# Declining population of wild ungulates in the Masai Mara ecosystem: a sign of resource competition

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#### Abstract

This study reveals that loss of wildlife wet season range and habitat fragmentation through land use changes has a much wider impact on the dynamics of wild ungulates than do the effects of climatic variations. If climate were the only factor affecting the wild herbivores in the Serengeti-Mara ecosystem (SME), we could expect similar changes in species population in both the Masai Mara ecosystem (MM) and the Serengeti ecosystem (SE). But the results shows a higher of wild ungulates in the MM, with most declines occurring after 1985, whereas the decline in the Serengeti has involved only a few species. The declines were more rapid among the larger-bodied ungulates than among the smaller-bodied ones during the non-migratory period. There are signs of possible competition between species during the non-migratory (decline of 10 out of 13 wild ungulates) or periods of limited food supply than in the dry season (decline of 6 out of 13 wild ungulates). The declines in wildebeest and buffalo were mainly associated with intraspecific competition for food. The resident wildebeest population declined heavily during the period 1977-85, which was a period of low rainfall. The resident zebra population remained stable, dominating in areas of poor vegetation production (the Loita plain), and wildebeest dominated areas of high productivity (the Mara range unit). Thomson's gazelle, topi, kongoni, warthog, and buffalo declined as the zebra, wildebeest and elephant populations levelled off after 1985. The decline of Thomson's gazelle and topi was steeper during the migratory season than during the non-migratory season. The buffalo, kongoni and warthog the decline was steeper in the wet season than in the dry season. The study concludes that the loss of the wet season habitat (the Loita plains) has had a major impact on the population dynamics (changes in population densities and distribution) in the MM. Further loss of wildlife habitat to agriculture and the fragmentation of land will cause more declines wildlife population through resource competition as indicated in the high declines during both the non-migratory (low forage) and migratory periods (high forage).

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# **8.1** INTRODUCTION

The Serengeti-Mara ecosystem (SME) is renowned for its abundant and diverse assemblage of wild ungulates (Talbot and Steward, 1964; Gwynne and Bell, 1968; Sinclair, 1979a; McNaughton, 1985; Stelfox *et al.*, 1986). Studies of ungulates in the SME have provided one of the longest time series of population data in East Africa. Changes in the populations of several species over the last 30 years suggest several hypotheses for the regulation of ungulates in the SME, that consists of competition, facilitation, predation and diseases (Sinclair, 1973; Sinclair and Norton-Griffiths, 1982; Sinclair *et al.*, 1985; Borner *et al.*, 1987; Dublin *et al.*, 1990; Mduma *et al.*, 1999). However, the underlying processes of resource exploitation and resource supply (Sinclair, 1975; Western, 1975; McNaughton, 1985; Sinclair *et al.*, 1985; McNaughton, 1990; Mduma *et al.*, 1999), and their interaction with wildlife species, are still poorly understood (Sinclair and Norton-Griffiths, 1982; Prins and Douglas-Hamilton, 1990; Prins and Olff, 1998; Du Toit and Cumming, 1999; Voeten and Prins, 1999; Murray and Illius, 2000; Baird, 2001).

Recent studies in the SME indicate a sharp decline in the population numbers of ungulates in the Masai Mara (MM) (Broten and Said, 1995; Ottichilo et al., 2001a; Ottichilo et al., 2001b; Serneels and Lambin, 2001) compared with the Serengeti (Campbell and Borner, 1995; Sinclair, 1995a; Sinclair, 1995b; Homewood et al., 2001). The MM, which consists of the Masai Mara National Reserve (MMNR) and adjoining group ranches in Kenya, forms the northern portion of the Serengeti-Mara ecosystem. In the MM there has been a rapid conversion of rangeland (pastures mainly used by wildlife and livestock) to agriculture in the last 20 years (Epp and Agatsiva, 1980; Lamprey, 1984; Karime, 1990; Homewood et al., 2001; Serneels et al., 2001). Apart from the changes in land cover, the rainfall pattern has changed from what was observed in the late 1960s and 1970s (Mduma et al., 1999; Ottichilo, 2000; and this study), and its effect on the ungulate population still needs to be investigated. Previous studies in the SME on interactions between species or on the interactions of species with other parameters (such as food supply) generally focused on a single species (Sinclair and Norton-Griffiths, 1982; Sinclair et al., 1985; Borner et al., 1987; Dublin et al., 1990; Mduma et al., 1999; Ottichilo et al., 2001a; Serneels and Lambin, 2001) or on a number of species but for a single season (Broten and Said, 1995; Campbell and Borner, 1995; Ottichilo et al., 2001b).

In this paper we extend the study to 16 ungulate species and analyze the trends and spatial distribution patterns for both the wet (non-migratory) and dry (migratory) seasons. The aim of this study is first to establish the temporal and spatial changes in land cover/use and rainfall pattern in the SME. Secondly, the study will assess the significance of changes in the ungulate population density by using general linear models that incorporate the effects of (i) season and (ii) climate and/or period of land cover changes (time period derived from the first objective).

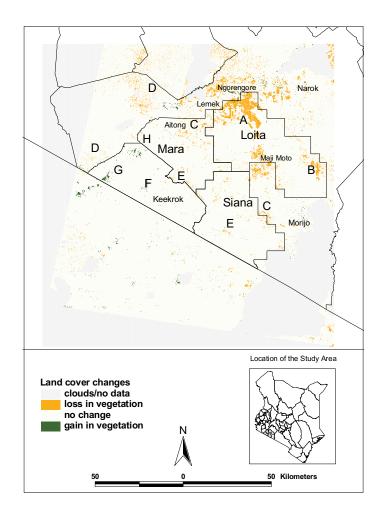
#### 8.1.1 Study area

The MM, which is part of the large SME, is located in southwestern Kenya, between  $34^{\circ}$  45'E to  $36^{\circ}$  00'E and  $0^{\circ}$  45'S to  $2^{\circ}$  00'S. The area is roughly triangular and covers about 6500 km<sup>2</sup>. It can be divided into three range units, based on their biogeography and climate (Stelfox *et al.*, 1986). These units are the Mara (composed mainly of *Themeda* grasslands – the reserve forms part of this unit), the Loita plains (composed of dwarf shrub and *Acacia drapanolobium* grassland) and the Siana (mainly hills and plains supporting *Croton* bush and other woody species interspersed with grassland). The main land uses in the area are pastoralism, tourism and recently agriculture. The Loita plains are the main wet season range for the wildebeest and zebra populations in the MM, while the Mara range unit forms the dry season range for the migratory wildebeest and zebra populations, in addition to a number of resident species.

The description of the land cover changes is based on remotely sensed time series change analysis conducted by Serneels *et al.* (2001) and previous land cover studies in the MM (refer to Epp and Agatsiva, 1980; Lamprey, 1984; Karime, 1990). There were minor land cover changes in the MM between 1975 and 1985, but the period 1985-95 showed small patches of intensively cultivated land spreading across the Mara and Siana range units (refer to Figure 8.1 and Table 8.1). However, the largest changes in the land cover occurred in the Loita plains. The large-scale cultivation of wheat in the Loita started in the 1970s and increased extensively during the period 1985-95 (Ottichilo, 2000; Homewood *et al.*, 2001; Serneels *et al.*, 2001). The area under cultivation increased fivefold between 1975 and 1995 (4,800 ha versus 26,700 ha), which accounted for about a 13% loss of wet season wildlife habitat or range to agriculture (refer to Table 8.1).

The rainfall pattern in the SME is described in detail in Brown and Cocheme (1973), Norton-Griffiths et al. (1975) and Pennycuick and Norton-Griffiths (1976). The annual distribution of rainfall is bimodal, characterized by two rainy seasons and two dry seasons (Stelfox et al., 1986; Broten and Said, 1995; Ottichilo, 2000). The main rains fall from March to May, with a peak in April and a second peak (although not noticeable) in the November-December period. The main dry season is from mid-June to mid-October, with a lesser dry season in January and February (see Figure 8.2). The long-term rainfall pattern in the SME shows changes over time. Sinclair (1979b) linked the increase in dry season rainfall in the 1970s (upwards of 250 mm) to the increase in wildebeest and buffalo populations in the SME. The rainfall pattern in time and space within the SME was studied using the rainfall data of 71 stations within the area. The cumulative deviations of the mean can be used to reveal periodicity in annual rainfall (refer to the methodology in Prins and Loth, 1988; Ottichilo, 2000). The pooled rainfall data for the different stations show a series of wet and dry years. The period 1977-97 experienced a decline in rainfall between 1977 and 1985 and an increase between 1986 and 1997 (Figure 8.3a). Coincidently, the period of increased rainfall also reflects the phase of increased agricultural activities. The MM received a mean of 965 mm of rainfall, with a dry season mean of 215 mm for the period 1977-85 and 295 mm for the period 1987-93. The Serengeti received an annual rainfall of 750 mm, with a dry season mean of 140 mm for the period 1977-93 (no significant change was observed before or after 1986 - see also Mduma et al., 1999). This would partly explain the stability of most of the ungulate species populations in the Serengeti ecosystem (Dublin et al., 1990; Campbell and Borner, 1995; Mduma et al., 1999; Homewood et al., 2001).

Declining wild ungulate population - resource competition



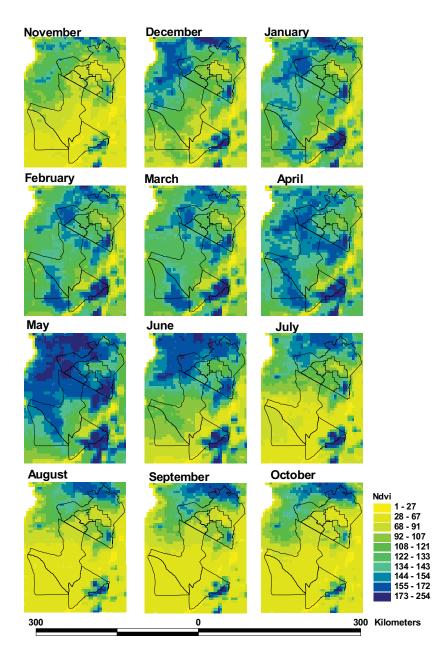
**Figure 8.1:** Land cover changes in the Mara ecosystem derived from 1975-1985-1995 TM and Landsat satellite images. Intensive agriculture was observed in the Loita plains (A) and (B). Patches of mosaic small-scale cultivation are developing in the Mara and Siana eco-units (C). Intensive small-scale cultivation replacing woodlands occurs in the Trans Mara region (D). Heavy decline in riverine vegetation was observed during the period 1975-85 near the Talek and Sekanali (E) gates. Increased vegetation in the park consisted of small bushes of *Croton dichogamus* (F), *Acacia* woodlands (G) and bushlands (H).

|                       |                 | Range units     | Range units Ecosystem |                 |
|-----------------------|-----------------|-----------------|-----------------------|-----------------|
| Land cover<br>changes | Loita<br>(ha)   | Mara<br>(ha)    | Siana<br>(ha)         | (ha)            |
| gradual decrease      | 1000 (0.5%)     | 20 (<0.1%)      | 10 (<0.1%)            | 1030 (0.2%)     |
| decrease 1985-95      | 26,710 (12.3%)  | 4690 (1.7%)     | 3000 (1.8%)           | 34,400 (5.2%)   |
| increase-decrease     | 550 (0.3%)      | 420 (0.1%)      | 190 (0.1%)            | 1,160 (0.2%)    |
| decrease 1975-85      | 4830 (2.2%)     | 4040 (1.4%)     | 2110 (1.3%)           | 10,980 (1.6%)   |
| no change             | 183,840 (84.3%) | 270,200 (95.5%) | 157,540 (95.8%)       | 611,580 (91.9%) |
| increase 1975-85      | 470 (0.2%)      | 360 (0.1%)      | 440 (0.3%)            | 1,270 (0.2%)    |
| decrease-increase     | 170 (0.1%)      | 10 (<0.1%)      | 10 (<0.1%)            | 190 (<0.1%)     |
| increase 1985-95      | 350 (0.2%)      | 3330 (1.2%)     | 70 (<0.1%)            | 3750 (0.6%)     |
| gradual increase      | 10 (<0.1%)      |                 |                       | 10 (<0.1%)      |
| clouds                | 110 (<0.1%)     |                 | 1210 (0.7%)           | 1320 (0.2%)     |

**Table 8.1:** Land cover changes in the Masai Mara ecosystem and the three range units, based on the three satellite images of 1975-1985-1995 (the figures in parenthesis are land cover changes in percentage).

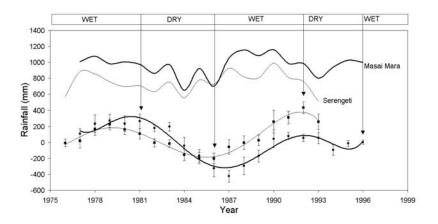
The monthly normalized vegetation difference index (NDVI – a proxy index for primary production; refer to Justice *et al.*, 1985; Justice, 1986; Box *et al.*, 1989) anomaly patterns clearly highlight the response of the plants and grass growth to rainfall. The pattern shows lower than average primary production for the period 1982-85. The decade 1987-97 had above average net primary production, with a sharp drop in plant biomass in 1991 and 1993 due to drought events (Figure 8.3b). The NDVI anomalies were calculated from the time series data by using the *z*-transform ( $(x_i - u)$ /std), with  $x_i$  being the NDVI value for a given month in year *i*, *u* the mean NDVI value for that month across all years, and std the standard deviation of the NDVI values for that month across all years (Anyamba *et al.*, 2001; Serneels *et al.*, 2001).

A review of the land cover and rainfall changes establishes that the period 1975-85 experienced fewer changes in land cover and that the rainfall was lower than in the preceding decade, which had experienced an increase in the number of wildlife species in the Serengeti ecosystem. The period after 1985 experienced a significant change in land cover, especially in the Loita (wet season range for resident wildebeest and zebra populations). The rainfall pattern and vegetation response during this period show mostly above average production of biomass, except in the drought years of 1991 and 1993. We hypothesize that the wild ungulate population should show a declining trend between 1977 and 1985 if food supply is the limiting factor. However, the period 1986-97 should show either an increase or decrease, depending on the effects of interaction between climate and land cover change on ungulate populations.

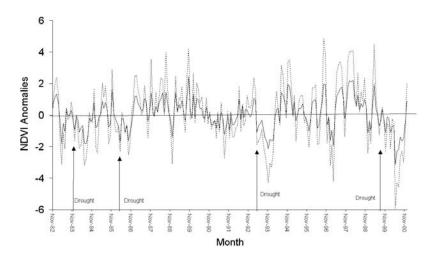


**Figure 8.2:** Spatial monthly variation in NDVI in the Serengeti-Mara ecosystem. The migratory species of wildebeest, zebra and Thomson's gazelle move between the Serengeti ecosystem and the Mara during the dry season (June-July), when the vegetation in the Serengeti is drier than in the Masai Mara. The animals move back to the Serengeti after October, when it starts to become green. The movements are dictated by local rainfall events and differ from year to year.





**Figure 8.3a:** Temporal changes in mean annual rainfall and cumulative deviation of rainfall in the Masai Mara (39 stations) and Serengeti (32 stations) between 1976 and 1996. Pooled cumulative deviations of the annual rainfall of wet and dry periods alternate but the length of the period varies.



**Figure 8.3b:** Temporal monthly changes of NDVI in the Masai Mara (—) and Serengeti (-----) ecosystems between 1982 and 2000. The severest droughts occurred in 1993 and 2000 and the impacts were felt more in the Serengeti ecosystem.

## **8.2 MATERIAL and METHODS**

#### 8.2.1 Data

The wildlife and livestock populations and distributions were compiled from aerial censuses conducted by the Department of Resource Surveys and Remote Sensing (DRSRS). The method as used and adapted by DRSRS is described in detail in Norton-Griffiths (1978), Dirschl *et al.* (1981) and Ottichilo and Sinange (1985). Population estimates for wildlife and livestock were calculated using Jolly (1969). Between 1977 and 1997 a total of 42 counts of ungulates in the Mara were undertaken, with regular wet (15 surveys) and dry (12 surveys) season counts (12 surveys were conducted in 1979 on a monthly bases). Three surveys were conducted in between the wet and dry seasons and could not be classified as either wet or dry season. The classification of the seasons was based on Ottichilo *et al.* (2001a).

#### 8.2.2 Analysis of species trends

We analyzed the changes in ungulate populations between 1977 and 1997 for both dry and wet seasons for the entire MM. Secondly, we assessed the significance of changes in the population density by incorporating the effects of season and the significance of changes in linear trends before and after the land cover and climatic changes. We identified the time period of change to be between 1977-85 (a declining rainfall period) and 1986-97 (a period of increased rainfall and land cover activities). We tested how these factors impact on the trends of the individual or groups of species by analyzing the trends before and after 1985. Animal densities were derived by converting the individual body weights (W in kg) of wildlife and livestock to metabolic body mass ( $W^{0.75}$ ), a value that reflects energy expenditure by different species in a comparable way (Moen, 1973). The average weights of the various wildlife species were derived from Prins and Olff (1998) and those of livestock from Peden (1987).

## 8.3 RESULTS

#### 8.3.1 Long-term population trends of the ungulates

The long-term population trends of both wild ungulates and livestock are summarized in Table 8.2. All species except zebra, elephant, impala and cattle showed significant population changes in either the wet or dry season, or in both periods. Wildebeest, Grant's gazelle, eland and waterbuck showed a decline in population in the wet season and a non-significant change in population in the dry season. Thomson's gazelle, topi, buffalo, warthog, giraffe and kongoni showed a declining population in both periods. The populations of Thomson's gazelle, topi, warthog, giraffe and kongoni were higher in the wet

season, and only wildebeest showed a higher population during the dry season. We did not find any significant seasonal changes in zebra, buffalo, Grant's gazelle, eland, waterbuck, elephant and impala populations. The trends in livestock populations were mixed with the cattle population remaining constant throughout the study period. Sheep and goats showed an increase in population during the dry season. The donkey trends were mixed, with declines in the wet season and increases in the dry season.

The marked changes in the population sizes of individual species were reflected in the total change in wild ungulate biomass over time. There were moderate declines in wildlife (though these were not significant) in the wet season  $(In(Y) = 13.16 - 0.050x, r^2 = 0.75, P < 0.001)$  compared with the dry season  $(In(Y) = 14.99 - 0.027x, r^2 = 0.32, P < 0.052)$ . The declines in the wet season were reflected in a greater loss of the large-bodied (>100 kg) wild ungulates  $(In(Y) = 13.79 - 0.081x, r^2 = 0.87; P < 0.001, n = 15)$  than of the small-bodied (<100 kg) ungulates  $(In(Y) = 8.37 - 0.03x, r^2 = 0.45, P = 0.006, (t = 97, P < 0.0001, df = 26)$ , whereas in the dry season there was no significant differences between the two populations (t = 1.81, P = 0.08, df = 20). Livestock population remained constant during both the wet and the dry seasons.

The large-bodied ungulates that showed sharp declines in their populations are the wildebeest, buffalo and giraffe (Table 8.2). The wildebeest population suffered declines during both the wet  $(In(Y_{wet}) = 17.02 - 0.13x, r^2 = 0.86, P < 0.001, n = 8)$  and dry seasons in the period 1977-85  $(In(Y_{dry}) = 31.89 - 0.29x, r^2 = 0.65, P < 0.001, n = 6)$ . The resident wildebeest population declined from an average of 120,000 animals in the late 1970s to less than 50,000 in the 1990s. The period 1977-85 had a moderate impact (declining trends approaching statistical significance) on the buffalo population, but the numbers dropped sharply during the wet season in the period 1986-97 (In( $Y_{wet}$ ) 18.15 - 0.15x,  $r^2 = 0.64$ , P < 0.05, n = 7). The buffalo population crashed from more than 20,000 animals observed in the late 1970s to a population of less than 5000 buffalo observed in the 1990s. The giraffe population continued to decline throughout the study period (In(Y) = 10.645 - 0.076,  $r^2 =$ 0.87, P < 0.001, n = 15), dropping from more than 5000 animals in the 1970s to less than 2000 in the 1990s. The long-term trends of both Thomson's gazelle and topi seem to be similar. Both have a higher wet season population and their populations declined significantly in the dry season, and especially after 1985. The declines in the dry season were significantly higher than those in the wet season for both Thomson's gazelle (t =53.44, P < 0.001, df = 12) and topi (t = 18.78, P < 0.001, df = 12). The decline in kongoni was significantly higher in the wet season than in the dry season (t = 51, P < 0.001, df = 12) and a similar pattern was observed for Grant's gazelle (t = 24, P < 0.001, df = 12).

|                   | Wet Season                    |                                                             |                                          | Dry Season                    |                                                             |                                          |                                     |    |  |
|-------------------|-------------------------------|-------------------------------------------------------------|------------------------------------------|-------------------------------|-------------------------------------------------------------|------------------------------------------|-------------------------------------|----|--|
|                   | Trends<br>1977-97<br>(n = 15) | Change in slope of<br>linear trend before and<br>after 1985 |                                          | Trends<br>1977-97<br>(n = 12) | Change in slope of<br>linear trend before and<br>after 1985 |                                          | Season                              |    |  |
| Species           | r <sup>2</sup> of<br>model    | Trends                                                      | r <sup>2</sup>                           | r <sup>2</sup> of<br>model    | Trends                                                      | r <sup>2</sup>                           | Season with<br>a high<br>population | Р  |  |
| Wildebeest        | 0.75***                       | B: decline<br>A: no                                         | 0.86***<br>0.01 <sup>ns</sup>            | 0.31 <sup>ns</sup>            | B: decline<br>A: increase                                   | 0.65*<br>0.03 <sup>ns</sup>              | Dry                                 | ** |  |
| Burchell's zebra  | 0.15 <sup>ns</sup>            | B: no<br>A decline                                          | $0.22^{ns}$<br>$0.45^{ns}$               | 0.01 <sup>ns</sup>            | B: decline<br>A: no                                         | 0.54 <sup>ns</sup><br>0.01 <sup>ns</sup> |                                     | ns |  |
| Thomson's gazelle | 0.46**                        | B: no<br>A decline                                          | 0.03 <sup>ns</sup><br>0.36 <sup>ns</sup> | 0.78***                       | B: no<br>A: decline                                         | 0.13 <sup>ns</sup><br>0.69*              | Wet                                 | ** |  |
| Торі              | 0.48**                        | B: no<br>A: decline                                         | 0.01 <sup>ns</sup><br>0.53 <sup>ns</sup> | 0.73***                       | B: no<br>A: decline                                         | 0.25 <sup>ns</sup><br>0.63*              | Wet                                 | *  |  |
| Buffalo           | 0.80***                       | B: decline<br>A: decline                                    | 0.44 <sup>ns</sup><br>0.64*              | 0.35*                         | B: decline<br>A: no                                         | 0.46 <sup>ns</sup><br>0.17 <sup>ns</sup> |                                     | ns |  |
| Warthog           | 0.77***                       | B: decline<br>A: decline                                    | 0.32 <sup>ns</sup><br>0.47 <sup>ns</sup> | 0.40*                         | B: no<br>A: no                                              | 0.02 <sup>ns</sup><br>0.01 <sup>ns</sup> | Wet                                 | ** |  |
| Grant's gazelle   | 0.51**                        | B: decline<br>A decline                                     | 0.16 <sup>ns</sup><br>0.36 <sup>ns</sup> | 0.25 <sup>ns</sup>            | B: no<br>A: no                                              | 0.11 <sup>ns</sup><br>0.05 <sup>ns</sup> |                                     | ns |  |
| Eland             | 0.50**                        | B: decline<br>A no                                          | 0.42 <sup>ns</sup><br>0.02 <sup>ns</sup> | 0.22 <sup>ns</sup>            | B: decline<br>A: increase                                   | 0.41 <sup>ns</sup><br>0.82*              |                                     | ns |  |
| Giraffe           | 0.87***                       | B: decline<br>A decline                                     | 0.55*<br>0.80**                          | 0.61**                        | B: no<br>A: decline                                         | 0.01 <sup>ns</sup><br>0.36 <sup>ns</sup> | Wet                                 | *  |  |
| Waterbuck         | 0.37*                         | B: no<br>A decline                                          | 0.01 <sup>ns</sup><br>0.29 <sup>ns</sup> | 0.07 <sup>ns</sup>            | B: no<br>A: no                                              | 0.16 <sup>ns</sup><br>0.01 <sup>ns</sup> |                                     | ns |  |
| Elephant          | 0.11 <sup>ns</sup>            | B: no<br>A no                                               | 0.09 <sup>ns</sup><br>0.12 <sup>ns</sup> | 0.01 <sup>ns</sup>            | B: increase<br>A: no                                        | 0.41 <sup>ns</sup><br>0.15 <sup>ns</sup> |                                     | ns |  |
| Impala            | 0.16 <sup>ns</sup>            | B: no<br>A: no                                              | 0.16 <sup>ns</sup><br>0.01 <sup>ns</sup> | 0.16 <sup>ns</sup>            | B: no<br>A: no                                              | 0.01 <sup>ns</sup><br>0.03 <sup>ns</sup> |                                     | ns |  |
| Kongoni           | 0.38*                         | B: no<br>A: decline                                         | 0.02 <sup>ns</sup><br>0.74*              | 0.37*                         | B: decline<br>A: no                                         | 0.42 <sup>ns</sup><br>0.24 <sup>ns</sup> | Wet                                 | ** |  |
| Cattle            | 0.02 <sup>ns</sup>            | B: no<br>A: no                                              | 0.23 <sup>ns</sup><br>0.03 <sup>ns</sup> | 0.01 <sup>ns</sup>            | B: decline<br>A: no                                         | 0.75*<br>0.21 <sup>ns</sup>              |                                     | ns |  |
| Sheep and goats   | 0.16 <sup>ns</sup>            | B: decline<br>A: no                                         | 0.31 <sup>ns</sup><br>0.02 <sup>ns</sup> | 0.36*                         | B: no<br>A: no                                              | 0.01 <sup>ns</sup><br>0.01 <sup>ns</sup> |                                     | ns |  |
| Donkey            | 0.44**                        | B: no<br>A: decline                                         | 0.14 <sup>ns</sup><br>0.47 <sup>ns</sup> | 0.48*                         | B: increase<br>A: no                                        | 0.51 <sup>ns</sup><br>0.01 <sup>ns</sup> |                                     | ns |  |

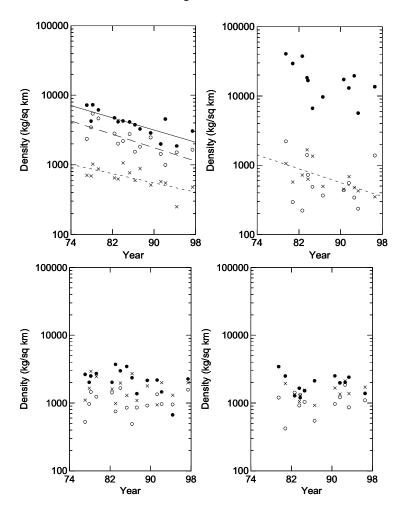
#### Table 8.2: Wildlife ungulates and livestock population trends in the Masai Mara.

Note: Significance assessed by log-linear models (P values: <0.05; \*\*<0.01; \*\*<0.001; ns = not significant). Notation B represents before and notation A after 1985. A total of 15 censuses were conducted in the dry season, with eight censuses surveyed before and seven after 1985. As for the wet season there were 12 censuses, with six conducted before 1985 and six after 1985.

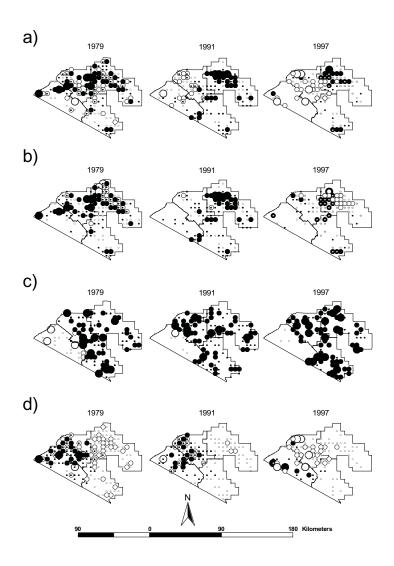
#### 8.3.2 Changes in spatial distribution of species

There were significant changes in the wild ungulate population trends in the Mara  $(\ln(Y) = 12.60 \pm 0.92 - 0.055x \pm 0.01, r^2 = 0.63, P < 0.001, n = 15)$ , Loita  $(\ln(Y) = 12.45 \pm 1.11 - 0.055x \pm 0.13, r^2 = 0.58, P < 0.001, n = 15)$  and Siana  $(\ln(Y) = 9.77 \pm 0.99 - 0.038x \pm 0.02, r^2 = 0.46, P < 0.005, n = 15)$  during the wet season. In the dry season there were no changes in trends in the Mara and Loita, but the Siana  $(\ln(Y) = 11.52 \pm 1.80 - 0.058x \pm 0.02, r^2 = 0.002, r^2 = 0.002,$ 

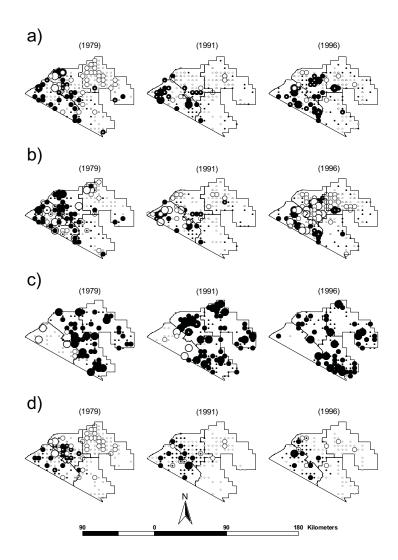
0.44, P < 0.02, n = 15) showed a decline in ungulate population (Figure 8.4). The spatial analyses of individual species trends for the wet and dry seasons for the three range units are summarized in Table 8.3. Thomson's gazelle and topi are the only species that showed declining populations in all three range units. The resident wildebeest trend shows declines in the Loita and Siana. The distribution patterns of giraffe, kongoni, waterbuck and buffalo showed that significant declines occurred in the Mara range unit, while declines in the zebra and warthog populations were observed in both the Mara and the Loita range units. The wildebeest and impala revealed localized declines in the Loita and Siana range unit respectively. The change in trends of livestock occurred in the Mara, where donkey as well as sheep and goats showed a declining population. Cattle and sheep and goats remained constant in both the Loita and Siana range units.



**Figure 8.4:** Changes in wildlife (top) and livestock (bottom) populations in the Mara ( $\bullet$ ), Loita ( $\circ$ ) and Siana (x) range units for the wet season (left) and dry season (right).



**Figure 8.5a:** Distribution of species during the dry or migratory season. Species patterns show changes in both distributions and densities over the years. The distributions of the species are as follows: a) Thomson's gazelle ( $\circ$ ) and zebra ( $\bullet$ ); b) wildebeest ( $\circ$ ) and zebra ( $\bullet$ ); c) buffalo ( $\circ$ ) and livestock ( $\bullet$ ); and d) impala ( $\circ$ ) and topi ( $\bullet$ ). 1979 represents the peak herbivore biomass, 1991 represents a drought year, and 1997 was a year that had similar rainfall to that of 1979.



**Figure 8.5b:** Distribution of species during the wet or non-migratory season. Species patterns show changes in both distributions and densities over the years. The distributions of species are as follows: a) Thomson's gazelle ( $\circ$ ) and zebra ( $\bullet$ ); b) wildebeest ( $\circ$ ) and zebra ( $\bullet$ ); c) buffalo ( $\circ$ ) and livestock ( $\bullet$ ); and d) impala ( $\circ$ ) and topi ( $\bullet$ ). 1979 represents the peak herbivore biomass, 1991 represents a drought year, and 1996 was a year that had similar rainfall to that of 1979.

**Table 8.3:** Regression equation describing the best-fitting model between herbivore species and time. The formulas for the regressions are indicated if the models are significant at  $P \le 0.05$ . The trend analysis was conducted for the entire Masai Mara (MM) and the three range units (Mara, Loita and Siana).

| Species               | Unit          | Wet Season                         | r <sup>2</sup> | Р              |                  | Dry Season                         | r <sup>2</sup> | Р     |
|-----------------------|---------------|------------------------------------|----------------|----------------|------------------|------------------------------------|----------------|-------|
| D. (C.)               | 10/           | 15 715 0 101                       | 0.00           | 0.001          | D. (% 1          | 16.070 0.100                       | 0.25           | 0.044 |
| Buffalo               | MM            | 15.715 - 0.121x                    | 0.80           | 0.001          | Buffalo          | 16.272 - 0.132x                    | 0.35           | 0.044 |
|                       | Mara          | 16.913 - 0.119                     | 0.78           | 0.001<br>0.099 |                  | 18.039 - 0.136x                    | 0.36           | 0.040 |
|                       | Loita         |                                    | 0.81<br>0.03   |                |                  |                                    | 0.09           | 0.629 |
| Eland MM              | MM            | 10.690 - 0.085x                    | 0.03           | 0.648 0.003    | Eland            |                                    | 0.40<br>0.22   | 0.609 |
| Elaliu                | Mara          |                                    | 0.30           | 0.003          | Eland            |                                    | 0.22           | 0.120 |
|                       | Loita         | 11.496 - 0.088x                    | 0.28           | 0.155          |                  |                                    | 0.10           | 0.402 |
|                       | Siana         | 11.837 - 0.106x                    | 0.13           | 0.012          |                  |                                    | 0.10           | 0.490 |
| Elephant              | MM            | 11.057 - 0.100X                    | 0.42           | 0.229          | Elephant         |                                    | 0.01           | 0.220 |
| Elephant              | Mara          |                                    | 0.11           | 0.229          | Elephan          |                                    | 0.01           | 0.860 |
|                       | Loita         |                                    |                |                |                  |                                    | 0.01           | 0.800 |
|                       | Siana         |                                    |                |                |                  |                                    | 0.89           | 0.213 |
| Giraffe               | MM            | 10.645 - 0.076x                    | 0.87           | 0.001          | Giraffe          | 7.904 - 0.046x                     | 0.61           | 0.003 |
|                       | Mara          | 11.682 - 0.076x                    | 0.56           | 0.001          |                  | 9.530 - 0.055x                     | 0.70           | 0.001 |
|                       | Loita         |                                    | 0.16           | 0134           |                  |                                    | 0.05           | 0.488 |
|                       | Siana         |                                    | 0.18           | 0.113          |                  |                                    | 0.24           | 0.107 |
| Grant's gazelle       | MM            | 7.765 - 0.049x                     | 0.51           | 0.003          | Grant's gazelle  |                                    | 0.25           | 0.096 |
|                       | Mara          |                                    | 0.29           | 0.057          |                  |                                    | 0.17           | 0.181 |
|                       | Loita         |                                    | 0.47           | 0.005          |                  |                                    | 0.21           | 0.135 |
|                       | Siana         |                                    | 0.14           | 0.174          |                  |                                    | 0.18           | 0.168 |
| Impala                | MM            | 1                                  | 0.16           | 0.145          | Imapla           |                                    | 0.13           | 0.25  |
|                       | Mara          |                                    | 0.02           | 0.589          | F                |                                    | 0.03           | 0.575 |
|                       | Loita         |                                    | 0.02           | 0.671          |                  |                                    | 0.00           | 0.954 |
|                       | Siana         | 8.313 - 0.038x                     | 0.47           | 0.005          |                  | 9.184 - 0.050x                     | 0.36           | 0.039 |
| Kongoni               | MM            | 7.470 - 0.051x                     | 0.39           | 0.014          | Kongoni          | 0.144 - 0.041x                     | 0.30           | 0.03  |
| Rongom                | Mara          | 9.288 - 0.060x                     | 0.38           | 0.014          | Rongom           | 8.940 - 0.060                      | 0.50           | 0.010 |
|                       | Loita         | 9.200 - 0.000X                     | 0.01           | 0.857          |                  | 0.940 - 0.000                      | 0.01           | 0.398 |
|                       | Siana         |                                    | 0.26           | 0.055          |                  |                                    | 0.01           | 0.437 |
| Thomson's gazelle     | MM            | 8.080 - 0.039x                     | 0.20           | 0.006          | Thomson's        | 10.639 - 0.074x                    | 0.78           | 0.001 |
| ritoitisoit s gazette | Mara          | 8.080 - 0.039X                     | 0.40           | 0.000          | Thomson s        | 10.039 = 0.074x<br>11.704 = 0.069x | 0.78           | 0.00  |
|                       | Loita         | 10.017 - 0.064x                    | 0.23           | 0.0057         |                  | 11.704 - 0.009X                    | 0.85           | 0.001 |
|                       | Siana         | 9.775 - 0.072                      | 0.47           | 0.003          |                  | 12.097 0.106                       | 0.44           | 0.072 |
| Tomi                  | MM            |                                    | 0.44           | 0.007          | Toni             | 12.087 - 0.106x<br>10.189 - 0.013x |                | 0.02  |
| Торі                  | Mara          | 8.762 - 0.049x<br>10.414 - 0.051x  | 0.48           | 0.004          | Торі             | 10.189 = 0.013x<br>11.704 = 0.069x | 0.73<br>0.71   |       |
|                       | Loita         |                                    | 0.32           | 0.003          |                  | 8.037 - 0.077x                     | 0.71           | 0.001 |
|                       |               | 9.932 - 0.094x                     |                | 0.003          |                  |                                    |                | 0.042 |
| Waterbuck             | Siana<br>MM   | 7 786 0 060-                       | 0.17<br>0.37   | 0.165          | Waterbuck        | 12.054 - 0.115x                    | 0.45<br>0.05   | 0.024 |
| waterbuck             |               | 7.786 - 0.069x                     |                | 0.018          | waterbuck        |                                    | 0.03           |       |
|                       | Mara<br>Loita | 9.926 - 0.081x                     | 0.35           | 0.021          |                  |                                    | 0.09           | 0.364 |
|                       | Siana         |                                    | 0.04           | 0.570          |                  |                                    |                |       |
| Warthog               | MM            | 10.774 - 0.097x                    | 0.04           | 0.001          | Warthog          | 8.357 - 0.074x                     | 0.40           | 0.026 |
|                       | Mara          | 10.774 = 0.097X<br>12.425 = 0.101x | 0.73           | 0.001          | warnog           | 10.372 - 0.084x                    | 0.35           | 0.020 |
|                       | Loita         | 12.425 - 0.101X                    | 0.13           | 0.308          |                  | 10.372 - 0.084X                    | 0.00           | 0.04  |
|                       | Siana         |                                    | 0.15           | 0.002          |                  | 0.644 0.006                        | 0.56           |       |
| Wildebeest            | MM            | 12.623 - 0.076x                    | 0.33           | 0.002          | Wildebeest       | 9.644 - 0.096x<br>13.944 - 0.068x  | 0.38           | 0.020 |
| M                     |               | 12.025 - 0.070x                    |                |                | wildebeest       | 15.944 - 0.008x                    |                |       |
|                       | Mara<br>Loita |                                    | 0.06<br>0.74   | 0.401<br>0.001 |                  |                                    | 0.30<br>0.01   | 0.064 |
|                       | Siana         |                                    | 0.74           | 0.001          |                  |                                    | 0.01           | 0.730 |
|                       |               | 7 455 0 017                        |                |                | D 1 10 1         |                                    |                | 0.13  |
| Burchell's zebra      | MM            | 7.455 - 0.017x                     | 0.15           | 0.154          | Burchell's zebra |                                    | 0.00           | 0.980 |
|                       | Mara          | 12.541 - 0.073x                    | 0.38           | 0.015          |                  |                                    | 0.00           | 0.938 |
|                       | Loita         |                                    | 0.06           | 0.385          |                  | 11 100 0.072                       | 0.07           | 0.389 |
| C-#1-                 | Siana         |                                    | 0.01           | 0.703          | C-wl-            | 11.189 - 0.073x                    | 0.57           | 0.00  |
| Cattle                | MM            |                                    | 0.02           | 0.663          | Cattle           |                                    | 0.00           | 0.989 |
|                       | Mara          |                                    | 0.18           | 0.117          |                  |                                    | 0.01           | 0.83  |
|                       | Loita         | 1                                  | 0.16           | 0.140          |                  |                                    | 0.04           | 0.535 |
|                       | Siana         | 0.011 0.075                        | 0.10           | 0.721          | <b>D</b> 1       | 0.102 0.077                        | 0.07           | 0.43  |
| M<br>Lo               | MM            | 8.011 -0.055x                      | 0.44           | 0.007          | Donkey           | 8.193 - 0.061x                     | 0.48           | 0.01  |
|                       | Mara          | 9.688 -0.071x                      | 0.33           | 0.024          |                  | 11.073 - 0.087x                    | 0.54           | 0.00  |
|                       | Loita         | 1                                  | 0.13           | 0.183          |                  |                                    | 0.23           | 0.113 |
|                       | Siana         | 1                                  | 0.12           | 0.213          |                  |                                    | 0.03           | 0.58  |
| Sheep and goata       | MM            |                                    | 0.16           | 0.137          | Sheep and goats  | $3.138 \pm 0.020 x$                | 0.36           | 0.040 |
|                       | Mara          | 8.932 - 0.041x                     | 0.42           | 0.009          | 1                | 8.932 - 0.041x                     | 0.42           | 0.009 |
|                       | Loita         | 1                                  | 0.19           | 0.104          |                  |                                    | 0.13           | 0.258 |
|                       | Siana         | 1                                  | 0.04           | 0.500          | 1                | 1                                  | 0.27           | 0.085 |

## **8.4 DISCUSSION**

The results reveal a decline in 10 out of 13 wild ungulate species during non-migratory period and 6 out 13 species during the migratory period, with significant changes occurring in the period after 1985. Five species (Thomson's gazelle, topi, buffalo, kongoni, giraffe) show significant declines after 1985, and two species (wildebeest and giraffe) before 1985. We assume that if only food supply limits ungulate populations, then more ungulate species would have declined between 1977 and 1985 (a low rainfall period) and increased between 1986 and 1997 (a high rainfall period). However, it seems that the loss of the wet season range may have created an environment for resource competition. Resource competition takes place when there is a high degree of habitat and diet overlap between species (see Hansen et al., 1985; Voeten and Prins, 1999; Illius and O'Connor, 2000; Prins, 2000) and food supply is limited. And it can be demonstrated to occur when an increase in the population of one of two animal species causes a reduction in the population of the other (Sinclair et al., 1985; de Boer and Prins, 1990; Mduma et al., 1999). However, apart from the diet overlaps, other factors such as the long-lasting cohabitation strategy of wild herbivores of partitioning resources among the different species that is linked to vegetation preferences, and digestive and feeding styles also counts on the success of a species out competing the other (Gwynne and Bell, 1968; Jarman and Sinclair, 1979; Hansen et al., 1985; Illius and Gordon, 1991; Murray and Brown, 1993; Murray and Illius, 2000). Three broad patterns that impact on species trends are identified in this study: populations of species may either be (i) regulated by intraspecific competition for food; (ii) regulated by interspecific competition; or (iii) no signs that they are regulated by either of the above processes.

The wildebeest and the buffalo fall into the category of species whose populations may be regulated through intraspecific competition for food (Sinclair, 1979b; Sinclair, 1983; Sinclair et al., 1985; Prins, 1996; Mduma et al., 1999). Previous studies in the SE indicated that dry season rainfall was the most important extrinsic determinant of food supply for the wildebeest and buffalo (Sinclair, 1979b; Sinclair et al., 1985; Mduma et al., 1999). In contrast, a recent study in the MM showed that the wet and dry seasons are both important factors in determining the resident wildebeest population (Serneels and Lambin, 2001). The decline in wildebeest in the MM occurred between 1977-85. In this period both the wet and dry season rainfall declined, and there were high numbers of wildebeest migrating from the SE to the MM during the dry season (Ottichilo, 2000; Serneels and Lambin, 2001). The combination of sub-optimal conditions during the wet season and increased competition during the dry season in the MM probably led to high wildebeest and buffalo mortality during the period 1977-85. But the severe drought of 1993 sharply affected the buffalo and contributed to a significant crash in the population in the MM (Figure 8.6a; also refer to Dublin, 1994). However, prior to the sharp decline there seems to have been heavy pressure on the buffalo wet season population and this might be related to increased densities of elephant in the MM. Almost 500 elephants moved from the SE to the MM in the early 1980s due to poaching in the SE (Dublin and Douglas-Hamilton, 1987). Drent and Prins (1987) and de Boer and Prins (1990) observed forage competition between elephant and buffalo in the Lake Manyara National Park. In the MM the elephant population has remained constant and this may well affect the densities of buffalo in terms of competition for forage during periods of limited food supply.



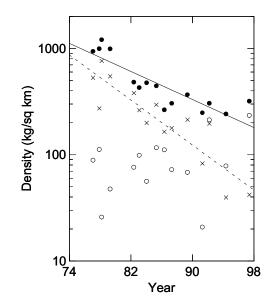
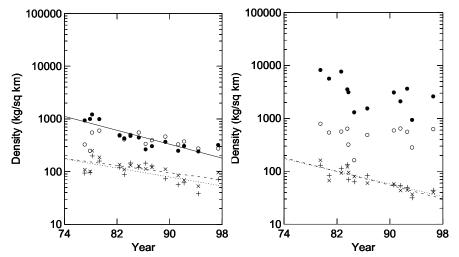


Figure 8.6a: The trends of both wildebeest (•) and buffalo (x) show declines over time during the wet or the non-migratory period, while the elephant ( $\circ$ ) population has remained constant throughout the study period. The wildebeest population during the wet season is predominately located in the Loita and has little interaction with buffalo, while both the elephant and the buffalo are located mainly in the Mara range unit both during the wet and dry seasons (refer to the distribution of these two species - Figure 6a and b).

The rapid decline in Thomson's gazelle, topi, kongoni and warthog coincided with the levelling out of the wildebeest, zebra and elephant populations (Figure 8.6b). The dominance of both zebra in the Loita (declining trends in the Mara – high productive areas) and wildebeest in the Mara (declining trends in the Loita and Siana – low productive areas) seems to have had an impact on a number of species. Hansen *et al.* (1985) found the highest diet similarities among the buffalo, kongoni, wildebeest, topi and Thomson's gazelle in the MM. In addition, Murray and Illius (2000) observed that herbivory by one species can modify the vegetation in a way that makes it less profitable for competing species. The situation seems to be much more severe during the migratory season, when the wildebeest and zebra dominate natural pastures and can preclude utilization of the resource by other selective ruminant species – especially if the grazing areas decrease as demonstrated in this study. The declines in Thomson's gazelle and topi were higher in the dry season than in the wet season, particularly in the period 1986-97. And there further declines of buffalo, kongoni and warthog even during a period of high forage availability. This would support the hypothesis of interspecific competition between species.

Among the wild ungulates the zebra, elephant and impala populations remained constant over time within the entire MM. However, the spatial based on range unit analysis show the distribution of the resident zebra population in the MM changed with local declines in the Mara range unit and dominance in the Loita over other species. The dominance of non-ruminant zebra in the Loita is partly explained by its tolerance of poorquality diets – a tolerance higher than that of hindgut ruminant species such as the wildebeest (Demment and Van Soest, 1985; Prins and Olff, 1998; Voeten and Prins, 1999). The overall trend of impala shows a stable population and this may be attributed to its high trophic diversity – its great choice of plants (both monocots and dicots) depending on the season (see Jarman and Sinclair, 1979; Hansen *et al.*, 1985). However, the spatial analysis

based on range units also showed localized declines in impala in the Siana, the area that had had an increase in livestock (especially sheep and goats). Several studies have indicated dietary overlaps between impala and sheep, which may have caused resource competition between the species. Habitat overlap between wildlife and livestock is likely to be high in areas where they co-occur, thus outside protected areas (Prins, 2000; Voeten and Prins 1999).



**Figure 8.6b:** The trends of wet (left) and dry season populations of wildebeest  $(\bullet)$ , zebra  $(\circ)$ , Thomson's gazelle (x) and topi (+). The decline in Thomson's gazelle and topi occurred as the populations of both wildebeest and zebra stabilized during the wet season in 1986-97 and the migratory populations of wildebeest and zebra slightly increased during the dry season in 1986-97.

In conclusion this study shows that in general competition appears an important process affecting large ungulates. The study has shown that when common resource (food supply) and key habitats are intact, climate changes (decline in rainfall) had a moderate affect of wildlife population, except during severe and prolonged drought. However, as resources become scarce through habitat modification (especially loss of critical habitats), competition for resources between species become evident - as reflected by the declines in a number of species (both during the dry and wet seasons), and especially after the large land use changes after 1985. This paper analysed on two possible regulatory processes governing ungulate population (rainfall and land use changes), diseases and predation are other factors that also regulate ungulate population but was not dealt in this paper.

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