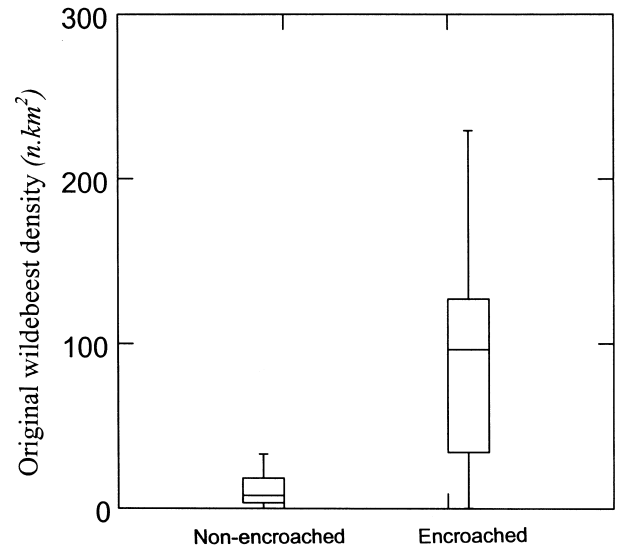


Fig. 8. Box plot of wildebeest density in 1977 in the Loita plains for areas subsequently (A) not encroached and (B) encroached upon by agriculture.

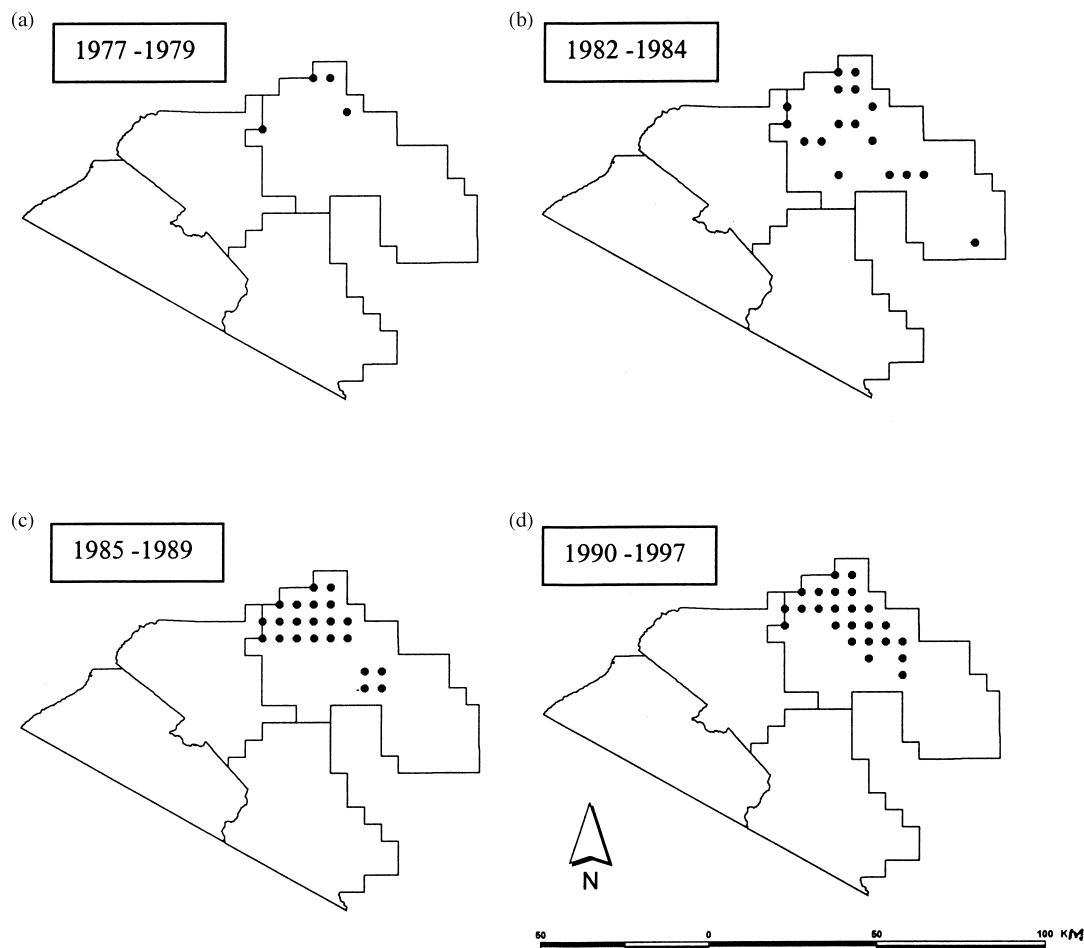


Fig. 7. Presence of large scale agriculture (wheat growing) in the Masai Mara ecosystem as recorded by the front seat observer in the DRSRS airplane, in (a) 1977–1979, (b) 1982–1984, (c) 1985–1989, (d) 1990–1997.



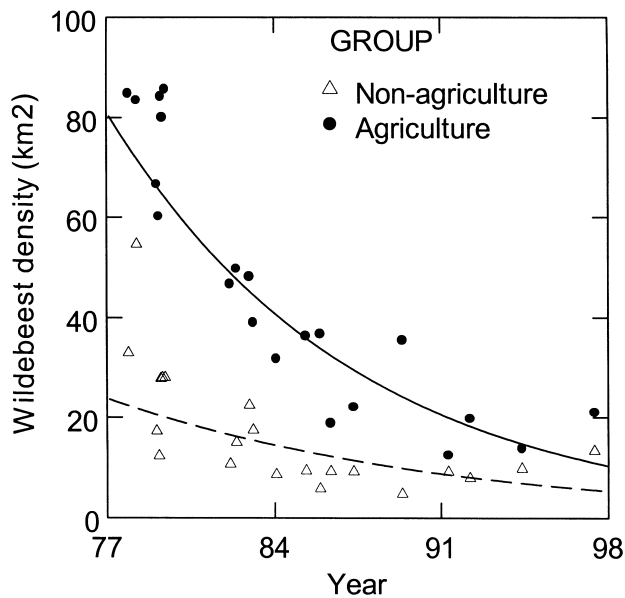


Fig. 9. Relation of density ( $n \text{ km}^{-2}$ ) of the resident wildebeest population in the Loita plains against time (year of observation) for agricultural and non-agricultural areas. Lines represent regression equations for areas encroached by agriculture (solid line;  $\text{Ln}(Y) = 11.942 - 0.098X$ ;  $R^2 = 0.803$ ;  $P < 0.0001$  and areas not encroached by agriculture (dotted line;  $\text{Ln}(Y) = 8.636 - 0.071X$ ;  $R^2 = 0.422$ ;  $P < 0.001$  respectively).

Regression analysis revealed no significant change in cattle densities in the Loita plains during the study period. This indicates that the cattle population size has remained stable despite the fact that a significant portion of the former grazing land has been converted into agricultural land. There was also no significant difference in the cattle density in the entire Loita plains during the dry and wet seasons, indicating that there were no significant movements outside the plains during the dry season. A paired *t*-test for wildebeest censuses in crop growing versus fallow periods in agricultural areas for the years 1982, 1983, 1984, 1986, 1991 and 1992 was significant ( $P < 0.05$ ). This indicates that cattle density during crop growing periods was low in comparison to non-growing periods. A similar test for non-agricultural areas was not significant but cattle density in the crop-growing season was higher than in the non-growing period. The results show that, in non-agricultural areas, high cattle densities occur during the cropping season while their densities in agricultural areas are low during the same period (Table 2). This is because during cropping season most cattle are moved out of cultivated areas to fallow or uncultivated areas. They are moved back to cultivated areas to feed on wheat stubble during the fallow period. We therefore reject our null hypothesis that the differences in cattle densities in cropped and not cropped areas were equal to zero. These results support our hypothesis that there is increase in cattle densities in non-cropped areas during the crop-growing period.

Table 2

Average density ( $n \text{ km}^{-2}$ ) of cattle in the areas occupied and those not occupied by agriculture during the crop-growing season and during the fallow period

Year	Cropping season		Fallow (August)	
	Agriculture	No agriculture	Agriculture	No agriculture
1982	18.34	42.94	24.82	31.95
1983	2.77	18.57	22.43	16.85
1984	19.23	30.04	36.01	15.93
1986	3.50	13.62	2.44	11.38
1991	17.20	35.79	37.83	17.91
1992	31.74	13.66	52.12	25.88
Mean	15.46	25.77	29.28	19.98
S.E.	4.45	5.03	5.30	3.07

## 6. Discussion

### 6.1. Wildebeest population trends

In this study we have shown a significant decline in the size of the resident wildebeest population from about 119,000 in 1977 to an estimated 22,000 in 1997, about 81%. The decline has occurred mainly in Loita plains which are the main calving and breeding grounds of wildebeest in southwestern Kenya (Talbot and Talbot, 1963; Lamprey, 1984). Population estimates from earlier counts indicate that in 1961 the resident wildebeest population in the Masai Mara ecosystem was c. 18,000 (Stewart and Talbot, 1962) and following control of rinderpest in the late 1960s, this increased to c. 94,000 in the mid 1970s (Stelfox et al., 1986). Thus, the resident wildebeest population in the Masai Mara ecosystem appears to have undergone a period of increase between 1960 and 1977 and a period of decline between 1977 and 1997 (Stelfox et al., 1986). The increase of the resident Kenyan population has been attributed to immigration of wildebeest from Serengeti into the Mara due to the population eruption in the Serengeti after eradication of rinderpest (Stelfox et al., 1986). In addition, the change in vegetation from bushlands and thickets to open grasslands (Dublin et al., 1990) could have affected the size of the population.

We demonstrate a clear association between the decline in resident wildebeest populations and the expansion of agriculture into prime and original wildebeest wet season ranges in the Loita plains. Our results further show that the highest decline of wildebeest densities in the Loita plains occurred in areas that are now occupied by crops, particularly wheat. The decline has been progressive, mainly in northern and central parts of the Loita plains where wheat farming has become a permanent activity. We, therefore, conclude that agricultural expansion is the prime cause of the decline.

Wheat growing, which started in the Loita plains in the early 1970s (Amuyunzu, 1984), has continued to expand (Serneels et al., in press) as a result of agricultural potential of the land (Norton-Griffiths, 1995), increasing human population (Ngene and Kariuki, 1999) and government land and food policies for arid and semi-arid areas (Republic of Kenya, 1979). This expansion may also be due to increasing awareness of the landowners that they can realize more economic benefits by diversifying their land use activities (Norton-Griffiths, 1995; Ngene and Kuriuki, 1999). With ever increasing agricultural expansion in the ecosystem (particularly in the Loita and now in the Mara ranches) (Serneels et al., in press), it can be expected that wildlife decline in these areas and consequently in the entire ecosystem will continue.

### 6.2. *Interactions between wildebeest and cattle*

The surprising finding that agricultural encroachment has occurred in the areas formerly most favoured by wildebeest can be attributed to the efforts of the Maasai to eliminate wildebeest from these areas in order to minimize transmission of malignant catarrh disease from wildebeest to cattle (Talbot and Talbot, 1963; Ngene and Kariuki, 1999) and to make them available for livestock grazing. Also it may be attributed to economic gains they receive for leasing the land to commercial wheat farmers. The selective leasing of former optimum wildebeest habitat was due to the suitability of these areas for wheat farming.

Results of a recent socio-economic survey conducted in the ecosystem by Kenya Wildlife Service indicate that overall, wildebeest is rated by the local Maasai (> 70%,  $n=178$  households) as the most problematic wild animal because it transmits disease to their cattle. This problem was probably limited in the 1960s but increased with the 10-fold increase in wildebeest population in the 1970s. The Maasai had to accept this increase since they had no legal means to control the population particularly after the ban of wildlife hunting and control in Kenya in 1977.

Since the Maasai did not benefit from wildebeest, they decided to put their land to other beneficial uses. In the early 1970s, they started leasing the land to commercial wheat growers (Azumi and MacDonald, 1993). Since then wheat growing in the area has become a profitable activity to both the landowner and the tenant hence its uninterrupted expansion. In the Lemek area of Loita plains, where wheat farming dominates, complaints about wildebeest have halved, whereas in Olkinyei where farming is not important and cattle and wildebeest interaction have increased due to wildebeest displacement from cropped areas, complaints have doubled (Ngene and Kariuki, 1999). In retrospect, it can be said that the conversion of parts of the Loita plains into

wheat fields has solved the problem of the wildebeest plague in those areas. The wheat companies destroyed the most suitable wildebeest habitat, which is legal under the current Kenyan law and, as a result, the wildebeest population size declined to the 1960s levels. This calls for serious re-examination of the rationale of making the control of wildlife populations in Kenya illegal while allowing the legal destruction of their habitats.

### 6.3. *Influence of rainfall on wildebeest population*

Fluctuations in rainfall and increased forage competition from cattle may have further contributed to the decline of resident wildebeest population in the ecosystem. Since there is a well established relationship between rainfall and primary production of grass in semi-arid tropics up to an annual total of about 1000 mm (Phillipson, 1975), it is assumed that during the years 1984 and 1986 when the Masai Mara ecosystem experienced droughts, primary production low and limiting. Therefore, it is possible that the wildebeest population experienced food shortages and could have suffered drought-induced mortality and reduced rate of natural increase.

Mduma et al. (1998) have indicated that the drought that occurred in the Serengeti in 1993 was the most severe since 1938 and led to a significant decline in wildebeest populations. Although the Masai Mara ecosystem experienced some drought conditions during the same year, they were not as severe as those of Serengeti (Table 1). However, the droughts of 1984 and 1986 were more severe in the Masai Mara than in the Serengeti (Ottichilo et al., in press). During these droughts, high mortality of livestock was reported in the ecosystem (Republic of Kenya, 1987). Since it has been shown that the energy requirements of cattle and wildebeest are similar (Rogerson, 1966), we expect that the drought may have also affected the wildebeest population. Contrary to available evidence that wildebeest population in the Serengeti is limited primarily by intra-specific competition for dry season food (Sinclair, 1985), it appears that the resident population in the Masai Mara ecosystem is limited by wet season food or rainfall (Fig. 6). Drent and Prins (1987) found the same relationship in Lake Manyara National Park in Tanzania. This may be because it is in wet season ranges where large concentrations of resident wildebeest occur and breeding and calving takes place. Thus decline in wet season rainfall may result into poor quantity and quality of food and this in turn will affect the reproduction and survival rates of the population. Mwachabe (1988) and Said (1993) have reported that these areas are overgrazed during the wet season since they support a large biomass of wildlife and livestock during the period. Amting (1997) has reported low grass biomass in these areas in comparison to inside the Reserve. We therefore

conclude that occurrence of drought conditions in the ecosystem may have further indirectly contributed to the observed decline of resident wildebeest population.

## 7. Conclusions

Overall, we have shown in this study that the resident wildebeest population in the Masai Mara ecosystem has drastically declined in the past 20 years. We have further shown that this decline is mainly related to habitat loss, due to agricultural encroachment. Therefore, it is extremely urgent that concerned authorities and stakeholders take necessary measures that will strike a balance between wildlife conservation and agricultural development if the current downward wildebeest population trend is to be reversed. Also there is an urgent need to revise both the wildlife policy and the relevant legislation so that wildlife habitats outside protected area system are protected from further undesirable destruction.

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## References

- Amuyunzu, C.L., 1984. Land resources inventory as a basis of land evaluation and rural development: the role of remote sensing techniques. MSc thesis, ITC, The Netherlands.
- Amting, E., 1997. Temporal and spatial variation in grassland biomass in Masai Mara game reserve and adjoining areas, Narok District-Kenya. MSc thesis, University of Amsterdam, The Netherlands.
- Azumi, E., MacDonald, M., 1993. Wildebeest and Wheat: Crafting a Land Policy in Kenya's Maasailand. Ministry of Planning and National Development, Long Range Planning Division, Nairobi, Kenya.
- Bell, R.H.V., 1970. The use of herb layer by grazing ungulates in the Serengeti. In: Watson, A. (Ed.), *Animal Populations in Relation to their Food Sources*. Blackwell, Oxford, pp. 111–124.
- Bell, R.H.V., 1971. A grazing ecosystem in the Serengeti. *Scientific American* 224, 86–93.
- Broten, M.D., Said, M., 1995. Population trends of ungulates in and around Kenya's Masai Mara Reserve. In: Sinclair, A.R.E., Arcese, P. (Eds.), *Serengeti 11: Dynamics, Management and Conservation of an Ecosystem*. The University of Chicago Press, Chicago.
- Caughley, G., Sinclair, A.R.E., 1994. *Wildlife Ecology and Management*. Blackwell Science, London.
- De Leeuw, J., Prins, H.H.T., Nguguna, E.C., Said, M.Y., De By, R., 1998. Interpretation of DRSRS Animal Counts (1977–1997) in the Rangeland Districts of Kenya. Ministry of Planning and National Development, Nairobi, Kenya.
- Dirschl, H.J., Norton-Griffiths, M., Wetmore, S.P., 1981. Training observers for aerial surveys of herbivores. *The Wildlife Society Bulletin* 9, No. 2.
- Douglas-Hamilton, I., 1988. Identification Study for the Conservation and Sustainable Use of the Natural Resources in the Kenyan Portion of the Mara-Serengeti Ecosystem. European Development of the European Economic Community, Nairobi.
- Drent, R.H., Prins, H.H.T., 1987. The herbivore as prisoner of its food supply. In: Van Andel, J., Bakker, J.P., Snaydon, R.W. (Eds.), *Distributions in Grasslands: Species and Population Responses*. Dr. W. Junk Publishing, Dordrecht, pp. 133–149.
- Dublin, H.T., Sinclair, A.R.E., McGlade, J., 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology* 59, 1147–1164.
- Grunblatt, J., Said, M., Warugute, P., 1996. National Rangeland Report. Summary of Population Estimates of Wildlife and Livestock. Ministry of Planning and National Development. DRSRS, Nairobi.
- Hansen, R.M., Bauni, S.M., Mugambi, M.M., 1985. Diets and trophic ranking of ungulates on northern Serengeti. *Journal of Wildlife Management* 49, 823–829.
- Jansen, D.H., 1986. The eternal external threat. In: Soule, M.E. (Ed.), *Conservation Biology, the Science of Scarcity and Diversity*. Sinauer, Sunderland, pp. 286–303.
- Johan, T.T., 1995. Determinants of the composition and distribution of wildlife communities in Southern Africa. *Ambio* 24 (1).
- Jolly, G.M., 1969. Sampling methods for aerial censuses of wildlife populations. *East African Agricultural and Forestry Journal* (special issue). Nairobi, Kenya.
- Karime, N.I., 1990. The Changing Land Use Patterns on the Ngorongore Loita Plains. Department of Resource Surveys and Remote Sensing (KREMU), Ministry of Planning and National Development, Kenya.
- Khaemba, W.M., Stein, A., in press. Spatial statistics for modelling of abundance and distribution of wildlife species in the Masai Mara Ecosystem, Kenya. *Environmental and Ecological Statistics*.
- Lado, L., 1996. Problems of wildlife management and land use in Kenya. *Land Use Policy* 9 (3), 169–184.
- Lamprey, R.H., 1984. Maasai Impact on the Kenya Savanna Vegetation: A Remote Sensing Approach. PhD thesis, University of Aston, Birmingham, UK.
- Maddock, L., 1979. The "migration" and grazing succession. In: Sinclair, A.R.E., Norton-Griffiths, M. (Eds.), *Serengeti: Dynamics of an Ecosystem*. University of Chicago Press, Chicago, pp. 104–129.
- Mduma, S., Hilborn, R., Sinclair, A.R.E., 1998. Limits to exploitation of Serengeti wildebeest and the implications for its management. In: Newbery, D.M., Prins, H.H.T., Brown, N. (Eds.), *Dynamics of Tropical Communities*. Blackwell Science, Oxford.
- Mwichabe, E.S., 1988. The Grassland of the Loita-Aitong-Mara plains (Narok District, Kenya): Their Composition, Distribution, Ecology and Productivity. MSc thesis, ITC, The Netherlands.
- Ngene, S., Kariuki, A., 1999. Community attitudes towards natural resource management in the Mara ecosystem. Kenya Wildlife Service, Nairobi, Kenya.
- Norton-Griffiths, M., Herlocker, D., Pennycuik, L., 1975. The pattern of rainfall in the Serengeti ecosystem, Tanzania. *East African Wildlife Journal* 13, 347–374.
- Norton-Griffiths, M., 1978. Counting Animals. Handbook No. 1. African Wildlife Leadership Foundation, Nairobi.

- Norton-Griffiths, M., 1995. Economic incentives to develop the rangelands of the Serengeti: implications for wildlife conservation. In: Sinclair, A.R.E., Arcese, P. (Eds.), *Serengeti 11: Dynamics, Management, and Conservation of an Ecosystem*. The University of Chicago Press, Chicago and London.
- Ottichilo, W.K., Sinange, R.K., 1985. Differences in the Visual and Photographic Measurements in the Estimation of Strip Widths for Aerial Censuses of Animal Populations. DRSRS, Ministry of Planning and National Development, Nairobi, Kenya.
- Ottichilo, W.K., Leeuw, J., Skidmore, A., Prins, H.H.T., Said, M.Y., in press. Population trends of non-migratory wildlife in Masai Mara ecosystem, Kenya. *African Journal of Ecology*.
- Ottichilo, W.K., Khaemba, W.M., in press. Validation of observer and aircraft calibration for aerial surveys of animals. *African Journal of Ecology*.
- Ottichilo, W.K., Said, M.Y., Koster, H.N., Prins, H.H.T., De Leeuw, J., Hoitkonig, A. in press. Dynamics of migratory wildebeest in the Masai Mara ecosystem, Kenya; 1977–1997. *Oecologia*.
- Phillipson, J., 1975. Rainfall, primary production and carrying capacity of Tsavo National Park (East), Kenya. *East African Wildlife Journal* 13, 171–201.
- Prins, H.H.T., Loth, P.E., 1988. Rainfall in time and space in the Masi ecosystem of the northern Tanzania: the background to plant phenology patterns. *Journal of Biogeography* 15, 451–463.
- Prins, H.H.T., 1996. Ecology and Behaviour of the African buffalo. Chapman and Hall, London, pp. 11–16.
- Prins, H.H.T., Olf, H., 1998. Species-richness of African grazer assemblages: towards a functional explanation. In: Newbery, D.M., Prins, H.H.T., Brown, N. (Eds.), *Dynamics of Tropical Communities*. Blackwell Science, Oxford.
- Republic of Kenya, 1979. ASAL Land Use Policy. Government Printer, Nairobi.
- Republic of Kenya, 1987. Narok Development Plan. Government Printer, Nairobi.
- Rogerson, A., 1966. The utilization of metabolizable energy by wildebeest. *East African Wildlife Journal* 4, 149–156.
- Said, M., 1993. Modelling Relationships Between Large Large Herbivores, Vegetation, Soils and Climate in the Mara Ecosystem: A GIS approach. MSc thesis, ITC, The Netherlands.
- Serneels, S., Said, M.Y., Lambin, E.F., in press. Land-cover changes around a major East-African wildlife reserve: the Mara Ecosystem (Kenya). *Journal of Remote Sensing*.
- Sinclair, A.R.E., 1985. Does interspecific competition or predation shape the African ungulate community? *Journal of Animal Ecology* 54, 899–918.
- Sinclair, A.R.E., 1995. Serengeti past and present. In: Sinclair, A.R.E., Arcese, P. Serengeti (Eds.), 11: Dynamics, Management and Conservation of an Ecosystem. The University of Chicago Press, Chicago.
- Sokal, R.R., Rohlf, J.F., 1995. *Biometry: The Principles and Practice of Statistics in Biological Research*. W.H. Freeman and Company, New York.
- Sitati, N.W., 1997. The Change of Land use Patterns in the Masai Mara, and its Impact on the Large Herbivore Populations. MSc thesis. Moi University, Eldoret, Kenya.
- Stelfox, J.G., Peden, D.G., Epp, H., Hudson, R.J., Mbugua, S.W., Agatsiva, J.L. et al., 1986. Herbivore Dynamics in Southern Narok, Kenya. *Journal of Wildlife of Management* 50 (2), 339–347.
- Stewart, D.R.M., Talbot, L.M., 1962. Census of wildlife on the Serengeti, Mara and Loita plains. *East African Forestry Journal* 28, 58–60.
- Talbot, L.M., Talbot, M.H., 1963. The wildebeest in Western Masailand, East Africa. *Wildlife. Monograph*. Chestertown, vol. 12, 88 pp.
- Walford, N., 1997. Geographical data analysis. *Spatial Statistics*. John Wiley & Sons, New York (pp. 344–385).