DECLINE OF THE MARA WOODLANDS:

THE ROLE OF FIRE AND ELEPHANTS

by

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ABSTRACT

The Masai Mara Game Reserve of southwestern Kenya forms the northernmost extension of the Serengeti ecosystem and provides the critical dry season range for approximately 1.5 million migratory wildebeest. Over the past 100 years, major ecological changes have occurred. The area has experienced a transformation from open grassland to dense woodlands and back.

This study addressed the transition in the Mara woodlands from both an historical and a contemporary perspective. The study focused on two central questions: 1) what factor (or factors) were responsible for the decline of the woodlands in the 1960s? And 2) what factor (or factors) are currently responsible for inhibiting woodland regeneration?

In the 1880s an introduced disease, rinderpest, decimated wild and domestic ungulates in the Serengeti-Mara region. Local pastoralists, dependent on their livestock for survival, succumbed to disease and starvation. Elephant numbers had also been greatly reduced by indigenous hunters. Explorers, slave traders, and hunters described the area as an open grassland by 1900. In the following decades, conditions were conducive to the establishment of woodlands; burning rates were low and elephant browsing was negligible.

By the 1930s, the area was covered by dense woodland. These woodlands began a steady decline several decades later. Unusually high rainfall, high grass productivity, and severe fires characterized the period of greatest decline (1961 - 1967). Although woodland losses were intially viewed as

"elephant problems", findings from this study suggest that fire was the primary factor in the disappearance of woodlands, while elephants merely accelerated the rate of decline.

Elephants preferred open grasslands, swamps, and relict thickets in the wet season. However, in the dry season, elephants selected wooded habitats. Average group size was significantly higher in the wet season than the dry.

Mara elephants fit the same feeding patterns reported for many African elephant populations. Elephants concentrated on grasses and herbs in the rainy season and browse in the dry season. In general, males browsed more than females, while females ate more diverse diets containing more herbaceous matter. Elephants utilized seedlings under 1m more than any other height class of trees throughout the year. This pattern of selective feeding significantly reduced seedling survivorship.

Large-scale field experiments subjected plants to three treatments: browsed only, browsed and burned, and neither browsed nor burned. Although fire, at current fuel loadings and intensities, produced an almost total topkill, the majority of burned individuals resprouted within six months. Elephants removed a significant proportion of seedlings and severely damaged others. Wildebeest inhibited seedling growth through trampling, thrashing, and accidental browsing. Only those seedlings protected from both burning and browsing increased in height. Woodland dynamics in the Mara are currently more affected by elephants, wildebeest, and other browsers than by

fire. Elephants can be considered a "keystone" species in this system.

I concluded that elephants were not capable of initiating the woodland declines which started over two decades ago. However, once tree densities had been reduced by previous perturbations (such as increased burning rates following a reduction in wildebeest numbers and an increased frequency of man-made fires), elephants accelerated the rate of decline. My findings did not support Caughley's "stable limit cycle" hypothesis. Today, elephants are holding the Mara in a grassland phase, despite low burning rates. This pattern suggests that the Mara may have two locally stable states, woodland or grassland, and that an external factor such as fire is necessary to move the system between the two. Elephants, alone, apparently cannot move the system from one state to another, but once it is in the grassland phase, they can hold it there.

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CHAPTER 1. GENERAL INTRODUCTION

The Masai Mara Game Reserve forms the northernmost portion of the Serengeti-Mara ecosystem (Figures 1.1 and 1.2). The Mara's extensive grasslands have expanded significantly in recent years (Glover and Trump 1970, Taiti 1973, Dublin 1984, Lamprey 1985). Today they provide the critical dry season range for approximately 1.5 million migratory wildebeest, Connochaetes taurinus (Sinclair et al. 1985). Although grasslands were extensive in the Mara around the turn of this century (Woosnam 1913, White 1914, 1915, Buxton 1927), these grasslands were replaced by woodlands and thickets over the following 30 years (Lewis 1935, Darling 1960, S. Downey, pers. comm.). In the late 1950s these woodlands began a steady decline which continued through the 1960s and 1970s leaving few intact stands of trees within the Reserve boundaries today.

The progression of these declines was not well-documented in the Mara. While a wealth of biological information had been collected in the Serengeti National Park over the three decades of woodland change, little information was available for the Mara Game Reserve. It was not until Norton-Griffiths (1979) quantified rapid woodland declines in the neighbouring northern Serengeti that attention was drawn to the status of woodlands in the Mara.

Like many similar declines in parks and reserves throughout east, central, and southern Africa (Laws 1970, Caughley 1976), woodland losses in the Serengeti-Mara were initially viewed as "elephant problems" (Darling 1964, Glover 1965, Lamprey et al. 1967, Russell 1968, Glover and Trump 1970). Ecological doctrine

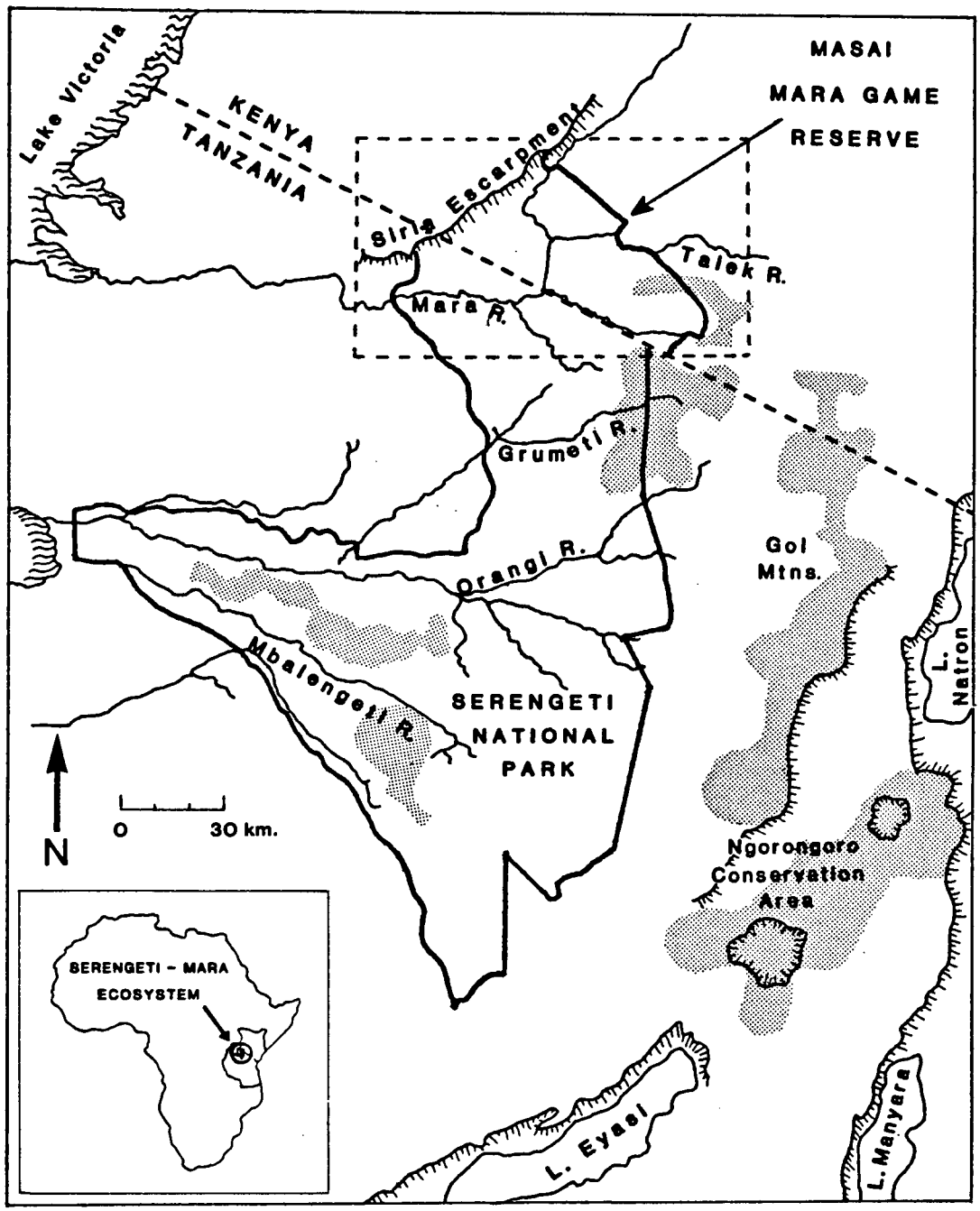

Figure 1.1. A map of the Serengeti-Mara ecosystem.

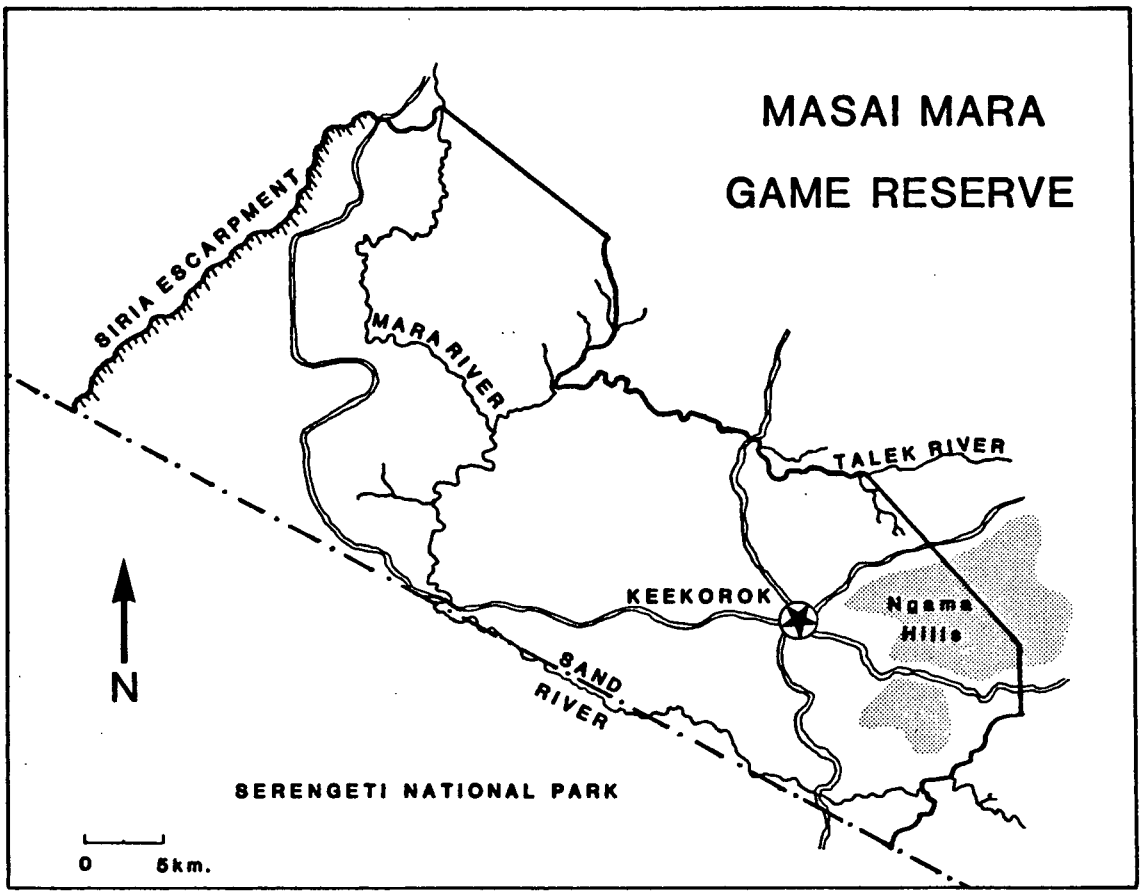

Figure 1.2. A map of the study area, the Masai Mara Game Reserve.

of this period argued that elephant (Loxodonta africana) densities in parks and reserves, such as the Serengeti-Mara, were becoming artificially high as human settlement pressures grew and forced elephants into protected areas. Once concentrated in these areas elephants exceeded the capacity of the lands to support them. Consequently, elephants destroyed their habitats through over-utilization, and elephant-related tree mortality was exceeding natural regeneration. This effect was documented in the parks of Uganda (Buechner and Dawkins 1961, Buss 1961, Laws 1970, Spence and Angus 1971, Field 1971, Laws et al. 1975, Field and Ross 1976, Malpas 1978), Tanzania (Lamprey et al. 1967, Savidge 1968, Laws 1970, Douglas-Hamilton 1972, Croze 1974a & b, Barnes 1982, 1983), southern Africa (Pienaar et al. 1966, Anderson and Walker 1974, Caughley and Goddard 1974, Thomson 1975, Hanks et al. 1981, Hall-Martin 1984) and other parks in Kenya (Glover 1963, Glover and Sheldrick 1964, Agnew 1968, Laws 1969, 1970). Controlled culling of elephants was instituted in the national parks of Zimbabwe (Cumming 1981, 1983), Malawi (Bell 1983), South Africa (Pienaar 1969, van Wyk and Fairall 1969, de Vos et al. 1983, Owen-Smith 1983, Pienaar 1983), and Uganda (Laws et al. 1975) and recommended in others (Ross et al. 1976, Barnes 1983) as a solution to the elephant/woodland dilemmas. Pressure was placed on park managers in other areas experiencing woodland declines to pursue similar options.

Lamprey et al. (1967) described an influx of elephants into the Serengeti-Mara in the late 1950s and early 1960s where they had not been present in significant numbers for at least

the previous 40 years. Dublin (1984) reviewed the anecdotal history of these movements and the geographical origins of immigrating elephants. In a review of all elephant censuses conducted in the Serengeti-Mara, Dublin and Douglas-Hamilton (in press) document this gradual re-colonization by elephants and the eventual merging of their southern and northern populations between the late 1950s and the late 1970s.

This increase in elephant numbers and densities coincided closely with the reported decline of woodlands in the Serengeti-Mara and was cited as evidence in support of the hypothesis that elephants were responsible for the observed reversion to open grassland. In the mid-1970s, park authorities and researchers decided to cull elephants experimentally in an attempt to reduce their impact on local woodlands. The culling operations met with little success and woodland losses continued. Croze (1974a & b) concluded from his studies, in the central Serengeti woodlands around Seronera, that elephants were not responsible for the observed woodland declines. His results showed that there was sufficient regeneration to offset the number of trees killed by elephants.

These findings inspired researchers in the Serengeti to look further for possible causes of woodland decline. Fire had long been recognized as a means of controlling bush encroachment and as an agent in the reduction of natural woodlands in Africa (Phillips 1930, 1965, Buss 1961, West 1965). Glover (1965, 1972) studied initially the detrimental effects of fire on woodland regeneration in the Serengeti. Norton-Griffiths (1979) further investigated these effects in a detailed study

correlating the frequency of fires with the loss of woodland canopy cover. He found that losses in the Serengeti were primarily correlated with the incidence of fire over the decade studied and only secondarily with the use of the area by elephants during the dry season. Although his investigation did not include the Mara, Norton-Griffiths (1979) hypothesized that similar factors were operating there as well.

In 1982 this study was initiated to investigate changes in the Mara woodlands over the past 30 years. Viewing these changes from both an historical and a contemporary perspective, the study was aimed at addressing two central questions: 1) what factor (or factors) were responsible for the observed decline of the woodlands in the 1960s? And, 2) what factor (or factors) are currently responsible for the inhibition of woodland regeneration? These questions were answered through experimental and observational findings.

Specifically, I focused on the hypotheses that in the 1960s and 1970s: 1) elephant-related mortality, in addition to other mortality factors, was responsible for the observed losses in woodland cover density in the Mara Reserve. By killing mature trees, elephants increased tree mortality rates to a level above recruitment rates, resulting in a population decline; and 2) fire, alone, was responsible for the rapid decline of the woodlands and thickets. Through an increase in fire frequency or severity, fires destroyed the younger, smaller size classes and reduced recruitment rates below the adult mortality rates experienced during the time of the declines.

Currently, the Mara woodlands do not appear to be returning

to their former status. To study the current dynamics of the woodlands, I hypothesized that: 3) present day fire regimes, in addition to other factors, prevent woodland recovery by continually top-killing seedlings and preventing them from growing to more fire-tolerant height classes; 4) elephants in the Mara today feed heavily on seedlings and prevent their successful escape into the larger height classes, where they are no longer susceptible to fires. Furthermore, elephants kill mature trees which reduces the number of seed-producing individuals and raises the adult mortality rates above current recruitment; and 5) an increase in the migratory wildebeest population is having a major inhibitory effect on woodland regeneration. By damaging small trees, wildebeest keep recruitment rates below adult mortality rates, thereby reducing the potential for woodland recovery and furthering woodland declines.

I begin in Chapter 2 with a summary of both qualitative and quantitative documentation of the decline of the Mara woodlands and thickets. Using the writing of explorers and hunters and interviews with long-time residents of the area, I reconstruct the history of the Mara's vegetation over the past 100 years. The loss of woodland cover, which began in the 1950's, is analyzed and quantified from a series of aerial photographs spanning the time period 1948 - 1982. The chapter provides an historical overview of the woodland declines within the Reserve boundaries and also discusses woodland changes which have been documented in the Serengeti National Park.

Chapter 3 presents an analysis of habitat selection by

elephants in the Mara. Using both aerial and ground censusing techniques, elephants are plotted by habitat on monthly and seasonal bases. These distributions of elephants by habitats are compared to the availability of the different habitat types over the same area. By comparing elephant sightings with the habitat availabilities, elephant habitat preferences are established for both the wet and dry seasons. This analysis describes the differential use of habitats by elephants in the Reserve at different times of the year.

In Chapter 4, I examine the foraging habits of Mara elephants with a view towards understanding their influence on woodland dynamics. I examine what plant species they select, what parts of these plants are eaten, what growing condition the preferred plants are in, and at what heights elephants prefer to feed. The feeding behaviour of both adult male and adult female elephants was recorded on a monthly basis and is summarized here on a seasonal basis. The balance between grazing on grasses and browsing on woody species is an important aspect of elephant foraging ecology and critical to management decisions aimed at preserving specific habitat and plant types. The feeding patterns observed in this study are, therefore, discussed in the context of current vegetation dynamics in the Mara Reserve.

Chapter 5 summarizes the experimental work in the Acacia woodlands of the Mara. This chapter provides an overview of the factors to which Acacia seedlings and trees are currently exposed, including: browsing by elephants and other browsers, trampling, thrashing, and inadvertent harvesting by migratory wildebeest, and intermittent burning by wildfires in the

Reserve. I discuss the results of experiments on both large-scale and multiple burns, the exclusion of both browsers and burning, and the germination rates of seeds exposed to varying fire intensities. The potential for recovery of woodlands in the Mara is then discussed in light of these findings. Results from these experiments and controlled studies are used in Chapter 6, where I summarize my research and present a simple model utilizing these data.

The central questions of what factor or factors were responsible for the dramatic woodland declines observed in the 1960s and the inhibition of woodland recovery in the Mara today are addressed in Chapter 6. Several hypotheses are put forth to explain the patterns of woodland change. A simple simulation model which incorporates the impacts of fire, elephants, wildebeest and other browsers is constructed to test predictions under the conditions measured in the 1960s and today. The model is then used to generate scenarios under various browsing and burning regimes that might realistically occur in the Mara in the future. Lastly, the findings of this study are summarized and implications for management of the Reserve are discussed.

CHAPTER 2. THE SERENGETI-MARA WOODLANDS: AN HISTORICAL PERSPECTIVE

Introduction

Over the past 30 years, dramatic woodland declines have taken place in many of the national parks and reserves of east, central, and southern Africa. The affected areas have experienced a rapid reversion from dense woodland to open grasslands (Caughley 1976). One hypothesis to explain these changes states that elephant browsing has actively inhibited tree regeneration and recruitment as well as increased adult tree mortality through felling and bark-stripping. This overall phenomenon is frequently referred to as the 'elephant problem' and largely attributed to the concentration of elephants into protected areas (Laws 1969, 1970).

The role of elephants in woodland dynamics has been studied in Kenya (Glover 1963, Agnew 1968, Laws 1969, Western and van Praet 1973, Parker 1983), Malawi (Jachmann and Bell 1985), Tanzania (Lamprey et al. 1967, Savidge 1968, Watson and Bell 1969, Croze 1974 a&b, Barnes 1980, 1982, Weyerhaeuser 1982, Barnes 1983, 1985, Weyerhaeuser 1985), South Africa (Pienaar et al. 1966, Pienaar 1969, Hanks et al. 1981, Hall-Martin 1984), Uganda (Buss 1961, Buechner and Dawkins 1961, Brooks and Buss 1962, Buechner et al. 1963, Buss and Savidge 1966, Laws and Parker 1968, Laws 1970, Wing and Buss 1970, Field 1971, Laws et al. 1975, Field and Ross 1976, Smart et al. 1985), Zambia (Caughley and Goddard 1974, Caughley 1976), and Zimbabwe (Anderson and Walker 1974, Thomson 1975, Guy 1976, 1981, Cumming

1981). Many of these studies supported the hypothesis that elephant foraging was the major factor in woodland losses.

Norton-Griffiths (1979) put forth an alternative hypothesis to explain the loss of woodlands in Tanzania's northern Serengeti National Park. Norton-Griffiths argued that the rinderpest epidemic that profoundly reduced the population of grazing ungulates in the Serengeti resulted in an underutilization of the highly productive grasslands. This unused grass provided the fuel for wildfires which annually burned the entire area in the late 1950s and early 1960s. Tree recruitment was therefore inhibited and some woodland communities were eventually destroyed by fire. In the long-run woodlands declined because the reduction in recruitment due to extensive burning could no longer offset the loss of mature trees to the activities of immigrating elephants.

The Masai Mara National Game Reserve, which borders the northern Serengeti, fits the general pattern of woodland losses in Africa. In this paper, I examine new lines of evidence not previously available to compare these alternative hypotheses and evaluate their relevance to woodland dynamics in the Mara. I review both qualitative and eyewitness accounts of the Serengeti-Mara area from the late 1880s to the early 1980s. These accounts allow a step-wise reconstruction of historical events and provide strong evidence that major changes in the faunal and floral diversity, structure, and extent of woodlands have taken place over the past century. In addition, I have analyzed the loss of woodland canopy cover from five sets of aerial photographs of the Reserve area taken in 1950, 1961,

1967, 1974, and 1982. The qualitative and quantitative evidence taken together reveals that the Serengeti-Mara ecosystem has experienced a transition from open grassland to dense woodland and back in less than 100 years.

Methods

The Qualitative and Eyewitness Evidence of Vegetation Changes

The evidence comes from numerous sources. I obtained records for several decades before and after the turn of the century from the journals of slave traders, reports of early explorers, the descriptions of visiting hunters, and the personal records of Narok District Commissioners. All of these sources were found in the Kenya National Archives, mainly from the collection of Africana donated by Kenya's first vice-president, Joseph Murumbi.

Photographs and accounts from the time period covering the 1930s through the 1950s were compiled from several sources. The Martin and Osa Johnson Museum in Chanute, Kansas, provided photographs taken in the Serengeti in the 1920s and 1930s by the Johnsons. The landscape panoramas in the photographs were relocated using permanent landmarks. This allowed a comparison of present vegetation with that recorded 50-60 years ago.

Mr. Syd Downey told me his recollections of the Serengeti-Mara since the early 1940s. Some of his photographs, taken in the Mara in the 1940s and 1950s, were subsequently relocated. M.I.M. Turner, warden of the Serengeti National Park from 1956-1972, provided detailed accounts taken from his daily diaries of

the period. Rodney Eliott, a game warden of the Mara in the 1950s, sent me descriptions of the area at that time, taken from his field notes.

The Direct Evidence of Vegetation Changes

For quantitative analysis of changes in both *Acacia* woodlands and *Croton* thickets of the Mara Game Reserve, during the period from 1950 to 1982, I used a series of complete aerial photographic surveys. Five surveys were flown in 1950, 1961, 1967, 1974, and 1982 (Table 2.1). Vegetation analysis followed Norton-Griffiths (1979) but was modified to fit the available aerial coverage.

Woodland changes were estimated by a 'dot-grid' analysis. The measuring grids were prepared photographically as described by Lamprey (1985). Dot grids were made for each set of aerial photography to account for the differences in photographic scale. A grid of 100 regularly-spaced dots was constructed in a 10 x 10 pattern for the analyses. Each dot was 0.05mm in diameter on the 1:50,000 scale photography. Standardizing from the smallest scale photography (1974, 1:68,000), the minimum detectable canopy diameter was 2.5m on the ground (Lamprey 1985). This provided a "lowest common denominator" dot size for use across all years. The grids were then analyzed under strong illumination at 20x-magnification. For the larger scale photography, it was necessary to ignore all trees with a canopy diameter less than 2.5m, i.e. those smaller than the chosen grid dot size. Woodland canopy cover (canopy density) was measured

Table 2.1. The aerial photographic series used in the analyses of woodland cover loss in the Masai Mara Game Reserve. Each survey provided total coverage of the study area.

YEAR	SCALE	FLOWN BY	SOURCE
1950	1:30,000	Royal Air Force	Directorate of Overseas Survey
1961	1:50,000	Royal Air Force	Survey of Kenya
1967	1:57,000	Royal Air Force	Survey of Kenya
1974	1:68,000	Meridian Airways	Survey of Kenya
1982	1:48,000	Kenya Rangelands Ecological Monitoring Unit	Wildlife Planning Unit W.C.M.D.

as a proportion of the number of dots touching trees or woody vegetation out of the total number of dots on the sample grid. This procedure allowed direct comparisons with the vegetation trends analyzed by Lamprey (1985) in an area immediately adjacent to the Reserve over the same time period.

When working with a finite dot size on small scale photography, one always overestimates cover in a way related to to the dot's diameter (Kershaw 1964, Norton-Griffiths 1979). Lamprey (1985, Appendix F) used computer modelling to analyze the degree of bias in this dot-grid technique. He concluded that the chosen dot size, of 2.5m, would overestimate cover density by a factor of two or a 100% bias error. Since the dot size used was the same for all photographic sets, this bias was considered to be constant between the different sets and the direction of changes detected was assumed to be unbiased.

In both Acacia and Croton communities three measurements were calculated:

1) The mean cover density value for each year's aerial photography was derived using the above methods.

2) From these data, the annual absolute change was calculated by taking the difference in mean cover between two successive photographic series and dividing this by the actual number of years separating the two measurements. For example, if mean cover was 30% in 1950 and 20% in 1961, the annual absolute change would be 10% divided by 11 years or -0.91% cover loss per year.

3) The annual relative change was calculated from the mean cover density data. This measure corresponds to the percentage

of the preceding time period's cover which has been lost by the following time period. If, for example, the mean cover in 1950 was 30% and in 1961 20%, the annual relative rate of change for the entire time period would be -33.0% or -3.0% per year.

Absolute change provides a measure of the mean annual percent cover lost each year, whereas the relative change is a rate measuring what percentage of the cover density in an earlier time period is lost by the next period measured. All statistical analyses were performed on MINITAB (Ryan et al. 1985).

The Acacia woodlands

Although individual tree species cannot be identified from aerial photographs at these small scales, ground records verify that the communities chosen for analysis were dominated by Acacia with a complex variety of other species occurring to a much lesser degree (Lamprey et al. 1967, Glover and Trump 1970, Trump 1972, Taiti 1973, Herlocker 1976a & b, Lamprey 1985). Species identification was not deemed necessary for the analysis, as the decline in total woody cover density was the primary focus.

Due to a rainfall gradient in the Mara Reserve, ranging from 800mm per year in the east, to 1200mm per year in the west (Norton-Griffiths et al. 1975, Epp and Agatsiva 1980), the area was divided into east and west. The 1950 aerial photos were used as a baseline for all analyses. They were first assembled by flight line, then transects were drawn down the center of

each of the parallel flight paths. This guarded against overlap of sampling points on successive flight lines. Fifty points were then randomly selected in Acacia woodlands and cover density was measured. The same points were identified on the photographs of all later series and cover density was re-measured. Identification of points was greatly aided by use of the 1:50,000 scale topographical map compiled by the Directorate of Overseas Surveys, the Survey of Kenya, and the Tanzania Survey and Mapping Division from these same aerial photographs.

Five randomly-oriented dot grid counts were made at each sample point in each series of photographs. This provided a mean cover estimate and standard error for each sample point. All sample points were assumed to be independent of one another. All woodland cover density estimates were arcsine transformed before statistical comparisons were performed (Zar 1984).

The Croton thickets

Because Croton thickets occur in discrete, clumped units, I measured the areas of thickets and their changes in addition to changes in cover density within individual thickets. Cover density was estimated on all five photographic series. Change in area was measured only on the 1950 and 1982 photographs. These two sets were photographed at the largest scale and, therefore, thicket outlines were clearly delineated and easily compared.

Croton thickets are far more abundant on the east side. Therefore, to select an equal number of sample points from each

side, sample sizes would have been necessarily reduced by the limited occurrence of thickets on the west side. By considering east and west side thickets together, I was able to select 50 sample points and examine the general trend in Croton cover loss across the entire Reserve.

Cover was estimated as described above for Acacia woodlands. Area loss was determined by selecting 15 individual thickets or thicket groups which were clearly photographed in both 1950 and 1982. Tracings were made of the outlines of these thickets on the 1950 series. Area was then measured, in square kilometers, using an area dot grid. Each sample thicket was re-measured five times to reduce the variance. Using a Bausch and Lomb Zoom Transferscope, each of the 15 base samples were then adjusted to fit directly over the 1982 photos. Thicket area that remained was drawn directly from the 1950 base tracings and measured with the area dot grid.

As a comparative test, thicket areas were also measured using a digitizer. Area measurements using the digitizer became increasingly inaccurate as thickets became smaller and more fragmented.

Results

Vegetation Changes from 1880 to 1980: the qualitative evidence

The Serengeti-Mara ecosystem lies within an area broadly described as Maasailand. Of all the local tribes, it is the Maasai who have had the most significant influence on this system. Maasai tribal lore relates that these nomadic pastoralists first came to the area in the mid-1700s (Mol 1980). However, detailed records of Maasai history in the area do not actually begin until the latter part of the 19th century (Sandford 1919, Fosbrooke 1948, Jacobs 1965). It was around this time that the Maasai suffered a series of setbacks which continued well into the 1900s.

In the early 1880s, drought struck the area and domestic stock, already weakened by arid conditions, succumbed to bovine pleuro-pneumonia. Control of the disease was non-existent and Maasai herdsmen suffered tremendous losses of livestock (Thomson 1885). Within a few years, the next disaster hit - an exotic viral disease of ungulates - rinderpest (Plowright 1963, Plowright and McCulloch 1967, Atang and Plowright 1969). The actual introductory locus of this endemic Asian disease remains uncertain but several theories exist. Some say the disease was first introduced into Egypt by the Nile expedition in 1884 and moved rapidly south from there. Others suggest that rinderpest was transmitted by cattle from the Black Sea area, which had been brought into Khartoum. The most commonly held belief is that it entered through Ethiopia during the Italian invasion of 1889 (Branagan and Hammond 1965, Mack 1970, Ford 1971, Plowright

1982). According to all sources, cattle served as the introductory hosts. African cattle, carrying no immunity to this foreign disease, died rapidly and in great numbers. By September 1890 it had arrived in the Serengeti-Mara region and within a few short months over 90% of the cattle were dead (Sandford 1919, Mallett 1923).

The ensuing famine was inevitable for the Maasai due to their total dependence on livestock. The catastrophic loss of livestock created the conditions for devastating human epidemics, including smallpox (Sandford 1919, Fosbrooke 1948). The 1890s became known amongst the Maasai as, enkidaaroto, the destruction (Baumann 1894a & b). Europeans travelling in the area at this time described the once proud and self-reliant Maasai, who had resisted the intrusion of Arab slave traders only a few years earlier, as a people on the brink of extinction. Baumann (1894a) recalled of his trek through Maasailand, "The people gathered themselves around the barrier of our camp, in the meantime uttering cries of a pitiful nature, which is now the distinguishing characteristic of Maasailand. The women had been reduced to skeletons, from whose hollow eyes gleamed the madness of hunger, the children who were more like naked frogs than men, "warriors" who could scarcely crawl on all fours and were dazed, languishing old men. These people ate anything: dead asses, the hide, yes, even the horns of a slaughtered beast they would not refuse. They had fled from the Serengeti where hunger had depopulated the entire district and had become beggars to their fellow countrymen who themselves had scarcely enough to eat.". Bernsten (1979) recounts how Maasai

tried to join Baumann's caravan just to stay alive, while others eked out a Dorobo-like (nomadic hunter-gatherer) existence. Baumann (1894b) estimated that 75% of the people in the Serengeti-Mara region had died by the early 1890s. Thus, the area was left devoid of human influence by the turn of the century and for many years thereafter.

Wild ungulates of the area were also affected by the rinderpest outbreak. As cattle numbers dwindled, the virus persisted in numerous wildlife species including giraffe (Giraffa camelopardalis), warthog (Phacochoerus aethiopicus), and others. Two heavily affected species were buffalo (Syncerus caffer) and wildebeest (Sinclair 1977, 1979). Due to the gregarious, herd-forming nature of these species, the viral disease was quick to catch hold and spread amongst them. Although the actual numbers lost are unknown, accounts of buffalo in East Africa show that there were only a few herds left by 1900 and suggest a loss of up to 90%. In fact, White (1914) described shooting a buffalo as one of the major highlights of his 1911 hunting safari to the northern Serengeti-Mara area. Veterinary records show that many wild animals gradually developed immunity to the disease. However, recruitment of young animals into the populations must have been very low. The disease took its greatest toll on calves, who lost their acquired immunity after weaning, at about six months of age. Hence, it became referred to as "the yearling disease".

During this same period, the elephant population of the area was also experiencing a reduction in size. Heavy hunting pressure was generated by a lively ivory trade, and the

flourishing slave trade helped to transport this ivory, on the backs of slaves, to the coast for marketing and shipment abroad (Wakefield 1882, 1870, Farler 1882). According to the journals of early caravan leaders, the local Dorobo hunters referred to themselves as "the elephant people" (Fosbrooke 1968). Some of these very elephant hunters were the itinerant Maasai of whom Baumann (1894, p.323) wrote, "... They apparently turned to hunting as a means of staying alive. In a few cases, men stated to me that they received 30 cattle for a tusk 6-7 feet long, and nine cattle for a tusk 2-4 feet long. The accuracy of these figures is questionable. What is important is that for the first time many Maasai who had never been involved in the international ivory trade were now forced to do so by their sheer destitution.". Ivory export records compiled by Spinage (1973) substantiate these reports of widespread elephant slaughter. The Serengeti-Mara became known as an area without elephants. Grogan and Sharp (1900) reported that, "...ten years ago elephant swarmed in places like this, where now you will not find one.". This absence of elephants was interpreted in later years as their never having occurred in the area. Buxton (1927, p.67) wrote, "...excepting elephants, we could have shot nearly every kind of game in the course of our wandering [through the Serengeti-Mara area]" and Melland (1938, p.176) stated, "...so far as I know, the Serengeti does not and has never numbered elephants among its inhabitants.".

By the turn of the century elephant numbers had been greatly reduced by hunting, wild and domestic ungulates by rinderpest, and the Maasai people by famine and disease.

Explorers and hunters of the early 1900s encountered a Serengeti-Mara which looked much as it does today. Broad, open expanses of grassland and lightly wooded savanna predominated. Buxton (1927, p.67) remarked, "...we came out onto undulating grasslands, lovely fertile country which seemed almost uninhabited... Near us was a thickly wooded range of hills running north and south (presumably the Kuka Hills), but in every other direction were plains stretching on and on.". In some areas, these grasslands were dotted with Acacias of a variety of species. Woosnam (1913, p.275), a game warden assigned to determine tsetse fly distributions along the Mara River, gave similar accounts of the west side of the river, in the Mara Triangle area of the present Reserve. "It was a broad plain of park-like country, fine grazing land, studded with the occasional yellow-barked Acacia trees." And, White (1915, p.158), a hunter and writer who travelled extensively in the northern Serengeti and Mara throughout the period from 1910 to 1913, described the same area as "...a high grass plateau with a few scattered thorn trees" and (p.162) "...an open, grassy rolling country. Here and there are low, rocky, circular outcropping hillocks crowned with green thickets... The [Croton] thickets are nowhere continuous, and one can always march around them.". Eastman (1927, p.57) described the area near the Sand River, in the early 1910s where "...the river meanders through a vast, level, mostly smooth plain, bordered with low, rounded hills. The plain is sprinkled with trees of moderate size... We can run our cars anywhere at any speed up to 30 or 40 m.p.h.".

By the 1930s the area had changed. The same area which 30 years earlier had been open, grassy plains was described by Lewis (1935, p.445) as "...numerous intersecting and narrow belts of thorn-brush [Croton]. In order to reach the Mara River, it was necessary to cut out a path for vehicles to pass through densely-growing Acacia seyal and another species known [to the Maasai] as 'Ol-jerai'.". According to Huntingford (1976) and Mol (1980), this is a name used for several other species of Acacia found in the Mara area. Early photographic records from naturalists such as Martin and Osa Johnson in the 1930s, hunters like Syd Downey in the 1940s, and the first Royal Air Force aerial photography in 1950, showed widespread hilltop thickets and Acacia woodlands throughout the northern Serengeti and Mara. In fact, Syd Downey recalled 'taking' up to five leopards in a day in the dense bush of the Mara Triangle, an area which is now known for its wide, open grasslands, an unlikely habitat for leopards.

Colonial administrators, who realized the inherent value of the region, were quick to move for protection of the area. In 1937 the Tanganyika Serengeti, which comprised the majority of the ecosystem, was declared a game reserve. Just over a decade later Kenya's Mara followed suit, and the Serengeti gained national park status. The goal was to preserve this wooded area in what was perceived as its "pristine" condition. Feeling confident that they had succeeded in securing the area before any changes occurred, Park authorities stated, in a 1946 Royal National Parks Report (p.55), that, "The tsetse fly stands guard over this area, and even today it is virtually a glimpse into

Africa as it was before the white man ever crossed its shores.". These early conservationists had not realized that less than 50 years earlier, these same dense woodlands had been wide expanses of open grassland.

These thickets and woodlands which afforded habitats for a diverse assemblage of vertebrate fauna also provided prime shade and resting sites for tsetse flies, Glossina swynnertoni and G. pallidipes, (Lewis 1935, Sywnnerton 1936, Beaumont 1944, Buxton 1955, Ford and Clifford 1968, Glover and Trump 1970, Langridge et al. 1970, Ford 1971). In addition to inflicting a painful bite, tsetse flies transmit a parasitic blood disease known as trypanosomiasis in cattle and "sleeping sickness" in man. Because the Trypanasoma parasite can be maintained in many secondary hosts, the vector survived the losses of its human, domestic, and most of its wildlife hosts in the late 1800s (Ford 1971, Bourn 1978, Molyneux 1982, Rogers and Randolph 1985). The Maasai were keenly aware of its persistence in other organisms and the District Commissioner for Narok District wrote in a 1925 report that, "...the strange disease [trypanosomiasis] was known by the Maasai to be carried by toads (and possibly lung fish) and when trampled by cattle at watering holes, it would poison the water with its blood.".

Throughout the 1950's the Maasai used the area that is currently the central and western portion of the Mara Game Reserve for seasonal grazing by their sheep and goats. Unlike cattle these smaller stock were largely unaffected by trypanosomiasis. A 1955 Kenya National Parks report stated that, "The whole of this section is dominated by the tsetse fly

and possibly for that reason retains its full quota of game. It is of absolutely no use to the Maasai except for grazing their small stock...". As late as 1960, the area between Aitong (well north of the Mara Game Reserve), the Talek River, and south to the Serengeti remained uninhabited (Lamprey 1985).

Whereas earlier in the century the vegetation was inhospitable to tsetse occupation, by the 1930s and 1940s the woodland increase had allowed their proliferation. Also, many resident wild ungulates had, by this time, developed immunity to rinderpest (Taylor and and Watson 1967, Stewart 1968) and now became prime hosts for the trypanosomiasis vector (Sinclair 1979). Early attempts at mechanical bush-clearing and the elimination of wildlife hosts were largely unsuccessful having little, if any, impact on tsetse fly numbers (Langridge 1960). Despite repeated failures, efforts to eliminate the flies from Maasailand continued for several decades. Finally, after great expenditure of time, money, and effort, tsetse eradication programs were abandoned in the 1960s (Ford 1971). Although tsetse flies began declining around this same time, it was not believed to be in response to official control programs but rather to ecological factors which lead to a reduction in their habitats.

Two of the important ecological factors were the increase in fire frequency and an increase in elephant densities. Unusually high rainfall in the early 1960s (Figure 2.1) resulted in heavy grass production throughout the region (Glover and Gwynne 1961, Kenya Game Department Annual Reports 1961-1964, Tanzania National Parks Annual Report 1962-1964, Talbot and

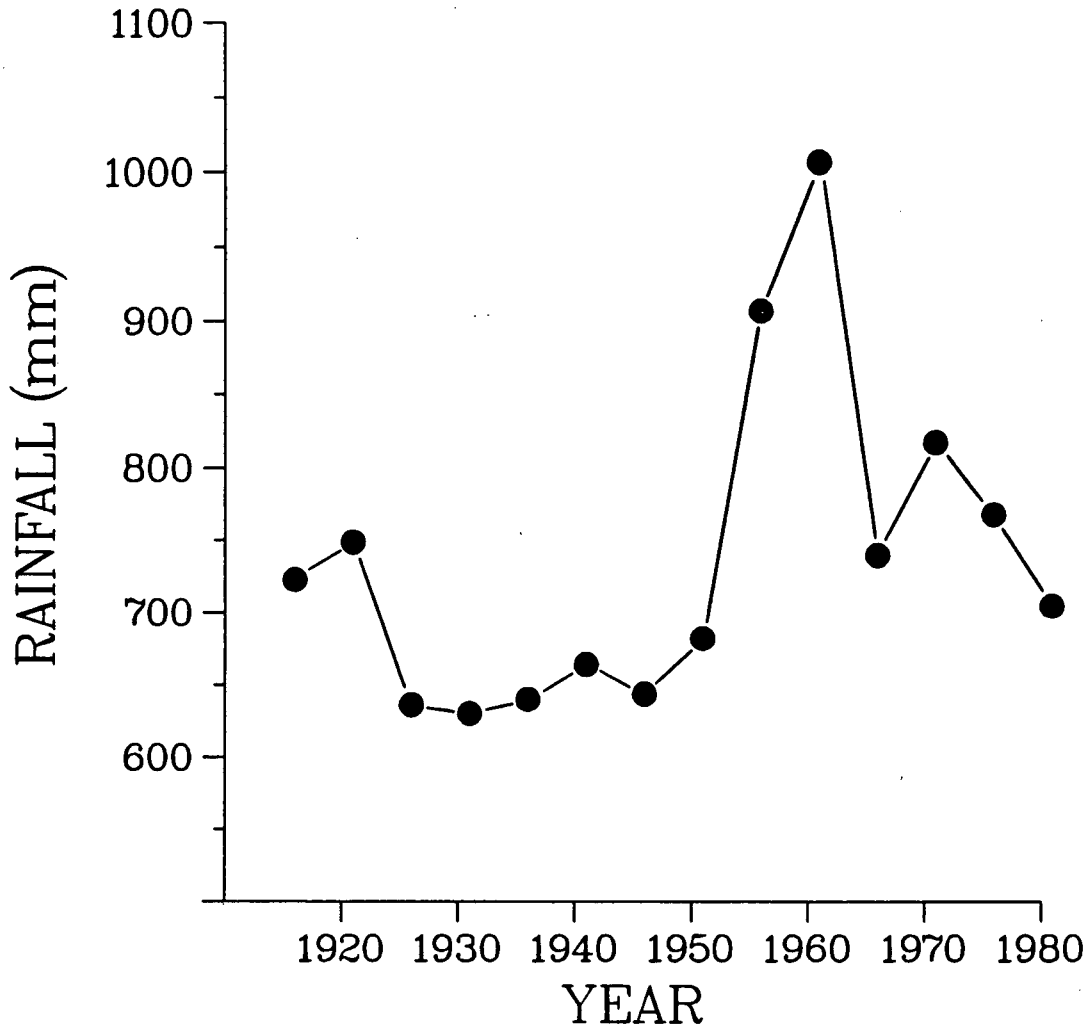

Figure 2.1. Five-year rainfall averages for Narok, Kenya over the period 1914 - 1980.

Talbot 1963, Glover and Trump 1970). M. Turner recalled grass swards above the bonnet of his Land Rover and the fiercely hot fires which prevailed during this time. The greatly reduced ungulate populations were unable to remove these tremendous fuel loads.

Langridge et al. (1970, p.204 and 208) described this phenomenon in the Mara Game Reserve: "...between 1961 and 1963 rainfall was very heavy throughout the district and produced luxuriant grass cover which allowed the bi and tri-annual burning... (meaning twice and three times per year). As soon as they are dry enough, the grassy plains are fired by the Maasai. Sometimes conditions are such that new growth of grass after a fire is ready for burning within the same season. Thus a single area may be burned twice within a season or even three times during a year... The very fierce fires caused accelerated destruction of the vegetation with marked changes in the numbers of trees and shrubs...".

Between the late 1950s and the early 1960s, researchers working in the Serengeti-Mara noted that elephant numbers were increasing and subsequent browsing on woody vegetation was occurring (Lamprey et al. 1967, Watson and Bell 1969, Glover and Trump 1970), It was not altogether clear where these elephant immigrants originated. It is most likely that they came from the areas immediately surrounding the Serengeti-Mara ecosystem. This included areas such as Loliondo, the Siria (also Oloolololo or Isuria) Escarpment, the Chepalunga Forest and the Lambwe Valley to the north and west (M. Turner, personal communication). These areas were experiencing rapid human

settlement, increasing livestock numbers and, in some cases, cultivation, and therefore elephants were being forced out.

This led to a compression of elephants into protected areas in the years that followed. The District Commissioner of Narok (1955) reported that, " Elephants created serious problems for settlement of these areas. This necessitated the shooting of a number of these elephants. The campaign against shamba [farm] damaging elephants in these areas has been, on the whole, satisfactory. The results of our persistent attack has been to drive a certain portion of elephants back to their old haunts. These places are in the Maasai Reserve where no cultivation exists". The Tanzania National Parks Annual Report (1962-1964, p.31) noted that "... Viewing of elephant became more common in the Serengeti National Park". With elephant densities increasing within the protected park and reserve lands (Watson and Bell 1969, Glover and Trump 1970, Norton-Griffiths 1979, Dublin and Douglas-Hamilton, in press), subsequent change in the woodlands was inevitable. Ring-barking and heavy browsing pressure on a variety of tree species followed (Glover 1965, Lamprey et al. 1967, Croze 1974a & b).

An analysis of long-term monitoring data by Norton-Griffiths (1979) showed that woodland cover loss in the Serengeti could be attributed primarily to the increased frequency and severity of fires and secondly to the impacts of browsing elephants. Burn and bark-stripping scars found in the tree cores of two species in the Mara suggested that both fire and elephant browsing figured prominently in their individual histories during the 1960s (Dublin, unpublished data).

Vegetation Changes from 1950 to 1982: the direct evidence

The Acacia woodlands

Results of the cover density analysis for the Mara Reserve show that in 1950, mean woody cover was approximately 30% in Acacia woodland stands (Figure 2.2). Cover estimates ranged from 8% to 56.8% in the east and 10.7% to 50.4% in the west. Fifty sample points were followed through time on both the east and west sides. The Mara has suffered continual woodland loss since the early 1950s. Both east and west showed highly significant cover losses in each successive time period. A two-way ANOVA showed that there was a significant interaction between year and the east and west sides of the Mara ($F = 3.91$, $P<.01$). Tukey's multiple comparison test showed that cover density was the same for east and west in 1950, 1961, and 1967 but was significantly lower in the west in 1974 and 1982 at the 1% level. This is most likely the result of higher rainfall on the west side which produced more grass fuel for dry season fires subsequently killing more trees in the west than the east after 1967.

The hypotheses that there were no differences between east and west in absolute or relative rates of change for the different time periods were also tested using two-way ANOVAS (Figures 2.3 and 2.4). Tukey multiple comparison tests on mean rates of change showed that the absolute rate was higher in the east for the period 1950 to 1961. From 1967 to 1974, significantly greater losses occurred in the west. Absolute losses were not significantly different between east and west

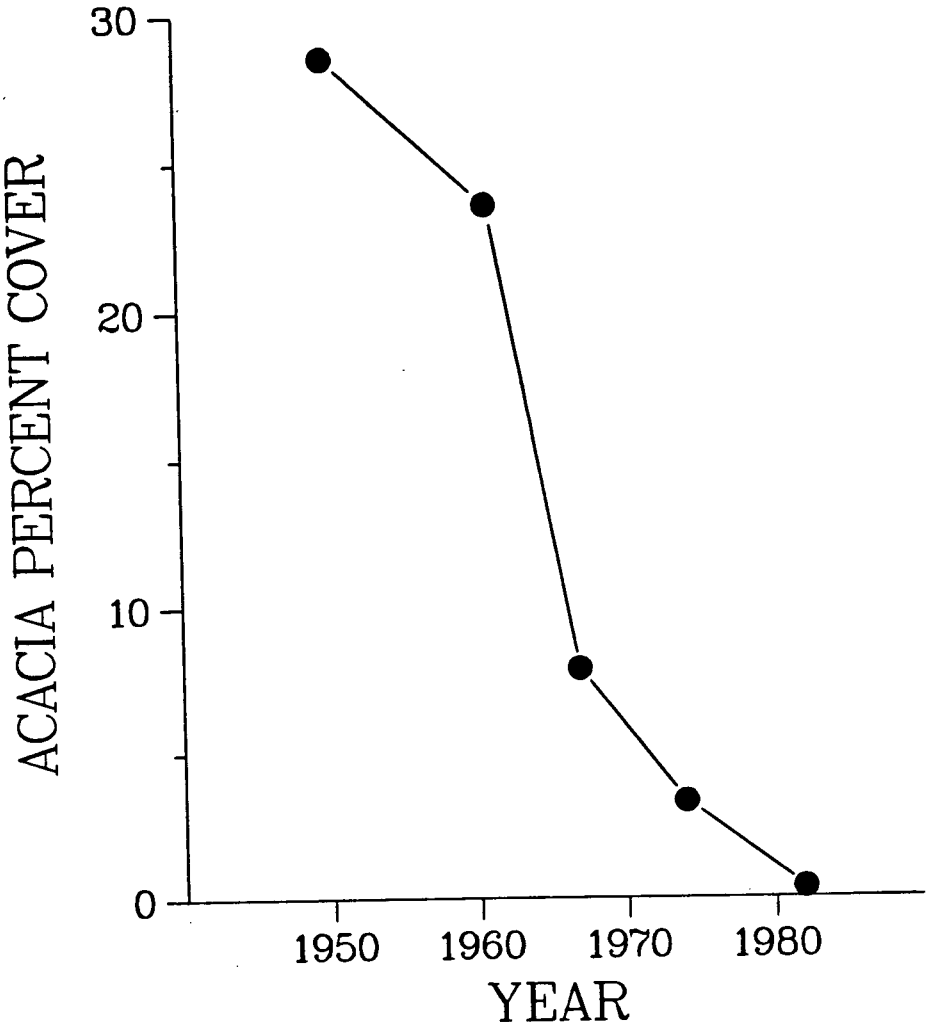

Figure 2.2. Mean cover density of Acacia woodlands in the Masai Mara Game Reserve. Percent cover densities are derived from dot-grid analyses of five sets of aerial photographs.

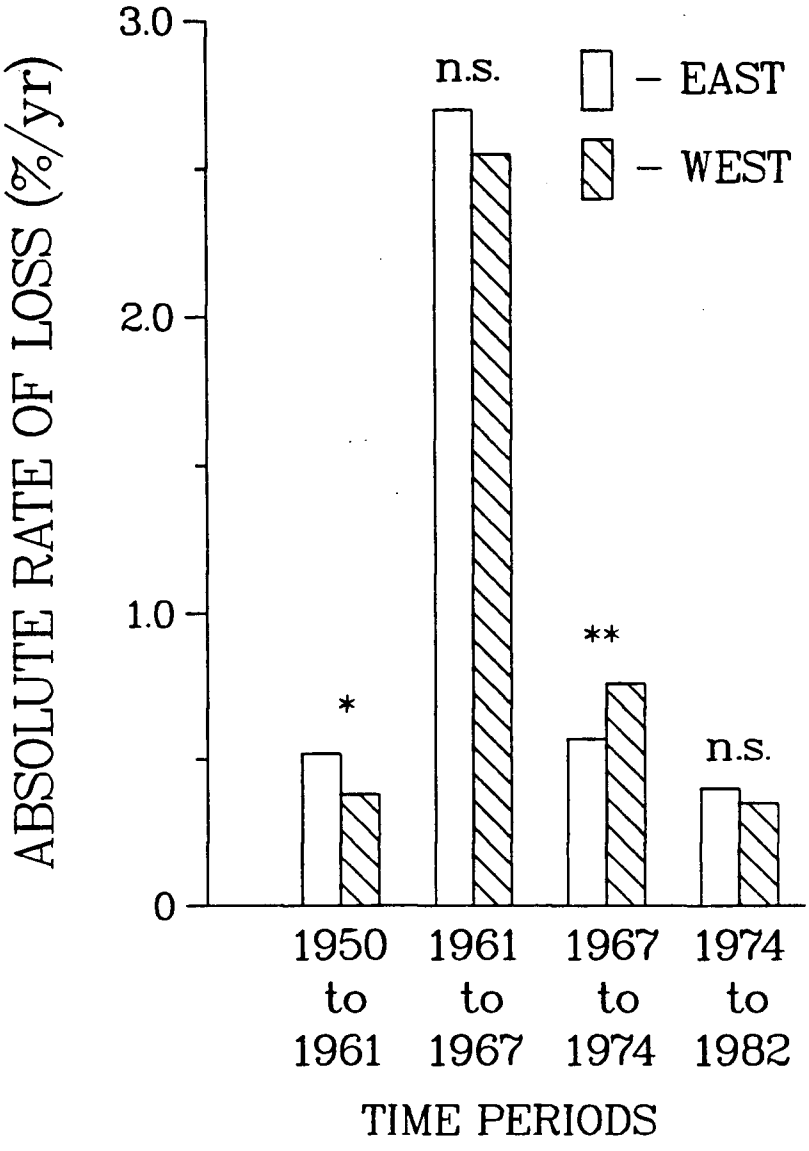

Figure 2.3. Absolute rate (percent/year) of cover loss for Acacia woodlands in the Mara Mara Game Reserve. The Reserve was broken into east and west sides for analysis, (* = P<.05, ** = P<.01).

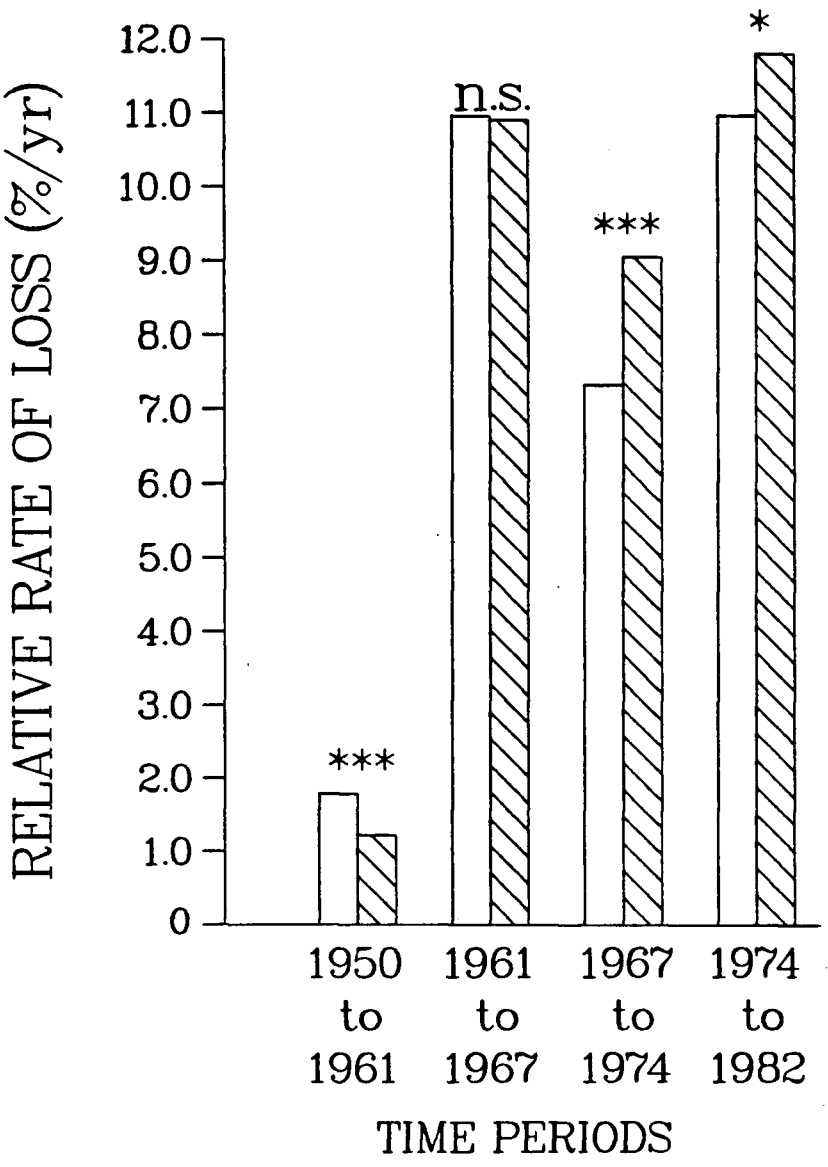

Figure 2.4. Relative rate (percent/year) of cover loss for Acacia woodlands in the Mara Mara Game Reserve. The Reserve was broken into east and west sides for analysis, (* = P<.05, *** = P<.001).

for the periods 1961 to 1967 and 1974 to 1982. Absolute rates of change were highest in the period 1961 to 1967.

Relative rates of change followed a similar trend. East side losses were greater than west from 1950 to 1961, rates in the west exceeded those in the east for the periods 1967 to 1974 and 1974 to 1982, and east and west sides were equal from 1961 to 1967. Looking at relative rates of change, across the entire Reserve, in the period from 1961 to 1967 alone, there was a 60% to 65% decline in tree cover density. In the 32 years, between the first aerial series in 1950, and the last in 1982, over 95% of the Acacia woodlands had vanished.

The Croton thickets

Croton thickets have changed in two ways over time. Both a loss in canopy cover within thickets and a loss of total area covered by individual thickets have taken place. The analyses show that both these losses have been highly significant over the past 32 years (Figures 2.5, 2.6, & 2.7, all P-values <.0001). The largest declines occurred from 1961-1967 (-2.33% per year absolute loss and -3.12% per year relative loss). The average area of the 15 individual Croton thickets or thicket groupings, followed through time, dropped from a mean of 4.12 km^2 to 2.80 km^2 (Figure 2.8).

It should be mentioned that variability was especially high in the Croton thicket area-loss measurements. The actual perimeters of some thickets did not change at all, though internal thinning (i. e. loss of cover density) occurred in all

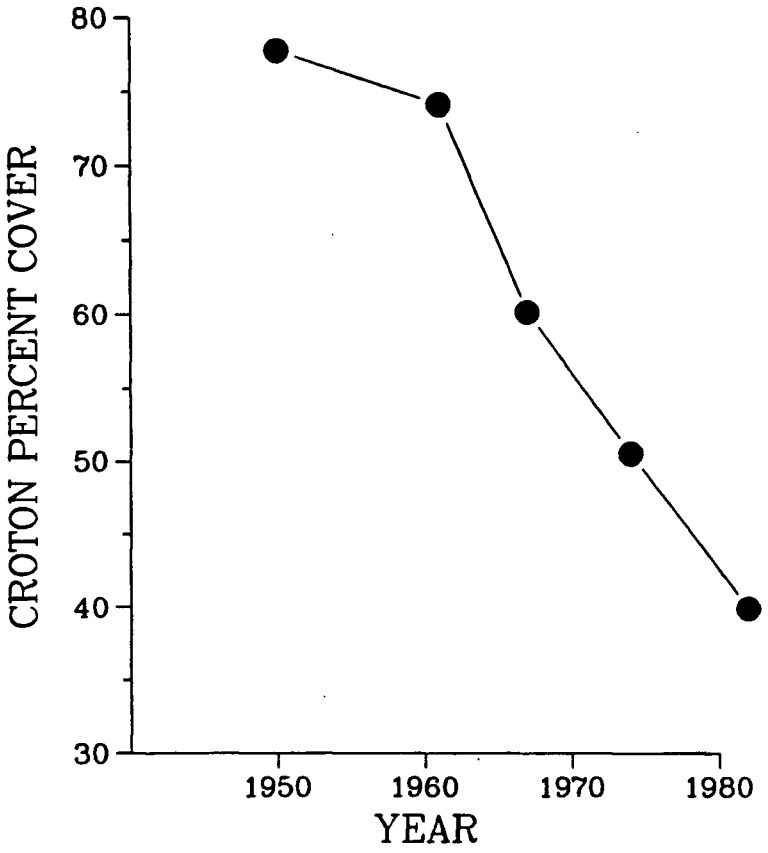

Figure 2.5. Mean cover density of Croton thickets in the Masai Mara Game Reserve. Percent cover densities are derived from dot-grid analyses of five sets of aerial photographs.

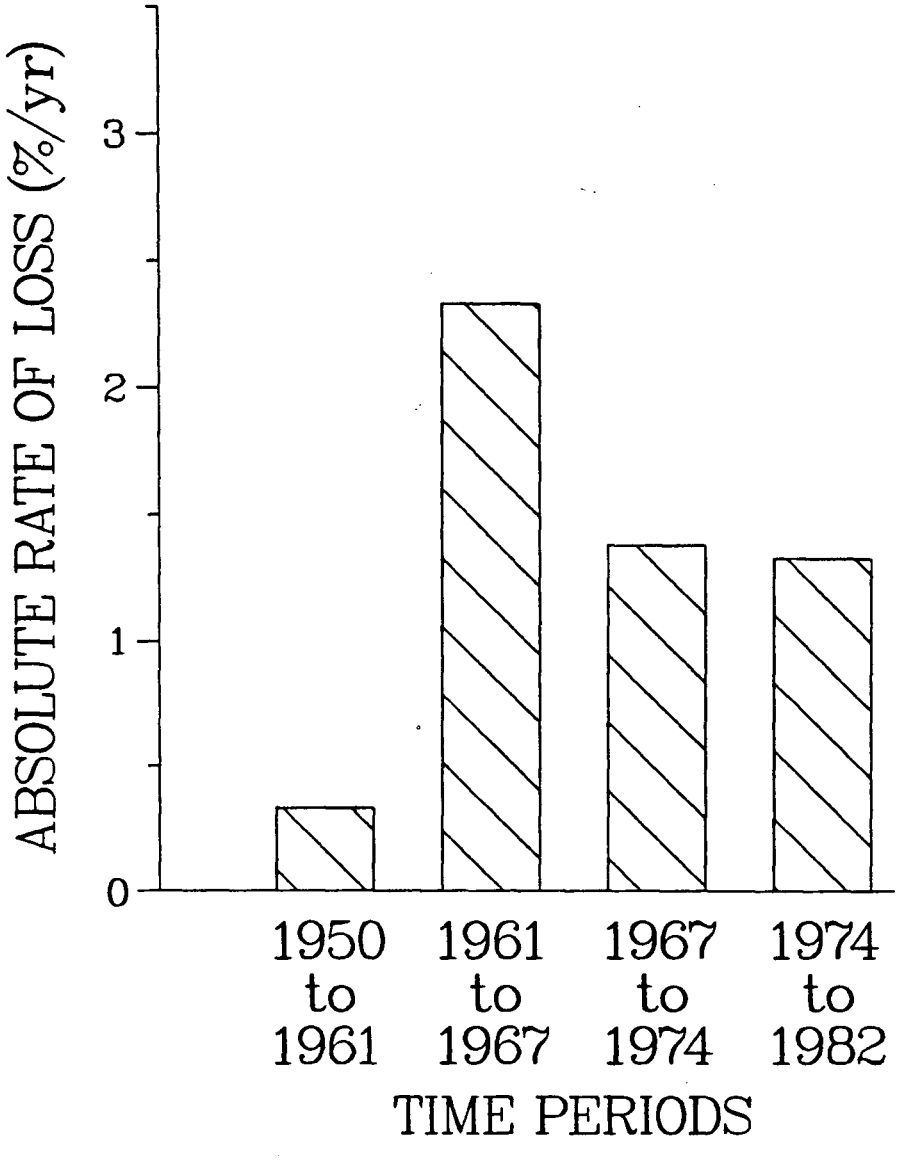

Figure 2.6. Absolute rate (percent/year) of cover loss for Croton thickets in the Masai Mara Game Reserve. All time periods are highly significant at the P<.0001 level.

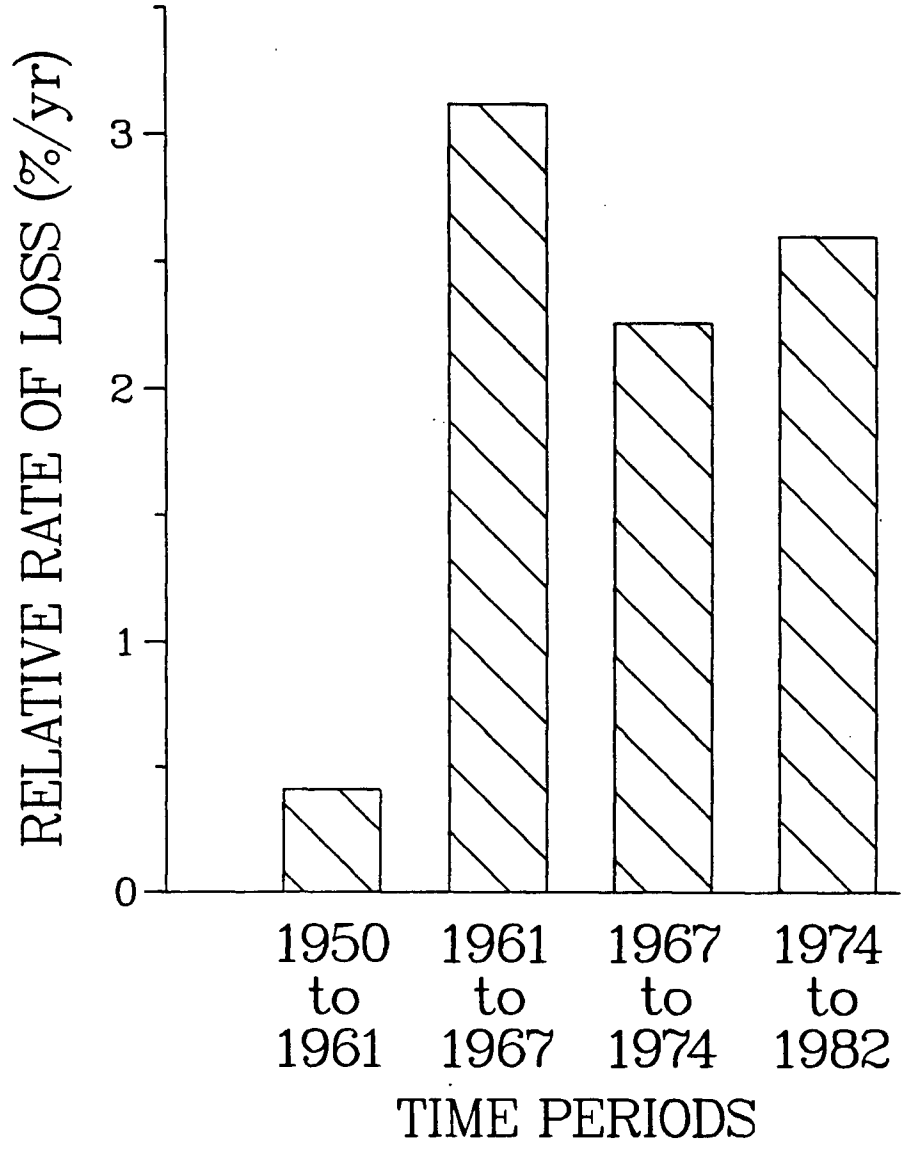

Figure 2.7. Relative rate (percent/year) of cover loss for Croton thickets in the Masai Mara Game Reserve. All time periods are highly significant at the P<.0001 level.

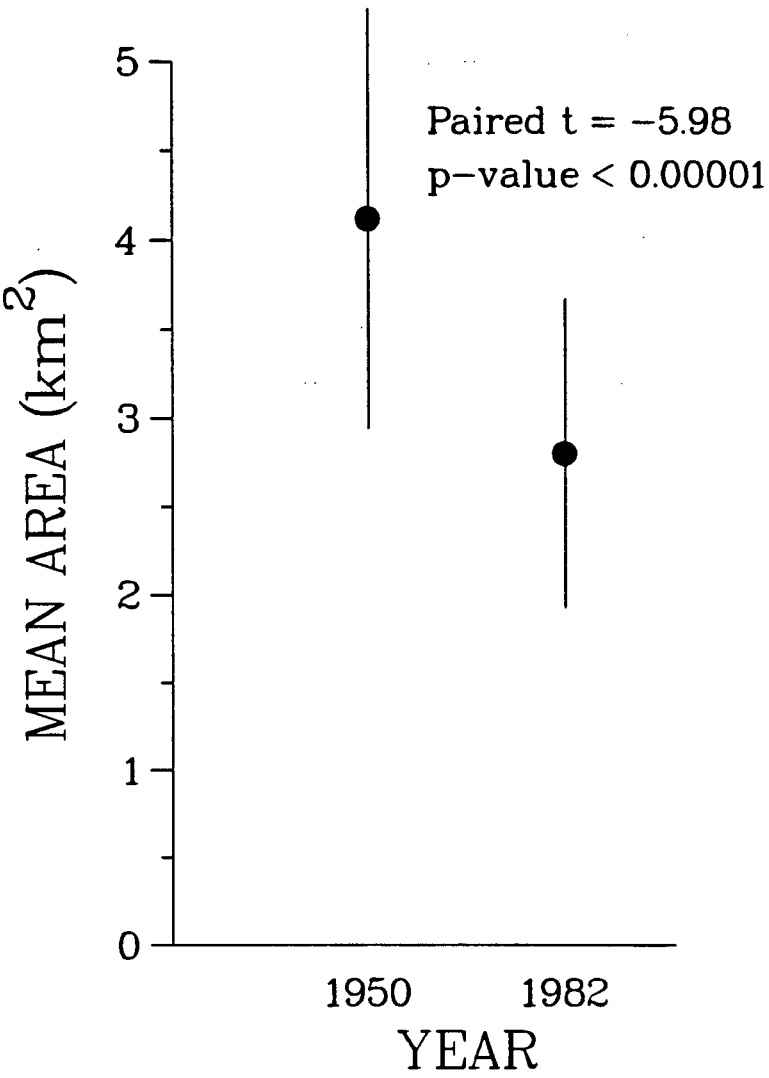

Figure 2.8. Mean area of fifteen Croton thickets sampled in the 1950 and 1982 aerial photography (± one s.d.).

thickets sampled. The reason for this stability through time is unclear but may have to do with the original shape of individual thickets. Thickets which were rectangular or circular in 1950 tended to be more resistant to change. Those that were long and narrow or had bottlenecks within them were more readily fragmented and the subsequent segments disappeared entirely, over time. The agents responsible for area and cover loss probably acted both together and individually.

Discussion

A synthesis of qualitative and direct evidence shows that the Serengeti-Mara ecosystem has experienced a change from open grassland to dense woodland and back in less than a hundred years. By 1900 elephant numbers had been greatly reduced by hunting, wildebeest, buffalo, and cattle populations were low due to rinderpest, and the Maasai people had been decimated by famine and disease. These events late in the last century set the stage for the establishment of extensive woodlands and thickets in what had formerly been open grasslands.

Shielded from the effects of heavy browsing and grazing and the annual hot fires set by the Maasai, bush and woodland formation progressed unimpeded. By the mid-1930s, the area which 30 years earlier had been open grassland now comprised dense woodlands and thickets. In 1937 the Serengeti was gazetted as a national reserve. Early conservationists and park authorities vowed to maintain this diverse, woodland dominated area in what they mistakenly viewed as its "pristine" condition.

These woodlands and thickets persisted for some time but, despite the desire to preserve them, precipitate declines began in the late 1950s and early 1960s. With the advent of modern medicines which protected and extended human life, coupled with advanced veterinary care, which vaccinated livestock against rinderpest and other diseases, unprecedented increases in human and cattle populations had occurred in areas surrounding the Serengeti-Mara (Figure 2.9, Morgan and Shaffer 1966, Kurji 1976, Lamprey 1985). It was the direct and indirect effects of these increases which finally brought about woodland declines and a return to the open grasslands seen today.

Two primary pathways stemming from the increase in human populations appear to have initiated woodland declines. The first was fire. Ungulate populations, still sparse as a result of the rinderpest, were unable to reduce significantly the standing crop of dry grass resulting from unusually high rainfall in the early 1960s. As the dry season progressed, fires became widespread. Some of these fires were intentionally set by the Maasai to improve grazing pastures and to clear tsetse-infested bush, while other burns facilitated hunting by neighbouring tribes, some were set by park authorities under overall fire management schemes, some were inadvertently lit by wandering honey hunters and still others by European hunters. Under conditions of normal rainfall, woodland regeneration would have been hampered by this sudden increase in fire occurrence. Under the high rainfall conditions of the early 1960s and the subsequent high fuel production these fires were devastating and served to clear the area of bush and attract game to the lush

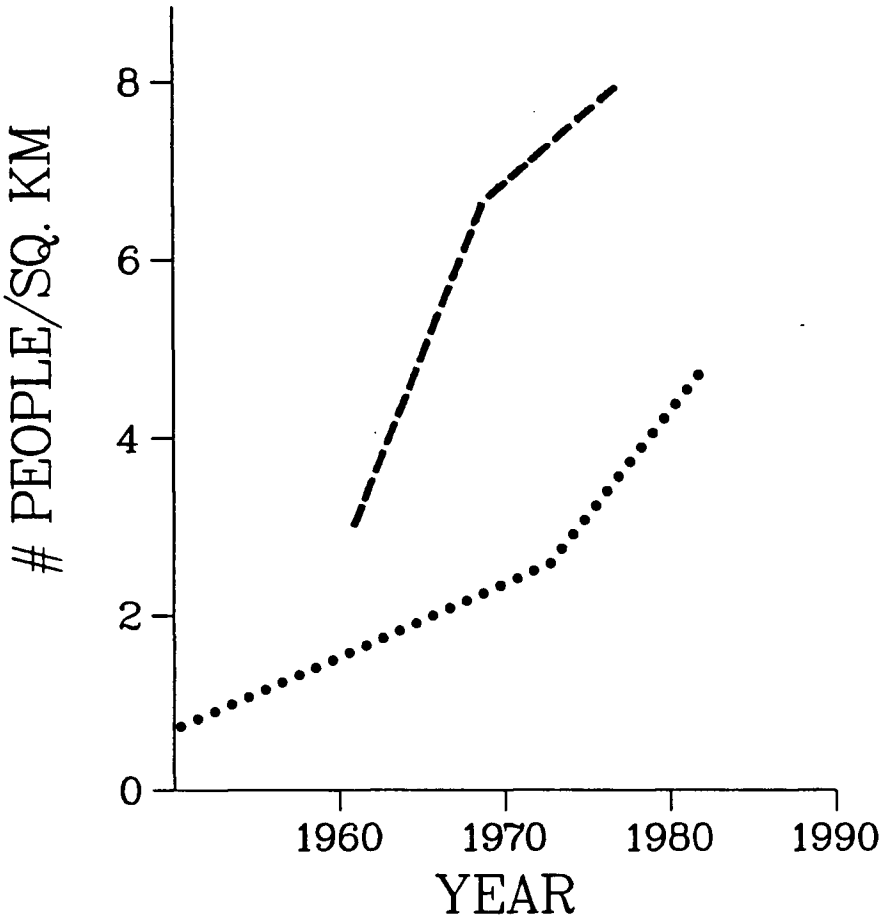

Figure 2.9. Human population density trends for the area near the Masai Mara Game Reserve. The dotted line (•••••) represents the trend calculated from settlement numbers in the area adjacent to the Game Reserve (Lamprey 1985). The dashed line (---) represents the trend calculated from national census data which included the densely populated Ololunga area. (Morgan and Shaffer 1966). This area is not adjacent to the Reserve. Graph adapted from Lamprey (1985).

grazing "lawns" created by fires.

The human increase also opened a second pathway to woodland loss in protected areas, the compression of elephants. The role of elephants in dramatic woodland declines had gained much notoriety and attention among ecologists, at this same time, throughout Africa (Buechner and Dawkins 1961, Brooks and Buss 1962, Simon 1962, Glover 1963, Darling 1964, Buss and Savidge 1966, Field 1971, Anderson and Walker 1974, Caughley 1976, Croze et al. 1981). In discussing elephants and woodland loss, Curry-Lindahl (1968, p.26) stated, "...except for man there is no other animal in Africa that is able to alter a habitat so drastically as does the elephant". Like so many other areas of Africa, the Serengeti-Mara woodlands felt the effects of increased elephant densities.

The quantitative analysis of aerial photography, which covered the major period of woodland decline, provided a better understanding of the exact timing of these losses. The highest losses, from 1961 to 1967, corresponded significantly to a period of unusually high rainfall and subsequent fires which occurred two or three times per year during this time (Langridge et al. 1970). While healthy trees may have withstood fire longer, in the face of such hot fires even many unbrowsed trees died. The additional heavy influx of elephants, in this same time period, drove these declines of tree density even further. Elephant impacts, such as branch breakage and bark stripping, could have exacerbated the effects of fire, by adding to existing fuel loads or by causing physiological stress to the trees and making them more vulnerable to fire. Elephants and

fires acted together, their relative contributions are not easily distinguished.

Separate analyses of east and west sides of the Mara Reserve uncovered some interesting differences in the pattern of woodland loss. Although the period of greatest tree density decline, 1961-1967, was not significantly different between the two, all other time periods showed greater relative losses on one side or the other. From 1950 to 1961, the east experienced greater losses of trees and from 1967 to 1974 and 1974 to 1982 the reverse was true. The greater eastern losses in the early time period may be attributed to a larger influx of elephants to that part of the Reserve, following their emigration from neighbouring areas (Narok District Commissioner, Annual Report, 1955). The east was always an area of greater woodland cover density relative to the west, with Acacia woodlands, Croton thickets, and Combretum woodlands throughout. Elephants tend to prefer dense woodlands and bushlands when these are available (Darling 1960, Glover 1963, Agnew 1968, Laws 1969, 1970, Laws et al. 1975). These woodlands were also devoid of humans because of the high tsetse fly infestations. The eastern woodlands and thickets, therefore, would have been colonized first by elephants and may have experienced greater elephant depredation in the earlier years.

Greater fire frequency and intensity may explain the higher rate of loss from 1967 to 1982, on the west side. Due to the strong east-west rainfall gradient, in normal years fire impact would be expected to be positively correlated to the amount of rainfall and the subsequent biomass production (Norton-Griffiths

1979). In the period from 1961 to 1967, when the greatest declines occurred and the least differences were seen between east and west, unusually high rainfall fell throughout the area. This high rainfall led to such high grass production throughout the Reserve that the effects of the normal rainfall gradient were probably swamped. With abundant dry grass fuel, fire could have affected both the east and west equally.

Trends in the Croton thickets paralleled those of the Acacia woodlands, over the past 30 years. Although some individual thickets, in both the east and west, did not experience fire effects to their peripheries, on average the area losses have been significant. There is generally an abrupt transition between vegetation types with little or no ecotone separating these thickets from open grasslands. Croton germination is most successful on the edge of thickets and less so in light gaps within the thickets but rarely in the shade under other trees or shrubs (personal observation). Thicket edges, however, are high risk growing sites because they are frequently subjected to grass fires and the trampling and grazing effects of herbivores (Norton-Griffiths 1979, Dublin, unpublished data). Under conditions of high fire incidence and herbivore use, growth and regeneration of thickets is very limited and area losses generally result.

The significant area losses found in the majority of thickets sampled in this study are contrary to the findings of Lamprey (1985). His findings did not reflect the general pattern of cover and area loss found in the Croton thickets within the Reserve boundaries in this study. Presumably, he

found no changes in the thickets he studied because of their location outside the Mara Game Reserve boundaries. Areas outside the Reserve have not experienced the same pressures as areas inside. Fire and elephants may have had little influence outside the Reserve, the former due to reduced fuel loads after heavy grazing by domestic stock and the latter due to the tendency of elephants actively to avoid human contact. Lamprey used a limited number of sampling points for his analysis and this may have limited his power to discriminate significant losses.

All thickets have suffered internal thinning, consistent with those reported by Norton-Griffiths (1979) in the northern Serengeti. In the Mara, this loss can be attributed primarily to utilization by elephants. Their movements and browsing within thickets results in extensive structural damage to the trees and shrubs. With the general loss of other woodland types, elephants now spend an inordinate proportion of their time within these thickets. This selective habitat preference is accentuated in the dry season when elephants move into thickets in search of shade and forage (Chapter 3).

The main body of the Croton thickets seem resistant to fire incursion, due to high soil moisture and sparse undergrowth (Langridge et al. 1970, Dublin, unpublished data). However, as thickets are opened, through the actions of elephants and other animals, they do become increasingly susceptible to the spread of fire through the grasses growing in these recently opened gaps (Norton-Griffiths 1979). My burning experiments showed that Croton bushes under 3m were frequently killed in hot fires

and those over 3m experienced a reduction in canopy and produced little or no seed crop in the next fruiting season. Elephant activity and subsequent fire damage probably accounts for the rapid loss of small thicket patches which have become isolated from the main body of the thickets. Area losses have been significantly lower in those thickets which have maintained their "structural integrity", as rectangular or circular configurations.

Further studies into the dynamics of these woodlands and thickets began in 1982, immediately following the last aerial photographic survey. Outside of the Reserve, overgrazing by cattle is now removing the standing crop so little or no burning is taking place and woody plants are becoming re-established (Lamprey 1985). This widespread "bush encroachment" provides prime habitat for tsetse flies, their numbers are increasing in areas adjacent to the Reserve and a high incidence of trypanosomiasis is occurring in cattle (Rossiter et al. 1983).

Inside the Reserve, similar conditions prevail. Wildebeest numbers have increased five-fold since the disappearance of rinderpest in the early 1960s (Sinclair 1973). Like cattle, the migratory wildebeest significantly reduce the standing crop of grasses (McNaughton 1976) and the frequency and severity of dry season fires are reduced. Norton-Griffiths (1979) predicted that under these conditions, the woodlands and thickets would re-establish themselves as they have outside the Reserve. Currently there is no evidence of woodland recovery in the Masai Mara Game Reserve.

Summary

The Serengeti-Mara ecosystem has experienced a transition from open grassland to dense woodland and back in less than 100 years. This chapter reconstructs the history of these changes through both qualitative and quantitative evidence. The changes in vegetation patterns are described and the biological factors implicated in these transitions are discussed.

At the turn of the century, the area was described by explorers and traders as an open grassland. However, by the 1930s this same area had become densely wooded. This transition is attributed to a concomitant reduction in man-made fires. In the late 1800s, wildlife and livestock numbers had been greatly reduced by the viral disease, rinderpest, and humans (dependent on these animals) had succumbed to starvation and disease on an epidemic scale. Elephant populations had been virtually eliminated by local hunters who supplied a flourishing ivory trade on the coast. With large herbivore populations at a low, conditions were ideal for the establishment of woodlands and thickets.

The areas set aside as the Serengeti National Park and the Masai Mara Game Reserve were characterized by dense woody vegetation in the 1930s and 1940s. However, by the 1950s these woodlands and thickets were already declining. An analysis of aerial photography flown in 1950, 1961, 1967, 1974, and 1982 showed the steady loss of cover in woodlands and thickets. The absolute and relative rates of woodland cover loss in the Mara Reserve were highest from 1961 to 1967, though declines continued into the 1980s. These declines coincided with an

increase in local elephant densities as well as an increase in fire frequency and severity. During this 30-year period, the mean cover density of Acacia woodlands dropped significantly throughout the Mara Reserve as did the mean cover density and area of Croton thickets.

Although burning rates are presently low and woodland recovery has been predicted under these conditions, there is currently no sign of a return to woodland vegetation in the Mara Game Reserve. The role of unprecedented numbers of resident elephants and migratory wildebeest in woodland dynamics of the Mara is still not fully understood.

CHAPTER 3. HABITAT SELECTION AND GROUP SIZE OF ELEPHANTS IN THE MASAI MARA GAME RESERVE

Introduction

The differential use of habitats by elephants can significantly alter the structure of affected plant communities (Curry-Lindahl 1968, Laws 1970, Field 1971, Thomson 1975). Utilization patterns are influenced by forage preference and availability (Leuthold and Sale 1973, Western and Lindsay 1985) as well as by external factors such as extreme weather conditions (Corfield 1973), human settlement and cultivation (Lamprey et al. 1967, Laws 1970, Lamprey 1985, Western and Lindsay 1985), and poaching activity (Douglas-Hamilton 1979). Over the past 25 years, these external factors have led to the concentration of elephants in protected refuges in many parts of their range. Today most of Africa's elephants survive in protected parks and reserves (Cumming and Jackson 1984). It is necessary to know the patterns of utilization of elephants in order to understand their impact on the habitats they occupy in parks and reserves, and to make decisions on local management.

The Masai Mara Game Reserve (the Mara) is a small area bordered on three sides by permanent settlements of the pastoral Maasai people and on the fourth by the Serengeti National Park of Tanzania. In the late 1970s the Serengeti provided elephants with a safe refuge from poaching pressure which was high at that time inside and to the north of the Mara Reserve in Kenya (I. Douglas-Hamilton, pers. comm.). Since about 1980, the situation has been reversed and poaching pressure has mounted on the

Serengeti side, thus cutting off this escape route to the south. In the mid-1980s, during this study, elephant seasonal movements in and out of the Reserve were severely curtailed, approximately 800-1100 elephants utilized the Mara year-round. This full-time residency produced noticeable browsing effects on the vegetation, significantly influencing the structure of many plant communities in the Reserve (Chapter 5).

This paper describes the seasonal changes in habitat selection and group size of elephants within the Mara. Habitat preferences are discussed as they relate to changes in feeding patterns between the seasons, while the details of elephant foraging are analyzed further in Chapter 4. The possible functions served by elephant aggregations are examined as well as the constraints placed on group size by food availability.

Study Area

The Masai Mara Game Reserve (34° 45' to 35° 30' E, 1° 15' to 1° 45' S) lies on Kenya's southwestern border with Tanzania and forms the northernmost extension of the 25,000 km^2 Serengeti-Mara ecosystem. In 1974, 1,530 km^2 were formally gazetted for the Game Reserve but, following recent boundary modifications, only 1,000 km^2 remains. The area to the north and east of the Mara is now permanently settled by pastoralists and large-scale agricultural schemes (Lamprey 1985). To the west, the Mara is bordered by the Siria (Esoit Oloololo) Escarpment, and to the south extends to the Serengeti National Park.

This small, protected area presently provides the essential dry season (June-October) range for many of the Serengeti migrants which include over one million wildebeest and over one hundred thousand zebras (Maddock 1979, Sinclair et al. 1985). These migrants are joined by thousands of Thomson's gazelles and wildebeest which move into the Mara from the dry, Loita plains to the north. At the start of the short rains, in late October, these migrants leave the Mara.

Climate

Rainfall in the Mara is bimodal, with short rains falling in November-December and long rains occurring in April-May (Figure 3.1). This pattern is influenced by the Intertropical Convergence Zone (ITCZ) which affects the East African region from Zimbabwe, in the south, to Sudan, in the north (Norton-Griffiths et al. 1975). This band of low pressure fronts follows the north and south movement of the sun with a lag of about 5 weeks. Driven by trade winds which converge in this area from both hemispheres, the system brings rain and cloudy weather. The ITCZ reaches its northern limit in late July and its southern extreme in late January, thus affecting weather patterns in the Mara twice each year.

The Mara also has a pronounced east-west rainfall gradient with the east side averaging approximately 800 mm/year and the west side approximately 1200 mm/year (Norton-Griffiths et al. 1975, Epp and Agatsiva 1980, Stelfox et al. 1986). The west

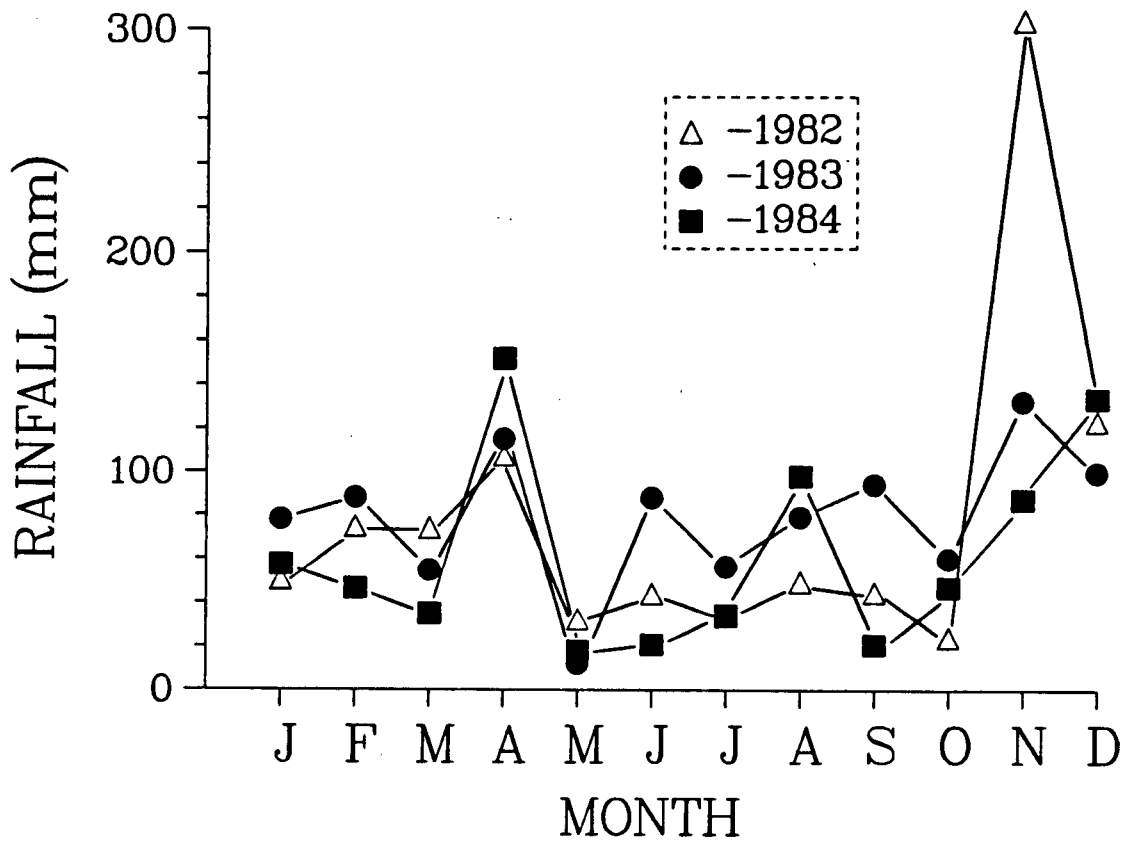

Figure 3.1. Monthly rainfall totals from Keekorok Lodge Meteorological Station located in the study area. The three study years 1982, 1983, and 1984 are presented.

side experiences much heavier rainfall because it is influenced by the convergence of the Lake Victoria and Mau Range weather systems and locally by the effects of the Siria Escarpment. This rainfall gradient results in a higher grass productivity on the west side of the Mara River compared to that on the east (A. Onyeanusi, pers. comm.).

Minimum and maximum daily temperatures in the Mara are constant throughout the year (Figure 3.2). The average daily maximum temperature for the years 1982-1984 was 28.1°C and the minimum was 14.8°C.

Plant Communities

In addition to the differences in annual rainfall patterns, east and west sides of the Mara are also characterized by differences in plant community composition (Taiti 1973, Epp and Agatsiva 1980, Lamprey 1985). The eastern portion of the Mara has more woody plant communities than the west, whereas the west is primarily open grassland with some woody vegetation along river courses and on hilltops. All trees and shrubs were classified according to Dale and Greenway (1961) and all grasses and herbs according to Edwards and Bogdan (1951).

The Ngama Hills, to the far east, are covered by *Combretum molle* - *Heeria reticulata* woodlands at the higher elevations, on the steeper slopes. These woodlands merge into relict or degraded thickets (referred to as *Acacia* - *Commiphora* woodlands by Lamprey (1985)) on the rocky, exposed slopes below. At the base of these hills, in the deeper soils, *Acacia gerrardii*

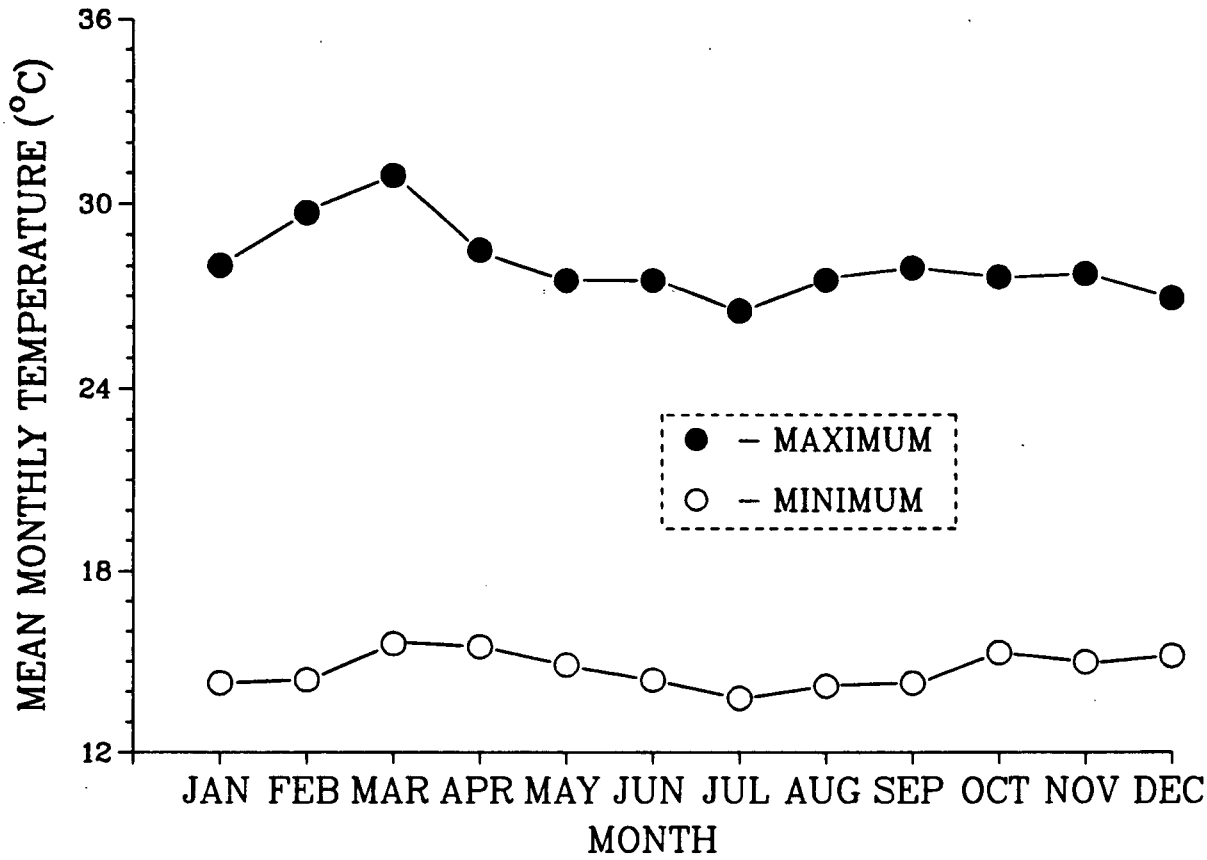

Figure 3.2. Mean monthly maximum and minimum temperatures from Keekorok Lodge Meteorological Station located in the study area. These maximum and minimum temperatures are averaged over the three study years 1982, 1983, and 1984.

woodlands form a mosaic with the relict thicket communities.

Relict thickets are widespread and diverse, containing seedlings and coppicing rootstocks of many species. These include: Acacia brevispica, A. gerrardii, A. hockii, A. senegal, Albizia amara, A. petersiana, Boscia angustifolia, Commiphora africana, C. trothae, Cordia ovalis, Dichrostachys cinerea, Grewia spp., Lippia javanica, Ocimum americanum, Ormocarpum trichocarpum, and Solanum incanum. Virtually all plants listed here are below 1 meter high. Standing dead trees are commonly seen in this community. Trump (1972) considered this community to be derived from Croton thickets, whereas Lamprey (1985) described it as a degraded phase of areas which had been thicker Acacia - Commiphora bushlands in the past. Large areas of the northern Serengeti now appear to be in an earlier phase of the degradation in this community with similar species composition but many more plants in the larger height classes.

The Acacia gerrardii woodlands occur as highly clumped cohort stands frequently found in association with the relict thickets mentioned above (Herlocker 1976a & b, Lamprey 1985). Although Trump (1972) did not distinguish this as a distinct community type, Lamprey (1985) documented the rapid increase of Acacia gerrardii woodlands in many areas of the Mara over the past decade. This proliferation is largely attributed to its fire-tolerance (Glover and Trump 1970, Spinage and Guinness 1972, Taiti 1973, Chapter 5). Individual plants persist through time by sprouting new shoots from underground rootstocks following burning or browsing. A variety of seedlings and root-coppicing species are commonly found in this community. These

include: Acacia senegal, Commiphora spp., Dichrostachys cinerea, and Ormocarpum trichocarpum which all remain under one meter in areas where burning is frequent or severe. The true age of individual trees or seedlings in this community, like those in relict thickets, is difficult to determine when their growth has been suppressed by browsing, trampling, and fires for indeterminate periods of time.

Ridge tops, small hills, and many seasonal drainage lines in both the eastern and western portions of the Mara are covered by Croton dichogamus thickets. Though Croton dominates the species composition, these discrete thicket clumps are still very diverse. While most species fall below the 4 - 5 meter Croton height, species such as Haplocelum foliolosum, Olea africana, Tarenna graveolens, and Teclea trichocarpa attain heights up to 6 and 7 meters. In the lower layer Acacia brevispica, Cordia ovalis, Grewia trichocarpa, Rhus natalensis, and Strychnos henningsii are found. This community is frequently marked by one or more adult Gardenia jovis-tonantis trees which occur 10 - 15 meters from the thicket edge and are never found inside the thickets proper. This community, referred to as "lion bush" by Darling (1960), is currently a primary source of shade, dry season browse, and cover for many animals in the Mara. This heavy use and repeated fires have led to internal thinning of the canopy cover and area loss in recent years (Chapter 2).

Balanites aegyptiaca woodlands occur only in the far western section of the Mara. This community, also referred to as Balanites - Acacia seyal woodland (Taiti 1973, Herlocker

1976b, Lamprey 1985), is prevalent on the open, grassy, park-like expanses of the Mara Triangle area. Taiti (1973) reported a decline in the density of Balanites stands in this area which Glover and Trump (1970) and Pellew (1981) attributed to heavy browsing by giraffe, still apparent today. The majority of remaining adult trees are well above the browsing reach of giraffes and elephants and regeneration may be limited both by seed predators (Lamprey et al. 1974, Pellew and Southgate 1984) and browsers (Belsky 1984, Chapter 5).

Also on the west side is a band of riverine forest which follows the course of the Mara River from Mara Serena north and occurs in small, discrete patches to the south along the river. This thick and diverse forest has been altered over the past 20 years. Though its borders have scarcely changed, its formerly closed, 15 - 20 meter canopy is now marked with large light gaps created by the loss of large trees. The causes for these losses are neither well-documented nor understood. However, it is believed that smaller trees may have been removed by elephants, while taller trees may have succumbed to disease or merely senesced. Elephants have also effectively thinned the understory of these forests leaving those species which are not highly preferred as food. The primary canopy trees are Albizia petersiana, Diospyros abyssinca, Euclea divinorum, and Warburgia ugandensis. Others include: Cassine buchananii, Ekebergia rueppelina, Syzygium cordatum, Pappea capensis, Phoenix reclinata and the occasional Podocarpus and Ficus trees. The understory has an equally diverse shrub component including: Carissa edulis, Chaetacme aristata, Croton dichogamus, Grewia

trichocarpa, Phyllanthus sepialis, Teclea trichocarpa, and Ziziphus mucronata.

The Mara is comprised of a combination of edaphically-derived and fire-induced grasslands dominated by the perennial grass, Themeda triandra, "red oat grass". Following the long rains other tall grasses such as Digitaria macroblephara, Hyparrhenia filipendula, Pennisetum mezianum, and Setaria sphacelata also flower in these grasslands. The overall grass productivity is high, ranging from 7,000 - 8,000 kg/ha/yr (Sinclair 1975, McNaughton 1979). The migratory zebra and wildebeest may remove 80 - 90 % of the standing crop biomass (McNaughton 1976, Stelfox et al. 1986) before returning south to the Serengeti. The short-cropped plains they leave behind then permit the growth and flowering of other, less competitve grasses such as Aristida adoensis, Eragrostis tenuifolia, E. racemosa, Harpachne schimperi, and Sporobolus stapfianus.

Geology and Hydrology

The hydrology of the Mara was described in detail by Glover (1966). The Mara River, the largest perennial river in the Serengeti-Mara ecosystem, drains the northern Serengeti and Mara region and flows into Lake Victoria some 100 km to the west. The Mara River originates in the Mau Range to the north and is fed by several major tributaries along its course. These include: the Talek River which arises in the Siana hills and Loita plains, the Olare Orok and Jagartiek watercourses which drain the Lemek valley to the north and join the Talek River

close to its confluence with the Mara River, and the Sand River which originates in the Loita Hills to the east and joins the Mara along the Kenya-Tanzania border. These rivers often flow year-round but in dry years become a series of small pools.

Williams (1964) has described the Mara region as an extensive peneplain comprised of metamorphosed pre-Cambrian sediments which have been modified over time by faulting, erosion, and volcanic activity. Soils in the area are mainly of volcanic origin and range from brown, sandy loams to black silt soils. Below this shallow layer of volcanic tuffs lies a basement system of gneisses, schists, and quartzites. The most significant relief in the area is the Siria Escarpment which forms the western boundary of the Mara and rises 100-300 meters above the plains below. Mean elevation in the Mara is approximately 1600 meters on the plains with the escarpment rising to 1900 meters.

Methods

Habitat selection by elephants was determined using two independent techniques. The first, total aerial counts, was used to distinguish selection only on a wet and dry season basis, whereas the second, monthly census circuits, allowed an analysis of habitat selection both by season and by sex.

Wet and Dry Season Total Counts of Elephants

Two wet season (late April 1984 and early May 1985) and one dry season total counts of elephants (late October 1984) were conducted in the northern Serengeti National Park, Tanzania, and the entire Masai Mara Game Reserve, Kenya. Herds were counted and mapped on all three flights but occurrence by habitat was recorded only on the October 1984 and May 1985 counts. Densely wooded areas were searched more intensively than open areas to correct for the relative visibility of elephants in different habitats.

To test the hypothesis that elephants were randomly distributed in the available habitats, the total number of elephants observed in each habitat type was compared to an expected frequency distribution. This expected frequency distribution was derived from a photo mosaic produced from an aerial survey of the area in early 1982 by the Kenya Rangelands Ecological Monitoring Unit. These photographs were at a scale of 1:50,000, large enough to distinguish habitat types on them. All habitat types distinguished on the photographs were checked on the ground using a 1:50,000 topographic map of the Reserve to relocate the areas. Thirty line transects were drawn on the photographic mosaic and analyzed for the proportions of different habitats. These proportions provided the theoretical random distribution for elephants if they showed no habitat selection (Table 3.1). For the purpose of analysis these expected distributions were converted to numbers, based on the observed sample size. Chi-square analysis was then used to compare the observed versus the expected numbers across all

Table 3.1. Percent of each habitat type measured from aerial photography of the Masai Mara Game Reserve flown in 1982 and monthly census circuits. These percentages were used to calculate the number of elephants to be expected in each habitat type under a random distribution.

HABITAT TYPE	GRASSLAND	RELICT THICKET	ACACIA WOODLAND	CROTON THICKET	BALANITES WOODLAND	SWAMP	OTHER
Aerial Photography (%)	41	29	8	6	4	4	8
Monthly Circuits (%)	43	34	4	6	7	0	6

habitat types.

Monthly Census Circuits

A 152 km. circuit was established within the Reserve. Initially, the entire circuit was driven and the habitat types which intersected this circuit were mapped to the nearest 0.1 km. (Table 3.1). The cumulative length of each habitat type was then expressed as a proportion of the total circuit length. From these proportions a random frequency distribution for elephants by habitat was produced. Using the observed sample sizes of elephants, this frequency distribution was then converted to numbers which allowed a comparison of expected with observed numbers of males and females in each habitat type for each month.

This circuit was driven once each month from November 1983 through May 1985. This period encompassed the 1983-84 wet season and the 1984 dry season. All elephants observed from the vehicle were recorded by age, sex, and the habitat in which they were seen. Visibility from the circuit was excellent and the sightability of elephants in the different habitats was assumed to be equal. Chi-square analysis was again used to compare the observed numbers of males and females by habitat type to the expected numbers for both the wet and dry seasons and to compare the sexes within each season.

Results

Habitat Selection

Seven hundred and eighty-five elephants were counted in the dry season and 912 in the wet season. Elephants surveyed during the aerial counts were not distributed randomly with regard to habitat type in either season (seasonal χ^2 values: wet = 126.3, dry = 347.7, d.f. = 6, $P<.001$). They showed distinct habitat preferences (Figure 3.3): in the wet season elephants selected grasslands, swamps, and *Croton* thickets more than expected by random use. In the dry season only *Croton* thickets were selected. All other habitats contained fewer elephants than expected.

These patterns were similar to those recorded on the monthly census circuits (Figures 3.4 and 3.5). Both sexes showed non-random use of habitats in both seasons (χ^2 values for males: wet = 11.5, number of males (n) = 111, $P<.05$, dry = 14.3, n = 25, $P<.025$, d.f. = 5, χ^2 values for females: wet = 13.9, n = 247, $P<.025$, dry = 38.9, n = 116, $P<.001$, d.f. = 5). Females selected grasslands and *Croton* thickets in the wet season whereas males selected grasslands and relict thickets. In the dry season males and females both chose *Croton* thickets and *Acacia* woodlands more than expected by random distribution. Males and females did not differ significantly in their distributions in either the wet (χ^2 = 8.0, d.f. = 5, n.s.) or dry season (χ^2 = 4.9, d.f. = 5, n.s.). Seasonal differences were significant for males (χ^2 = 33.2, d.f. = 5, $P<.001$) and females (χ^2 = 58.7, d.f. = 5, $P<.001$). Figures 3.4 and 3.5

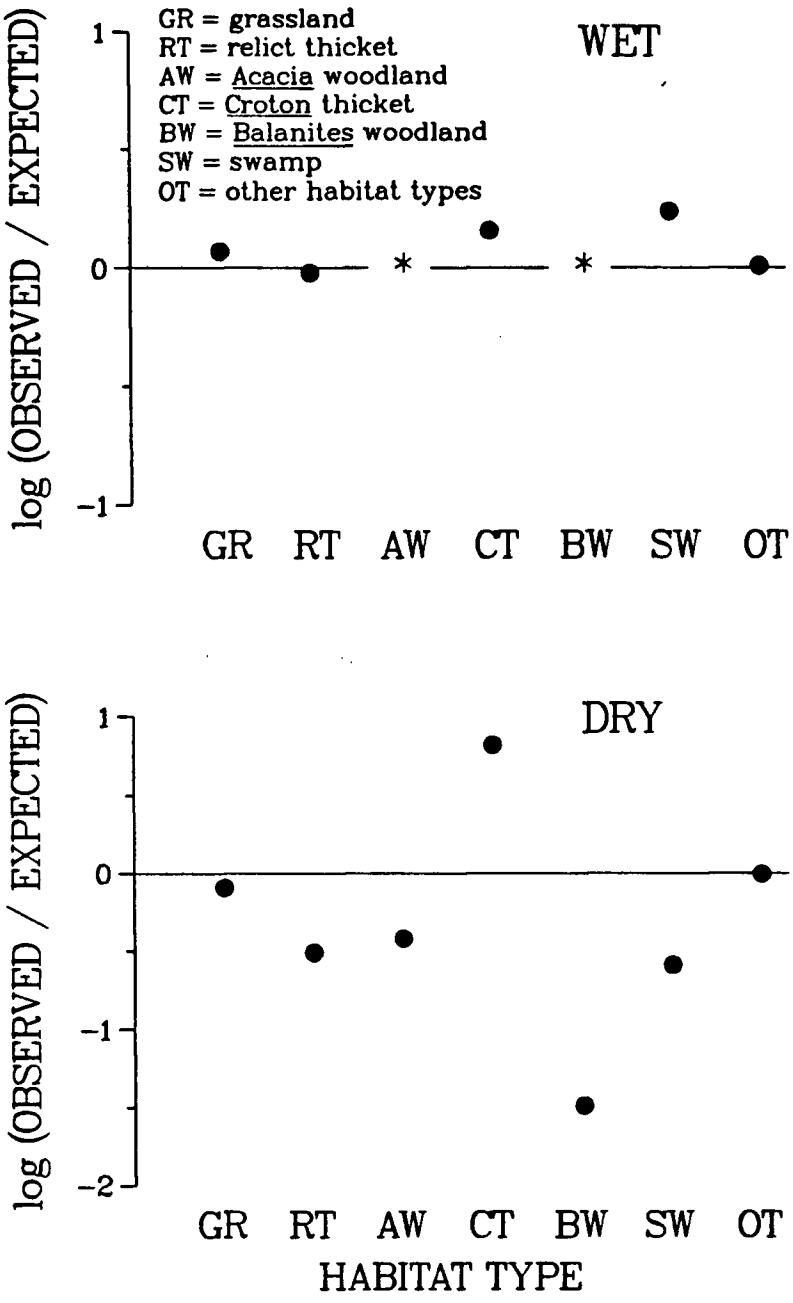

Figure 3.3. The habitat preferences of elephants in the Masai Mara Game Reserve in the wet and dry seasons. The expected values are calculated from a breakdown of the Reserve by habitat type using the 1982 total aerial photography. The observed numbers were taken from aerial counts flown in both seasons.

Notes : 1) Values greater than zero indicate habitats used more than expected if elephants were randomly distributed, while those values less than zero are habitats used less than expected and 2) * = those habitat types in which elephants were expected but were not seen.

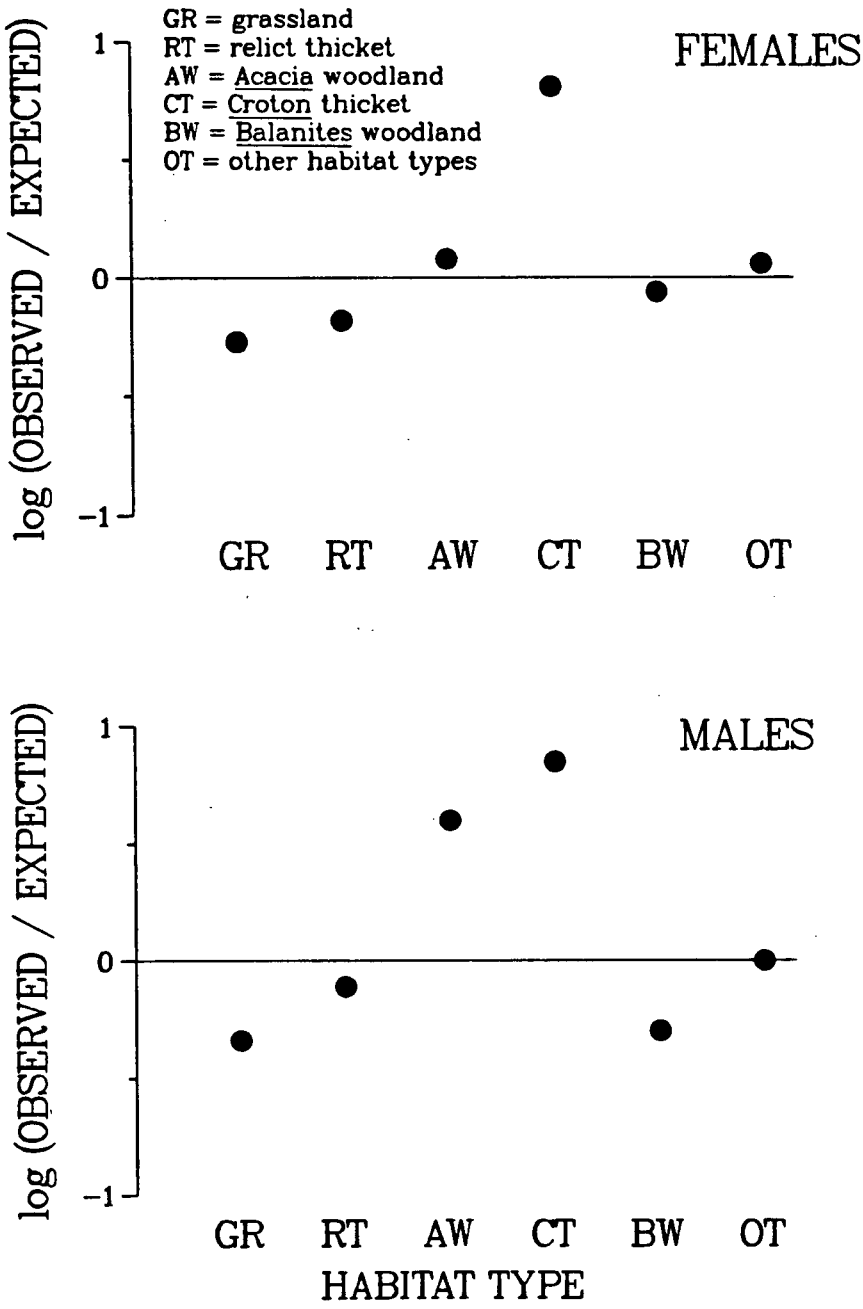

Figure 3.4. Dry season habitat preferences of male and female elephants in the Masai Mara Game Reserve. The expected values were calculated from a breakdown of the monthly circuit by habitat type. The observed numbers were derived from censuses driven on this circuit each month.

Note : Values greater than zero indicate habitats used more than expected if elephants were randomly distributed, while those values less than zero are habitats used less than expected.

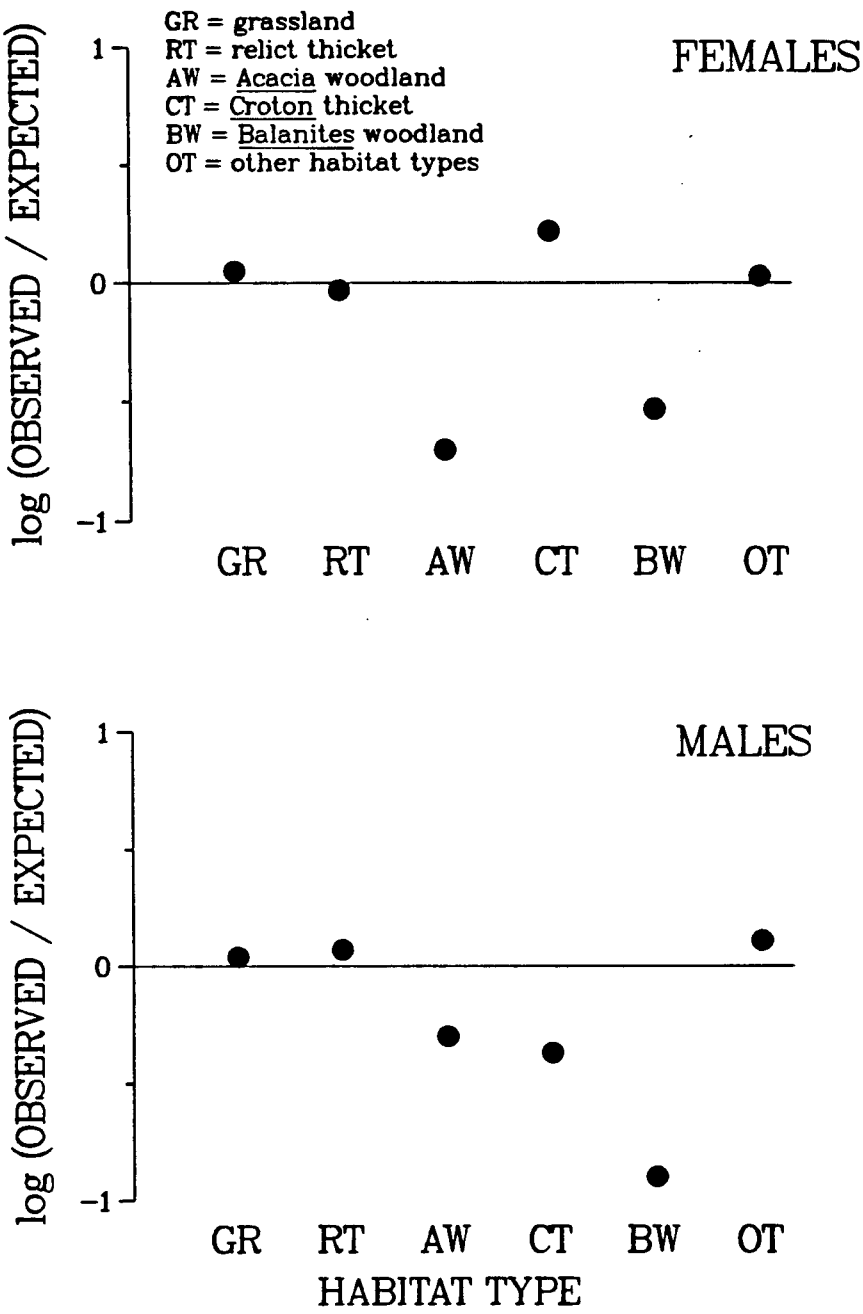

Figure 3.5. Wet season habitat preferences of male and female elephants in the Masai Mara Game Reserve. The expected values were calculated from a breakdown of the monthly circuit by habitat type. The observed numbers were derived from censuses driven on this circuit each month.

Note : Values greater than zero indicate habitats used more than expected if elephants were randomly distributed, while those values less than zero are habitats used less than expected.

illustrate the general pattern of these differences. Both males and females preferred grasslands during the wet season and Acacia woodlands and Croton thickets in the dry season.

Group Size

Seasonal variation in group size was calculated from count data. Average herd size in the wet season was 22.5 individuals/group and in the dry season it was 13.2 individuals/group. These averages differed significantly ($t = 2.84$, d.f. = 102, $P<.01$). However, even the larger wet season herds in the Mara never reached numbers such as the 700 recorded in seasonal aggregations in Tsavo (Laws 1969) or the 400 in Amboseli (Western and Lindsay 1985) National Parks. The largest recorded wet season aggregation was 158 animals and the largest dry season group only 40. Cow-calf herds which were accompanied by adult males averaged 14.8 individuals. Those herds with only females, subadults, and calves averaged 7.5 and all-bull groups averaged 1.9 on a year-round basis.

Mean group size did vary between seasons (Table 3.2). In general herds were larger in all habitat types in the wet season, whereas little difference occurred between habitats within a season. There was no significant correlation between average herd size and average numbers per habitat type for either the wet ($r_s = 0.43$, $n = 8$, n.s.) or dry season ($r_s = 0.54$, $n = 8$, n.s.). The largest groups were seen in relict thickets, Acacia woodlands, Euclea thickets and grasslands in the wet season.

Table 3.2 Average herd sizes for each habitat type in the wet and dry seasons. Number in parentheses is the number of herds observed in each habitat type during the monthly census circuits summed over the entire season.

HABITAT TYPE	GRASSLAND	RELICT THICKET	ACACIA WOODLAND	CROTON THICKET	SWAMP
Wet Season	11.6 (38)	11.8 (94)	14.5 (15)	10.2 (40)	9.2 (13)
Dry Season	8.9 (38)	7.4 (46)	6.0 (25)	9.6 (40)	7.8 (22)

Discussion

Habitat Selection

The Masai Mara Game Reserve has experienced vegetation changes in the past 30 years (Dublin 1984). The major result of these changes has been a significant reduction in *Acacia* woodlands and a thinning of riverine forests. At the present time the Mara is largely a wide, open grassland containing few surviving stands of *Acacia* woodland and patches of *Croton* thicket and high canopy riverine forests along the Mara River. Resident elephants which have been largely prevented from using their historical seasonal migration routes are now living in the Reserve year-round and their impacts on the remaining woodland habitats are pronounced (Chapter 5).

Elephants in the Mara ate woody species of all sorts, and their use of shrubs and trees increased significantly when dry conditions prevailed (Chapter 4). Facing an already reduced availability of browse forage and shade trees, elephants have begun concentrating their time within the *Croton* thickets. These thickets which are unique to the northern Serengeti and Mara region are discrete islands of bush sitting on hilltops and in river drainages scattered across the Reserve. With the significant loss of other woodland habitats in the Mara over the past three decades, these thickets now provide one of the last wooded refuges available to elephants. Here they are able to find shade, and also to forage on woody species, and herbs which thrive in the moist, shady conditions within these thickets. Consequently, damage to the internal structure of the *Croton*

thickets has become extensive. Many Croton bushes are shredded, their mainstems are split and broken. More preferred species within these thickets, such as Acacia brevispica, are browsed to within 10 cm of the ground (presumably this is the lower height limit of the elephants' foraging ability).

This constant use of Croton thickets for food and shade has opened large pathways through the vegetation. In subsequent rainy seasons, these light gaps grow thick swards of grass (Norton-Griffiths 1979). Most grazers avoid the risk of hidden predators in thickets so this grass is frequently left to dry and form litter in the herb layer. When fires occur in the Reserve these grass pathways through the thickets burn very hotly and destroy the trees and bushes along their boundaries. As the years progress these thickets become fragmented - like pies being cut and removed in ever smaller pieces.

Acacia woodlands have been subjected to similar pressures, primarily from elephant bulls, but occasionally from cow-calf groups as well. Most Acacia woodlands in the Mara are comprised of trees which are too small to be used for shade. However, in unusually dry seasons, bulls spend a lot of time in these woodlands and feed heavily on the trees (Lindsay 1982, Western and Lindsay 1985, Chapter 4 and 5). In the drought of 1984, a herd of approximately 6 bull elephants visited a 2 sq. km. mature Acacia stand near Emarti. Within 24 hours they had left 34% of the trees dead or fatally damaged and another 22% with many broken branches. Other stands experienced similar damage during this very dry period. Elephant damage to riverine forests was similar, all low-growing vegetation was removed.

Now these forests are comprised primarily of tall canopy trees whose leaves are well out of the reach of elephants. Many trees are beginning to die. Although the cause of these losses is not certain they are most likely due to disease or old age. But the effects of trampling by large mammals may also be implicated in the compaction of soil and the destruction of fine surface roots. Newly-formed light gaps left by fallen canopy trees would provide a good opportunity for forest regeneration but will probably suffer heavy pressure from elephant browsing.

Elephants do utilize the grasslands in the Reserve. Their preferred species is Cynodon dactylon, a grass which grows in low-lying areas, often inundated by surface water. The Mara grasslands, however, are primarily composed of Themeda triandra. The Cynodon areas are limited in extent and are also used by the migratory wildebeest and zebra after the initial standing crop of Themeda has been removed. The sheer number of wildebeest present during the dry season probably displaces elephants from Cynodon areas. Dry conditions alone can lead to extensive use of woodland areas by elephants and subsequent extensive damage. The additional factor of the competing migratory wildebeest during the dry season exacerbates the situation (Chapter 4).

Mara elephants may select habitats based on the availability of preferred forage types. Their foraging habits, as determined through direct observation, indicate that they feed on grasses and herbs immediately following the rains and switch to a browse diet in the dry season when a decline in the quality and quantity of herbaceous species occurs. The distribution of these forage types in different habitats

probably dictates the patterns of habitat selection between seasons. This is consistent with the findings of Leuthold and Sale (1973), Leuthold (1977a), and Western and Lindsay (1985) who found that seasonal movements were largely determined by the distribution of forage quality and quantity for elephants in Tsavo and Amboseli National Parks in Kenya. What is not quantitatively established for Mara elephants is whether their choice of habitats is most significantly correlated with forage quantity, forage quality, some combination of the two factors, or other factors such as disturbance.

During the rains when forage of all types was abundant, Mara elephants were primarily grazers, like those in other populations (Field 1971, Field and Ross 1976, Guy 1976, Barnes 1982, Western and Lindsay 1985). Mara elephants selected open grasslands, swamps, and Croton thickets during the wet season. This is consistent with the idea that forage quality is the determining factor in habitat choice because the new grasses and sprouting seedlings growing in these areas are highly nutritious. Although new browse leaves may have higher absolute crude protein levels than new grasses (Weinmann 1959, Dougall 1963, Dougall and Glover 1964, Dougall et al. 1964, Field and Ross 1976, McNaughton et al. 1985), they may also contain high levels of secondary compounds such as tannins which may interfere with feeding (Coley 1983, Sukumar 1985). For the most part, the habitats selected during the wet season were dominated by grasses.

Unlike Amboseli elephants (Lindsay 1982, Poole 1982), Mara elephants followed a dry season foraging pattern more like that

reported for elephants in other seasonal areas such as Queen Elizabeth and Kidepo Valley National Parks, Uganda (Field 1971, Field and Ross 1976), Sengwa Wildlife Research Area, Zimbabwe (Guy 1976), and Ruaha National Park, Tanzania (Barnes 1982). They switched to a predominantly browse diet in the dry season. Dougall et al. (1964), Field (1971) and Barnes (1982) pointed out that woody species maintained higher crude protein levels relative to grasses during water-limited times. The nutritional quality of grasses declines rapidly as they begin to age in the dry season. Habitat choices in the dry season may reflect these forage preferences. Elephants of both sexes were observed utilizing Croton thickets and Acacia woodlands.

Leuthold and Sale (1973) suggested that elephant habitat selection in Tsavo National Park was mostly limited by the quantity of food available and may be constrained further by the distribution of permanent water sources which are critical to their survival, particularly during the dry season (Corfield 1973). The findings of Western and Lindsay (1985) in Amboseli partially supported this idea. In the dry season, Amboseli elephants utilized the swamps most heavily. These swamps were the lowest in crude protein (quality) but the highest in forage biomass (quantity). However, elephants used the bushed-grassland habitat to a similar extent in the dry season. This bushed-grassland habitat was lowest in available forage biomass but significantly higher than swamps in available crude protein. From this evidence and my findings in the Mara, it seems likely that elephants may select primarily on the basis of forage quality but may be limited in their choice by the amount of food

available within their range of movement. The relative importance of quality versus quantity may be mediated by local elephant densities. In areas of high density, elephants may be more restricted by the absolute quantity of available food, regardless of the nutritional value of the type of forage eaten or habitat in which it is found. In the Mara, where elephant densities are not considered to be high, their choice of habitats may be influenced to a greater extent by forage quality than quantity as they appear to be in Amboseli, where local densities are much higher.

Group Size

It is possible that elephants form aggregations as a direct consequence of the numbers in a habitat (i.e. preferred habitats support higher numbers and densities and, therefore, larger herd sizes are found). However, the data do not support this hypothesis. In fact, there was no correlation between elephant numbers in specific habitats, and average group size in these same habitats. Group size appeared to be determined by factors other than random aggregations based on habitat preference.

Variation in mean herd size has been reported in other studies (Table 3.3), but the actual determinants of group size are not fully understood. In some areas, poaching activity has led to large aggregations which did not show seasonal changes (Laws et al. 1975, Douglas-Hamilton and Hillman 1981). But, in general, average herd size does seem to be correlated with season, larger herds form in the wet season when availability of

Table 3.3. Average herd sizes reported for a variety of African elephant populations. Table adapted from Laws (1969).

LOCATION	AVERAGE GROUP SIZE	SOURCE
Tsavo National Park, Kenya	13.5	Glover (1963)
	13.0	Watson and Bell (1969)
Amboseli National Park, Kenya	25.0	Western and Lindsay (1985)
Murchison Falls National Park, Uganda	12.1	Buechner et al. (1963)
	12.0	Laws et al. (1975)
Queen Elizabeth National Park, Uganda	5.9	Laws and Parker (1968)
Luangwa Valley, Zambia	3.9	Laws and Parker (1968)
Serengeti National Park, Tanzania (north)	52.0	Watson and Bell (1969)
	54.5	Dublin (unpubl. data)
Serengeti National Park, Tanzania (south)	19.0	Watson and Bell (1969)
Masai Mara Game Reserve, Kenya (wet season)	22.5	Dublin (unpubl. data)
Masai Mara Game Reserve, Kenya (dry season)	13.2	Dublin (unpubl. data)

preferred forage is greater. The variation in average herd sizes recorded for different elephant populations could, therefore, be the result of counts done in different seasons or on populations of elephants experiencing different levels of hunting pressure.

Seasonal variation in herd size has also been attributed to the seasonality of mating and birth peaks. Estrus and, hence, mating occurs during or slightly after the peak of the long rains (Hanks 1969, Dublin 1983, Moss 1983, Western and Lindsay 1985). At this time males temporarily join cow-calf herds to gain access to estrous females. Births then follow a 22-month gestation and occur just before or during the rains (Hanks 1969, Weyerhaeuser 1982). Mara elephant herds may show a similar pattern; the average size of herds containing adult males was considerably larger than exclusively cow-calf groups, and the average group size overall, was higher in the wet season.

Douglas-Hamilton (1972), Moss (1981), Moss and Poole (1983), and Western and Lindsay (1985) have all suggested that social benefits may provide a strong basis for herd formation. For example, elephants may aggregate on a periodic basis as a means of maintaining and strengthening bonds or establishing dominance hierarchies within kin groups or merely among individuals who may interact throughout their long lives (Moss 1981, S. Andelman, pers. comm.). Recent findings by K. Payne (unpubl. data) suggest that the low frequency sounds associated with certain behavioral patterns among elephants may actually be exchanges of information on levels previously unrecognized. Periodic aggregations would provide an opportunity for such

exchanges between individuals and herds. Laws et al. (1975) cited predation on elephants as a basis for aggregation. Western and Lindsay (1985) discussed the possible foraging benefits which larger groups may accrue through the exchange of information or through facilitation but emphasized that there is currently no hard evidence to support these ideas. Untangling the relative contributions of various factors to group formation and tenure is a difficult task. Larger herds seem to be desirable for a variety of reasons but are possible only when local food supplies are not limited. In an animal the size of an elephant, this condition could restrict the formation of large groups to the rainy season only.

Summary

In summary, Mara elephants fit the general pattern of habitat selection and group formation observed in other African elephant populations. Both sexes chose habitat types which produced large quantities of nutritious grasses during the wet season, and both switched to other habitats which provided browse vegetation in the dry season. In addition, average group size was larger, in virtually all habitats, in the wet season than in the dry. Seasonal differences in herd size were not the result of random aggregations forming in preferred habitats, but were more likely an indirect result of bulls joining cow-calf herds to breed during the rains and herds congregating, when food was not limited, to interact, to determine dominance hierarchies, and to re-establish bonds.

Before any progress can be made on a site-specific course

of management, it is essential that the local patterns of elephant habitat utilization and the potential impacts of elephants on these habitats be fully understood. The actual magnitude of their effects may be modified by local conditions such as weather, poaching activity, or the accessibility of seasonal migratory routes to allow dispersal and avoid overutilization of habitats. In future, these and other factors must be taken into account when formulating plans for the management of elephant populations and plant communities in protected areas.

CHAPTER 4. FEEDING ECOLOGY OF ELEPHANTS IN THE MASAI MARA GAME RESERVE

Introduction

The past 30 years have been a time of major change in the woodland habitats of east, central, and southern Africa. In many parks and reserves, woodlands have declined. Theoretical explanations for these changes have led to a great deal of controversy and much speculation (Pienaar 1969, Laws 1970, Caughley 1976). However, many researchers agree that the exponential growth of human populations during this century is linked to woodland loss. The subsequent expansion of cultivation and settlement has resulted in both concentration of elephants into protected areas, and an increase in frequency of human-induced fires.

Both fire and elephants have played roles in the documented woodland losses, though their relative contribution is in debate. Buss (1961), Lawton and Gough (1970), and Norton-Griffiths (1979) have supported the idea that fire played the primary role in woodland loss, but most research supports the converse. Elephants are widely thought to be the primary initiators of woodland change, with fires acting to maintain the vegetation in a grassland phase thereafter (Eggeling 1947, Buechner and Dawkins 1961, Brooks and Buss 1962, Lamprey *et al.* 1967, Laws 1969, Wing and Buss 1970, Field 1971, Spence and Angus 1971, Harrington and Ross 1974, Laws *et al.* 1975, Thomson 1975, Guy 1976, Field and Ross 1976, Barnes 1982, Smart et al. 1985). The potential synergistic effects of fire and elephants

have not yet been analysed.

Over the past 30 years, woodlands and thickets in the Serengeti-Mara have been disappearing. Similar events have taken place over eastern, southern, and central Africa, for example in Tsavo National Park, Kenya (Laws 1969, Parker 1983), Ruaha (Savidge 1968, Barnes 1982, 1983) and Lake Manyara (Weyerhaeuser 1982) National Parks, Tanzania, Queen Elizabeth and Murchison Falls National Parks, Uganda (Buss 1961, Buechner and Dawkins 1961, Brooks and Buss 1962, Buechner et al. 1963, Buss and Savidge 1966, Laws and Parker 1968, Field and Laws 1970, Field 1971, Laws et al. 1975, Field and Ross 1976) and the Sengwa Research Area, Zimbabwe (Anderson and Walker 1974, Guy 1976, 1981). These changes have coincided with intensive human settlement on park boundaries and subsequent concentration of elephants from peripheral areas into habitats unable to support their numbers (Anderson 1973, Guy 1976, Dublin and Douglas-Hamilton, in press). At the same time, fire frequency has increased due to both human activity and climatic factors (Langridge et al. 1970, Kurji 1976, Norton-Griffiths 1979). The separate and synergistic effects of man-induced fire and elephants have been implicated in these habitat changes, but, until recently, lack of data has prevented an accurate assessment of their relative importance.

In this study, elephant feeding behaviour was observed in conjunction with controlled experiments using browsing exclosures and varying fire regimes. I consider the effects of these experimental fires and mammalian herbivores in the structuring of woodland communities (Chapter 5). Direct

observation of free-ranging elephants covered two and a half years (1982-1985) in the Masai Mara Game Reserve where elephants were accustomed to humans and vehicles. I collected data on male and female elephants without disturbing their normal activities. This study investigated how recent increases in the resident elephant population may be impacting vegetation in the Reserve and, whether current elephant feeding patterns are playing a role in the inhibition of woodland regeneration. This chapter describes: a) seasonal and sexual differences in diet composition; b) absolute and relative diet diversity; c) average length of foraging bouts; and d) the characteristics of plants in the diet.

Methods

Observations covered three dry seasons (June - October 1982, 1983, and 1984) and two wet seasons (November - May 1982-83 and 1983-84). Data for the wet season 1983-84 and the 1984 dry season are more complete than the previous seasons due to the loss of some original data. More than 500 observation periods of bulls and more than 1,000 of females were recorded during the study (Table 4.1). Each observation period consisted of an uninterrupted block of 15 - 30 minutes with each focal animal. By choosing a different individual for each observation period rather than following one individual all day, I avoided the potential problem of idiosyncratic elephant feeding patterns. Short observation periods also allowed more different individuals to be observed in any given month.

Table 4.1. Study periods, number of focal animals, seasonal and mean monthly rainfall.

SEASON	FOCAL ANIMALS		TOTAL RAINFALL	MEAN MONTHLY
	M	F	(mm)	(mm)
Dry 1982	75	156	196.6	39.4
Dry 1983	104	221	378.1	75.6
Dry 1984	82	175	221.3	44.3
Wet 1982-83	152	289	775.7	110.8
Wet 1983-84	127	230	540.9	77.3

Focal elephants were observed from a distance not exceeding 25 meters. When necessary 10' x 40' Leitz binoculars were used for forage species identification. I observed elephants from a vehicle in open, exposed areas, but I observed on foot when elephants were in thick bush or woodland areas. Focal individuals were chosen on a daily basis from herds that were located from high vantage points or along random transects driven through the Reserve in the early morning. No individuals were sampled more than once per month though many resident individuals were observed repeatedly throughout the year. Bulls were more mobile than cow-calf herds and some individuals disappeared entirely for months at a time, while others remained in the Reserve year-round. Each month I attempted to sample equal numbers of both sexes, however, this was not always possible because the adult sex ratio was highly skewed towards females throughout the year.

The period from November through May is referred to as the wet season, while June through October constitutes the dry season. This is consistent with other analyses for the Serengeti-Mara system (Sinclair and Norton-Griffiths 1979). Diet choice was examined for differences between sexes within each season, between seasons within each sex and overall differences throughout the year.

The following components of foraging were analyzed: diet composition, absolute diet diversity, relative diet diversity or diet evenness, average duration of foraging bouts, and the characteristics of plants in the diet. Arcsine transformations were performed on percentage data where necessary. All

statistical analyses were performed using techniques described by Zar (1984).

Absolute dietary diversity is the total number of plant species included in the observed diets in a given month or season. Relative diversity of diet or diet "evenness", J, expresses the observed diversity as a proportion of the maximum possible diversity in a given data set, p_i is the proportion of the diet devoted to each forage species utilized, k is the number of distinguishable forage species consumed. This index is a variation on the Shannon-Wiener diversity index (Zar 1984) and is referred to as relative diversity or evenness by Pielou (1966). This relative diversity index was used by Barnes (1982) in a similar way for analyzing elephant diets. In this study I have used the same formula which is defined by Zar (1984) as:

$$J = -\sum_{i=1}^{k} p_i * \log(p_i)/\log(k)$$

Higher values of J indicate more even foraging among the selected plant species. Because k is generally an underestimate of the actual number of species in the diet, J will overestimate diet "evenness". However, it is a useful index for comparing general foraging patterns of males and females in the two seasons.

The length of a feeding bout was the amount of time a focal animal ate a given forage type before switching to another. It was assumed that the length of a feeding bout was positively correlated to the total amount of forage consumed in a given bout. Average feeding bouts were calculated for males and

females in each month and each season. Then average feeding bouts were summed for each forage type and divided by the number of individual bouts observed.

Forage use, with regard to the food plant's phenological condition, plant part eaten, and the height at which foraging took place were recorded. Plant phenological conditions included: leafless, dry leaves, green leaves, budding, leaves with flowers, and leaves with fruits. Plant parts were broken into the categories: roots, leaves and roots, leaves and shoots, branches and twigs, leaves only and bark only. Foraging heights were recorded as : 0 - 1m, 1 - 2m, 2 - 3m, and above 3m.

Results

Feeding differences between males and females

Diet composition by forage type

Seasonal diet composition differed between males and females. The frequency distributions of bull and cow diets over the five forage types (grasses, herbs, shrubs, trees, and tree seedlings) varied in all dry and wet seasons sampled (Figures 4.1 and 4.2).

The sources of these seasonal diet differences became apparent when seasonal means for each forage type (Figure 4.2) were compared for the 1983-84 data (Table 4.2). In the wet season, females devoted significantly more time to foraging on shrubs, while males ate more tree seedlings and trees. Males

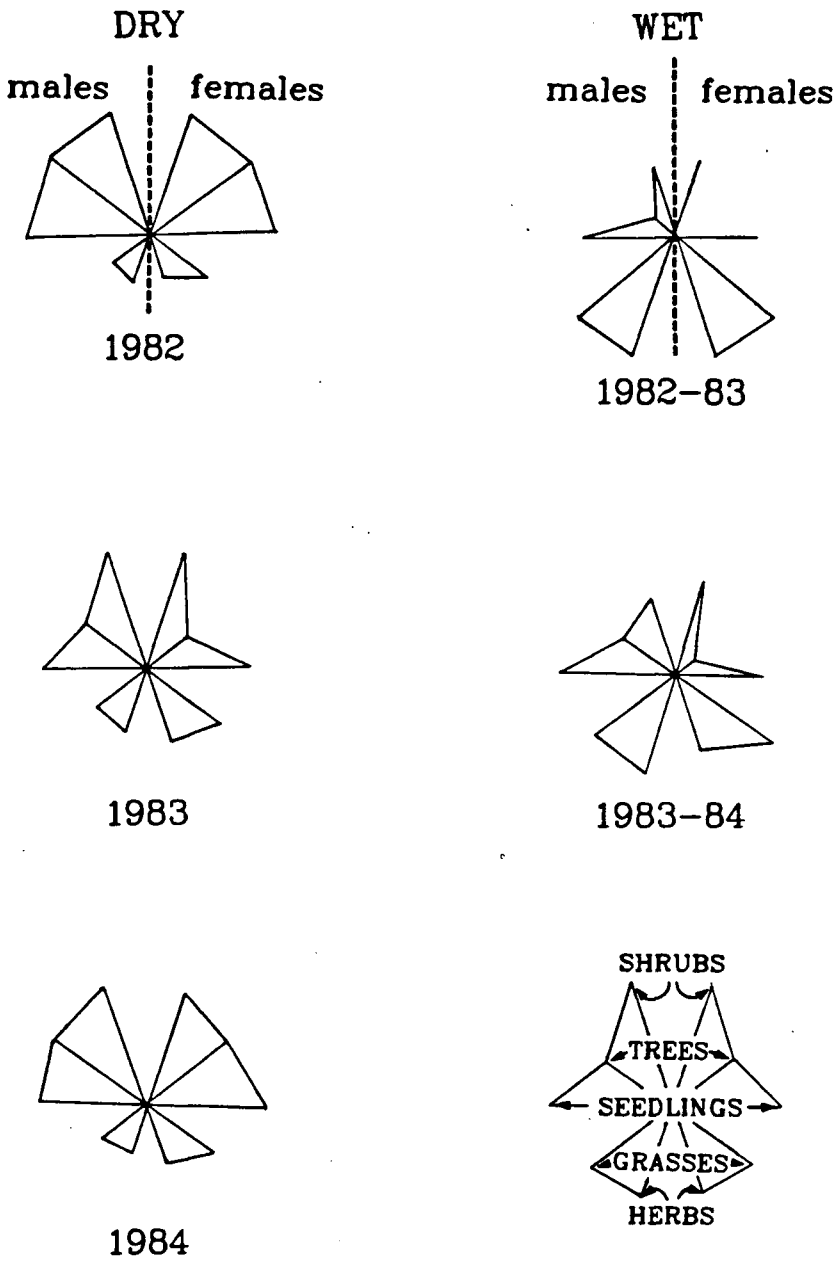

Figure 4.1. Mean percentage diet composition by forage type for females and males. The data covers three dry seasons (1982, 1983, 1984) and two wet seasons (1982-83 and 1983-84). The stars compare feeding patterns both between sexes and seasons.

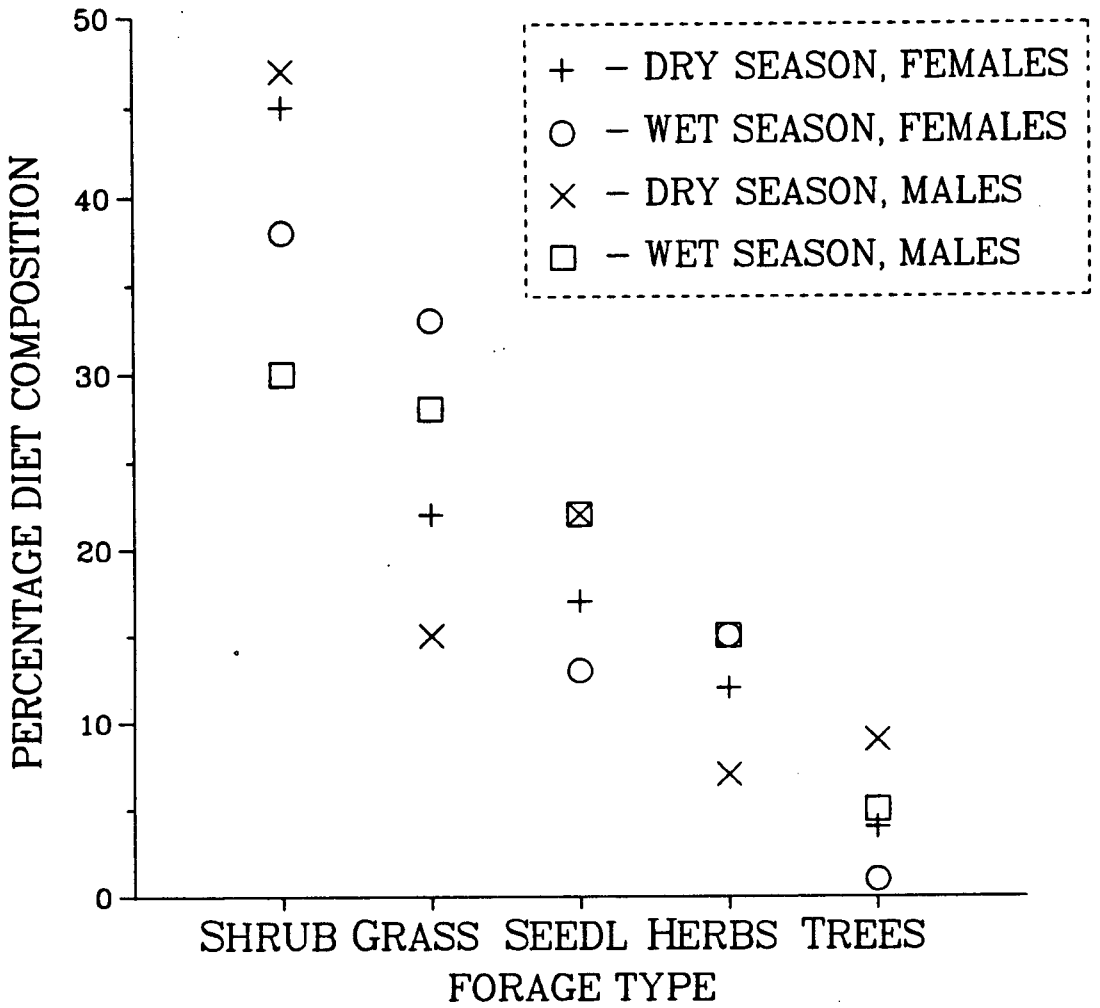

Figure 4.2. Mean percentage diet composition by forage type for females and males in the 1983-84 wet season and the 1984 dry season.

Table 4.2. Mean diet composition comparisons between sexes for all forage types. Tukey's multiple comparison tests (with unequal sample sizes) were performed. Significance levels are presented. (Dry season focal "n" = 257; wet season = 357).

FORAGE TYPE	SEASON	MEAN % FEMALES	MEAN % MALES	SIGNIFICANCE LEVEL
GRASSES	dry	22	15	n.s.
	wet	33	28	n.s.
HERBS	dry	12	7	0.01
	wet	15	15	n.s.
SHRUBS	dry	45	47	n.s.
	wet	38	30	0.01
TREES	dry	4	9	0.05
	wet	1	5	0.05
SEEDLINGS	dry	17	22	0.05
	wet	13	22	0.01

and females did not feed significantly differently on grasses in the wet season, the dry season as a whole, or the late dry season from August through October. At the height of the long rains, April and May, new grasses were highly preferred by both sexes. However, in the early dry season, June and July, females spent a significantly greater proportion of their time feeding on grasses than did males ($t = 2.37$, $d.f. = 99$, $P<.02$). Females also spent more time feeding on herbs in the dry season while males devoted more time to eating tree seedlings and trees.

In general, overall male diets were significantly higher in browse components (shrubs, tree seedlings, and trees) than overall female diets ($t = 2.45$, $d.f. = 612$, $P<.025$), this difference was seen in both the wet ($t = 2.09$, $d.f. = 355$, $P<.05$) and dry ($t = 2.67$, $d.f. = 255$, $P<.01$) seasons. Conversely, females utilized the herbaceous species (grasses and herbs) significantly more throughout the year ($t = 2.35$, $d.f. = 612$, $P<.02$) and particularly during the dry season ($t = 3.03$, $d.f. = 255$, $P<.01$). Grasses in the diet contributed more to this observed difference than herbs.

Among the grasses, Cynodon dactylon was the most important species in the diet throughout the year. Themeda triandra was chosen in a highly seasonal manner - during and immediately following the rains. Themeda was eaten more frequently when wildebeest were not present in the Reserve, that is during the short rains of November and December and during the long rains of April and May, just before the migrants arrived. Becium sp. was the preferred herb but more than a dozen other species were

eaten during their short periods of availability. Among the shrub species preferred were Acacia brevispica, Croton dichogamus, Euclea divornum, and Solanum incanum. Trees and seedlings of Acacia gerrardii, Dichrostachys cinerea, and Ormocarpum trichocarpum were important in elephant diets throughout the year.

Diet diversity

The absolute diversity of plant species contributing to elephant diets changed throughout the year. Identification of shrubs, trees, and tree seedlings to species was possible in all seasons but grasses could only be identified to genera during the dry season. Figure 4.3 presents the absolute number of plant species in the diets, across all forage types. Although this is an underestimate of dietary components, significant differences in elephant food choices were still detectable.

To test if diet diversity was independent of observation time the number of plant species recorded in the diets was compared with the total observation time for each month. No significant correlation was found between observation time and the number of species eaten for females (Figure 4.4, Spearman rank correlation, $r_s = 0.22$, $n = 12$, n.s.) or males (Figure 4.5, $r_s = 0.07$, $n = 12$, n.s.). From this, I assumed that absolute diet diversity was an independent measure of diet preference and not a function of the amount of time the elephants were observed in a given month. Females maintained a significantly broader diet than males across the year and in both the dry and wet seasons (Table 4.3).

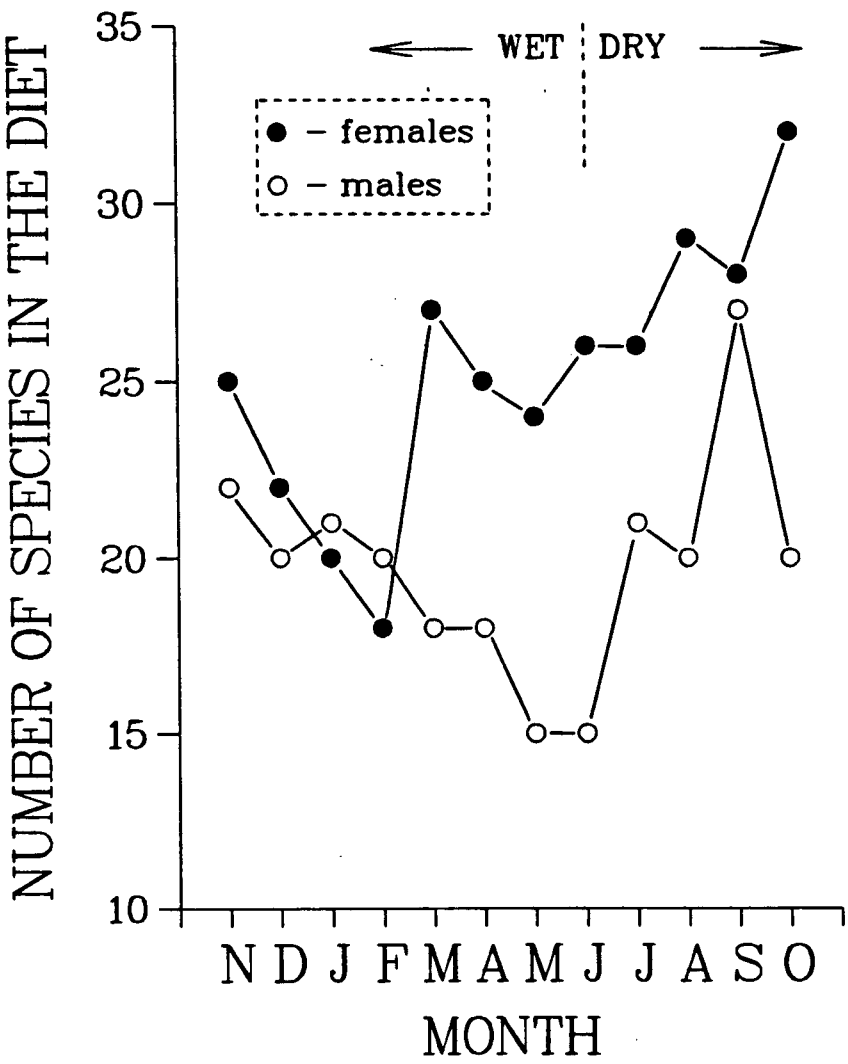

Figure 4.3. Absolute diet diversity (number of species in the diet each month) for females and males in 1983-84.

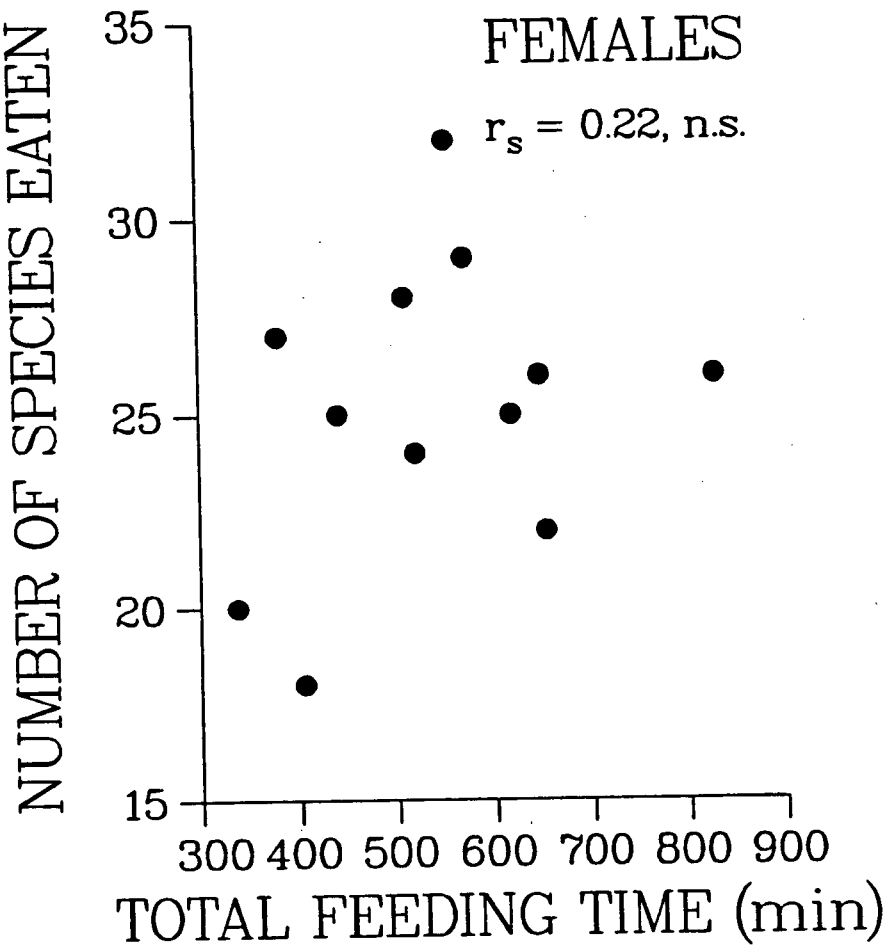

Figure 4.4. The number of species eaten versus the total feeding time observed in each month for female elephants.

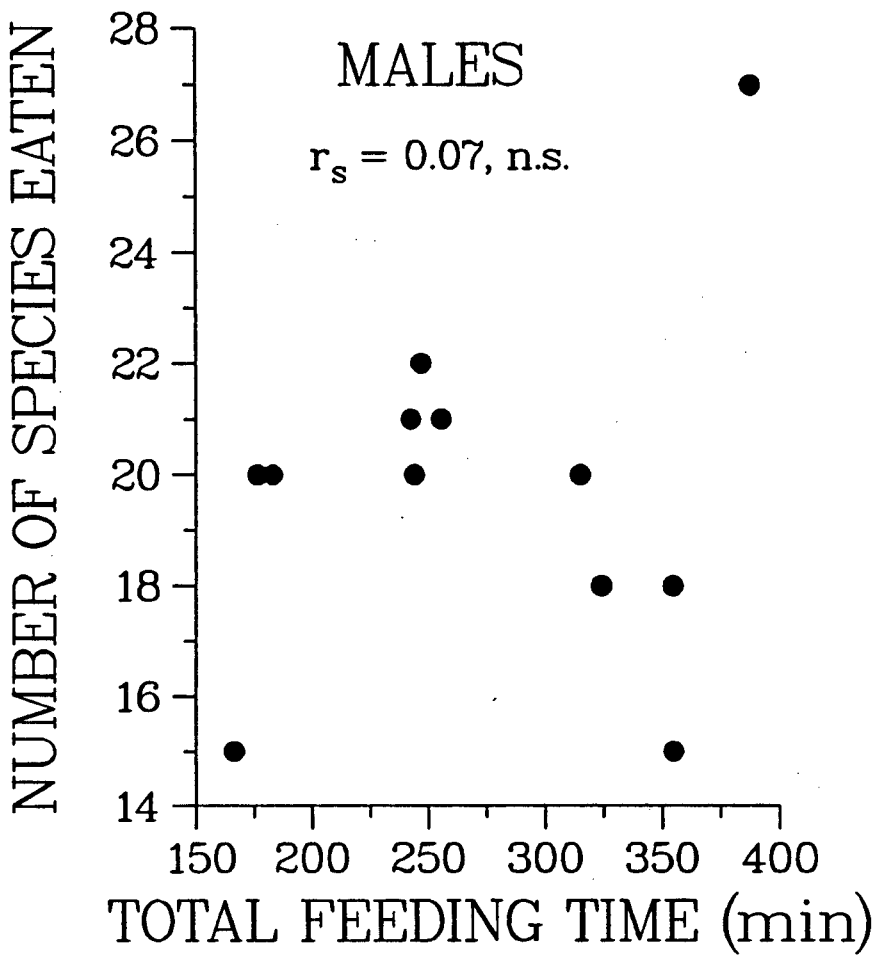

Figure 4.5. The number of species eaten versus the total feeding time observed in each month for male elephants.

Table 4.3. Absolute diet diversity comparison between males and females by season.

	d.f.	FEMALES	MALES	t-value	p-value
Annual mean	22	25.17	19.75	3.75	0.01
Dry season	8	28.20	20.60	3.43	0.01
Wet season	12	23.00	19.14	2.59	0.05

Relative diet diversity or "evenness" relates the distribution of diet choices to the numbers of different choices available (Figure 4.6). No significant differences were found between males and females across the year or in the wet and dry seasons (Table 4.4). On average females and males distributed their time evenly among all species in all forage types. However, in the months of November and April relative diet diversity fell below .65 for males and .50 for females. These months came at the end of long dry spells when forage quality and quantity was low and forage choice was reduced. The low diet "evenness" indicates that elephants fed disproportionately on a few preferred species in those two months. When relative dietary diversity was analyzed for browse species alone there were significant differences between males and females (Figure 4.7).

Averaged across the year, relative browse diets of males were distributed more evenly than those of females ($t = 2.55$, $d.f. = 22$, $P<.02$). This difference occurred in the wet season when males chose a significantly more even diet than females ($t = 3.51$, $d.f. = 12$, $P<.01$). In the dry season, males and females had similar browsing patterns ($t = 0.12$, $d.f. = 8$, n.s.). The lower relative diversity of browse species throughout the year in the diets of females indicated that they continually spent a disproportionate amount of their browsing time on a small number of highly preferred species. Males, however, demonstrated seasonal changes in the "evenness" of their browsing. In the dry season, they also selected a few preferred species to browse. However, in the wet season, when

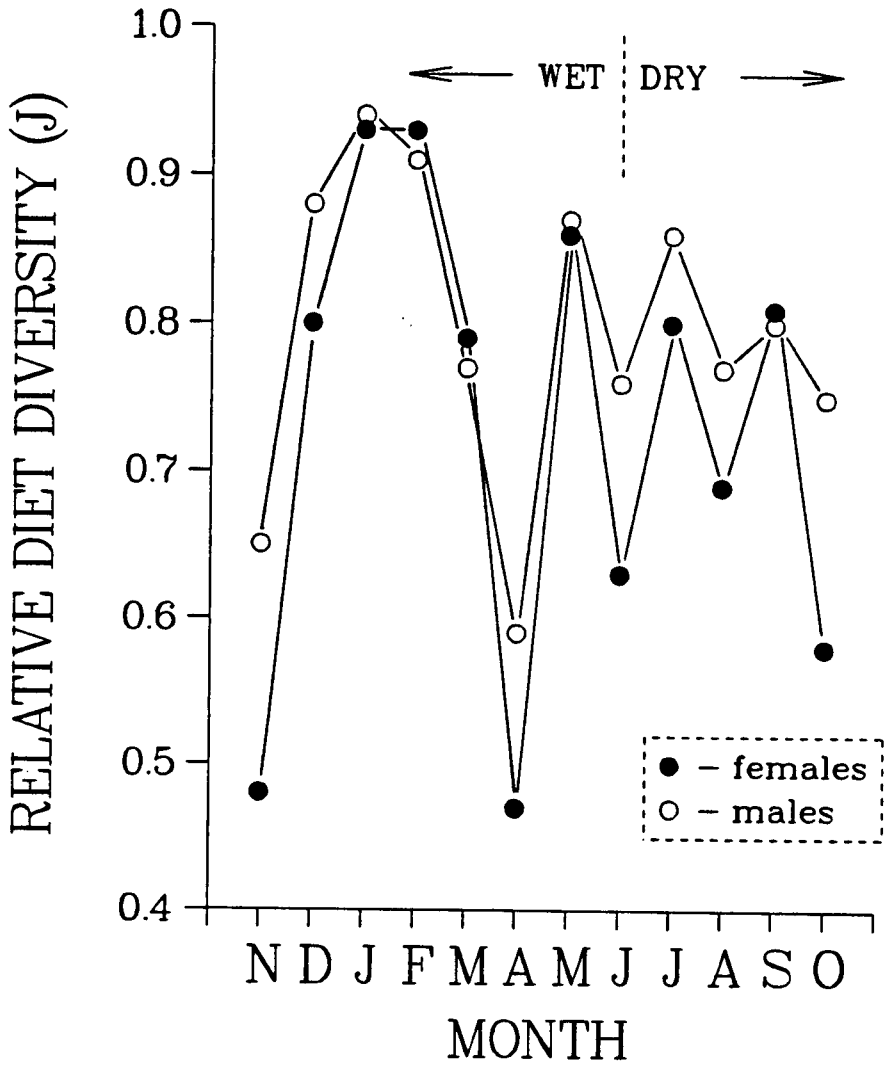

Figure 4.6. Relative diet diversity or diet "evenness" (J) for female and male elephants in 1983-84.

Table 4.4. Seasonal comparison of relative diet diversity between the sexes.

	d.f.	FEMALES	MALES	t-value	p-value
Annual mean	22	.73	.80	1.20	n.s.
Dry season	8	.70	.79	0.57	n.s.
Wet season	12	.75	.80	1.73	n.s.

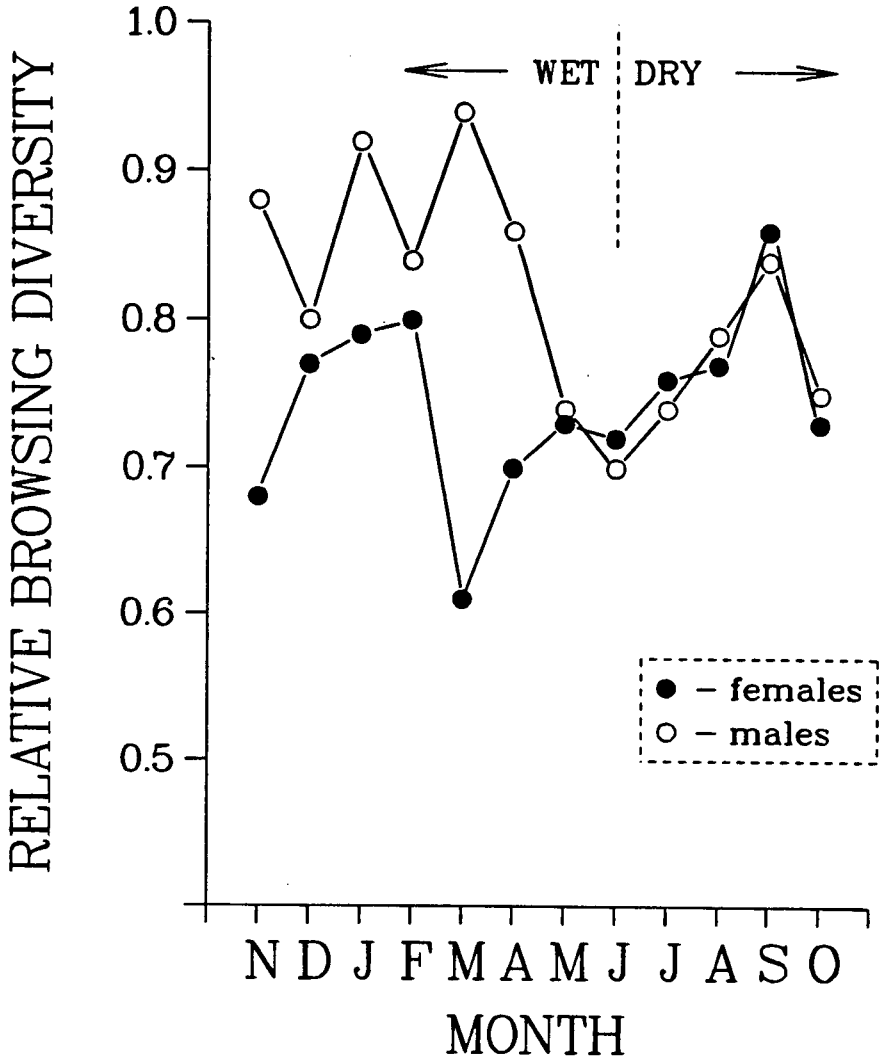

Figure 4.7. Relative browsing diversity or "evenness" for female and male elephants in 1983-84.

their diet was largely comprised of herbaceous species, males apparently sampled small amounts of a wide variety of available species.

Lengths of feeding bouts on forage types

Males and females spent similar amounts of time feeding on one forage type before switching to another (foraging bouts). This applied between seasons and across the entire year (Table 4.5a & b). In an analysis across all forage types, there were no significant differences in average length of foraging bouts between the sexes across the year or within either season.

Characteristics of plants in the diet

To see whether the sexes chose their food using the same criteria, utilization was examined in terms of the condition of the chosen plant, the specific plant parts eaten, and the height at which feeding took place. No significant differences were found between males and females for any of these conditional properties, for any forage type, in any season. Although no significant differences in the plant parts used were found, I could not rule out the possibility that more subtle choices were being made which I was unable to detect.

Elephants utilized forage in the green leaf stage more than all other categories of plant phenology (see Methods), when available. For herbs, shrubs, trees, and seedlings, the green leaf stage was used exclusively. For grasses, leaf condition was selected according to availability. So, more dry leaves

Table 4.5. Average length of foraging bouts across all forage types for males and females throughout 1983-84 (a); and between sex comparisons (b).

(a) Average length of foraging bouts in minutes

	N	D	J	F	M	A	M	J	J	A	S	O
Females	5.0	3.6	2.5	2.8	3.7	3.0	3.5	7.7	6.8	3.9	5.7	3.4
Males	3.7	4.4	2.4	2.9	3.8	3.0	4.5	6.4	6.0	4.1	5.0	4.2

(b) Between sex comparisons of mean length of foraging bouts in each season.

	d.f.	Females	Males	t-value	p-value
Annual mean	22	4.3	4.2	0.17	n.s.
Wet season	12	3.4	3.5	0.22	n.s.
Dry season	8	5.5	5.1	0.39	n.s.

were consumed during the dry season and more green leaves in the wet season. Males consumed significantly more grass in the dry leaf condition than females in both the dry (χ^2 = 8.59, d.f. = 1, P<.005) and wet season (χ^2 = 46.64, d.f. = 1, P<.001). This difference supports the idea that males, with their greater intake of bulk and lower relative energy demands (Sikes 1971), are better able to utilize poor quality, dry grasses. These differences are analyzed more fully below.

Male and female elephants fed almost exclusively on the leaves and shoots of all forage types with only occasional use of roots. Root feeding was not significant in any season, but bulls and cows followed the same general pattern of use. Shrub and tree bark was also consumed by both sexes in small amounts, primarily in the dry season.

Feeding height patterns apply only to the trees and shrubs. Throughout the year, elephants spent the majority of their feeding time on shrubs (males = 80%, females = 79%) in the 0 - 1m height class and on trees (males = 63%, females = 60%) in the 1 - 2m class. Their activity of selectively removing seedlings while foraging was termed "weeding". In a single foraging bout, individual male and female elephants removed as many as 35 seedlings (below 1m) in five minutes, a rate of over 400 per hour. Both sexes foraged at higher and higher levels as the dry season progressed. Seasonal differences within sexes are presented in the following sections.

Female feeding patterns

Diet composition by forage type

Females changed their diet with season (Figure 4.2). A two-way analysis of variance between season and forage type showed that the diets of females differed significantly with both season ($F = 5.59$, $P<.025$) and forage types ($F = 3.44$, $P<.01$). There was also a significant interaction between season and forage type ($F = 2.41$, $P<.05$). This interaction is due to the influence of season on relative quality between forage types.

Dry season diet composition showed a similar pattern between 1982 and 1984 but differed in 1983 (Figure 4.1). The decrease in browsing (trees, shrubs, and seedlings) and the increase in grazing (grasses and herbs) in 1983 may have been due to unseasonably high rainfall (378.1mm) during that period. Wet season diets also varied between the two seasons sampled. This difference was attributed to the significantly higher rainfall in the 1982-83 wet season (775.7mm) versus the 1983-84 wet season (540.9mm) when the rains largely failed and dry conditions prevailed. The main differences appeared to be in the herb and shrub forage types. In the wet season of 1982-83 herbs were probably more abundant due to higher rainfall and, therefore, constituted a larger proportion of the diet. From the 1983-84 data, it was apparent that females found new herbs highly desirable. On the other hand, feeding on shrubs was higher in the 1983-84 wet season when females were under more pressure to browse due to a shortage of green, herbaceous

forage.

Comparison of the 1983-84 wet season to the 1984 dry season shows a general tendency for a more herbaceous diet in times of higher rainfall and increased browse in the diet during the dry season, particularly from shrubs (Figures 4.2 and 4.8, Table 4.6a). The contribution of grasses to diets also differed between dry and wet seasons. To further analyze, the proportion of grasses in the diet was divided into the early (June and July) and late (August through October) dry season. In the late dry season diets, the grass composition (3.7%) was significantly less than in the wet season of (32.9% ($t = 3.39$, d.f. = 335, $P<.001$)) and in the early dry season (50.8% ($t = 2.83$, d.f. = 173, $P<.01$)). Herbs were more important in the wet season diets, and trees and tree seedlings contributed more to dry season diets, but not to a significant degree.

Diet diversity

The diets of females expanded in absolute diversity in the dry season and narrowed in the wet season (Table 4.3 and Figure 4.3, $t = 3.05$, d.f. = 10, $P<.02$). The relative diversity of diets of females did not vary by season either across all forage types ($t = 1.14$, d.f. = 10, n.s.) or for browse species alone ($t = 0.47$, d.f. = 10, n.s.). Cows showed their lowest relative diet diversity for browse species in March and November. Each of these months represented the end of long dry spells when high quality forage was scarce and browsing activity was high. Females travelled to permanent water sources where they fed on shrubs and trees by the water's edge. The low diet "evenness"

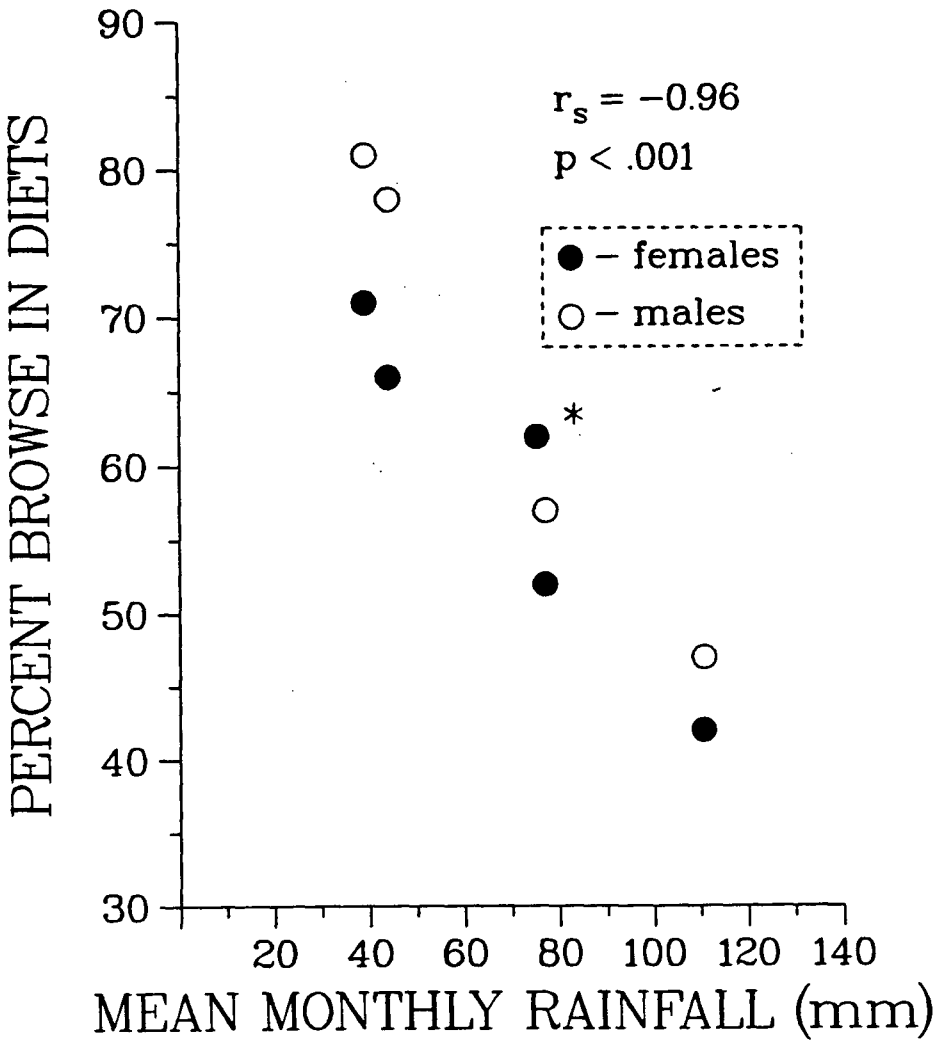

Figure 4.8. The relationship of percent browse in the diet to the mean monthly rainfall for female and male elephants.

Note : * = both males and females showed equal percentages of browse in the diets when mean monthly rainfall was 75.6mm.

Table 4.6. Between season comparison of diets by forage type within females and males. Tukey's multiple comparion tests (with unequal sample sizes) were performed. Significance levels are presented.

(a) FEMALES (dry season = 175; wet season = 230)

FORAGE TYPE	DRY	WET	SIGNIFICANCE LEVEL
GRASSES	22	33	0.01
HERBS	12	15	n.s.
SHRUBS	45	38	0.05
TREES	4	1	n.s.
SEEDLINGS	17	13	n.s.

(b) MALES (dry season = 82; wet season = 175)

FORAGE TYPE	DRY	WET	SIGNIFICANCE LEVEL
GRASSES	15	28	0.001
HERBS	7	15	0.01
SHRUBS	47	30	0.01
TREES	9	5	n.s.
SEEDLINGS	22	22	n.s.

indicates that females chose a few, favoured browse species and fed disproportionately on them.

Lengths of feeding bouts on forage types

Females did not maintain a constant bout duration on particular forage types in different seasons. In fact, foraging bouts of cows were significantly longer in the dry season (Table 4.7a). Variations in feeding patterns on several, but not all, forage types accounted for these significant seasonal differences. Foraging bouts on herbs, trees and seedlings were significantly longer in the dry season. Although feeding bouts on grasses did not differ significantly between the wet and dry seasons, a closer examination showed important differences between feeding patterns in the wet and early dry seasons. In the early dry season cows averaged 10.2 minutes per foraging bout on grasses, while in the wet season, they averaged only 4.34 minutes per bout, a significant difference ($t = 6.33$, d.f. $= 7$, $P<.001$). Early dry season grasses were a major component of the diet during this period. However, by the late dry season feeding bouts were similar in length to those in the wet season ($t = 0.42$, d.f. $= 8$, n.s.).

Characteristics of plants in the diet

All forage types, with the exception of grasses, were eaten only when in green leaf. The condition of grasses eaten differed between seasons ($\chi^2 = 835.6$, d.f. $= 1$, $P<.001$) and choice was determined by what was available. When green grass

Table 4.7. Between season comparisons of the length of foraging bouts on different forage types within females and males. Tukey's multiple comparison tests were performed. Significance levels are presented. Mean lengths are measured in minutes.

(a) FEMALES

FORAGE TYPE	DRY	WET	SIGNIFICANCE LEVEL
GRASSES	6.3	4.3	n.s.
HERBS	2.9	2.0	0.01
SHRUBS	4.6	3.7	n.s.
TREES	4.5	1.6	0.01
SEEDLINGS	3.5	2.1	0.05
OVERALL	5.5	3.4	0.05

(b) MALES

FORAGE TYPE	DRY	WET	SIGNIFICANCE LEVEL
GRASSES	6.9	3.4	n.s.
HERBS	2.0	2.8	n.s.
SHRUBS	4.6	2.6	0.01
TREES	6.9	3.6	0.02
SEEDLINGS	3.7	3.3	n.s.
OVERALL	5.1	3.5	0.01

leaves were ubiquitous, over 80% of the grasses chosen were in green leaf. However, in the dry season, dry leaves and stems made up 87% of the grasses eaten. Even in the most severe dry weather, females maintained over 10% of the grass component in the diet as green leaf, by moving to areas of perennial water where some green grasses could be found year round.

Females did not eat all plant parts equally. Leaves and new stems of all forage types predominated in the diet throughout the year. Roots, bark and woody branches were used in small amounts, primarily in the dry season.

There were sufficient data on shrubs to test whether females preferred to feed at particular heights in different seasons (Table 4.8a). In the wet season, female elephants preferred new shoots and leaves which frequently sprouted from shrubs below the 1m level. In the dry season, cows expanded their foraging to include greater proportions of other height classes and, therefore, less preferred leaves. This change in the dry season was probably a direct consequence of the reduced availability of newer shoots nearer the ground.

Male feeding patterns

Diet composition by forage type

A two-way analysis of variance of diet composition showed that the diets of bulls were significantly different both between seasons ($F = 15.72$, $P<.0005$) and between forage types ($F = 3.52$, $P<.01$). The frequency distribution of forage types in

Table 4.8. Feeding height preferences on shrubs and a test of the distribution of foraging heights between seasons for females and males.

(a) FEMALES

	HEIGHT CLASSES			TOTAL MINUTES
	0-1m	1-2m	2m+	
Dry season	855	249	83	1187
Wet season	1142	188	13	1343

$x^2 = 91.53$
d.f. = 2
$p < .001$

(b) MALES

	HEIGHT CLASSES			TOTAL MINUTES
	0-1m	1-2m	2m+	
Dry season	387	115	8	546
Wet season	538	55	3	611

$x^2 = 53.25$
d.f. = 2
$p < .001$

the diet varied within each season between the years sampled (Figure 4.1). The lower seedling and tree use in the dry season of 1983 may have been due to greater rainfall during that period than in either the 1982 or 1984 dry seasons (Table 4.1). This higher rainfall led to local forage conditions which were more similar to rainy season conditions than to dry season conditions. The observed decrease in browsing activity and the increase in grass and herb use merely reflected the relative change in quality between these forage types. The failed rains of the 1983-84 wet season led to a general pattern of increased browsing and reduced grazing (Figure 4.1).

The time spent eating grass was analyzed in more depth. Males followed a similar pattern to that seen in females. In the late dry season, grasses accounted for only 4.4% of male diets which was significantly less than 32.7% in the early dry season ($t = 3.44$, d.f. $= 80$, $P<.001$) and 27.8% in the wet season ($t = 2.52$, d.f. $= 174$, $P<.02$). The significant decline in grass eaten in the late dry season was both a product of its reduced availability following the arrival of the wildebeest and perhaps its reduced palatability due to phenological changes.

In the dry season, shrubs made up a significantly higher proportion of the diet than in the wet season (Figure 4.2 and Table 4.6b). Trees were also utilized more in the dry season but not significantly so. There was no seasonal change in seedling use among males. However, it is important to note that seedlings comprised almost a quarter of their overall diets, throughout the year, and males frequently consumed up to 400 seedlings in one hour of feeding.

Diet diversity

Among bulls, there was no significant change in absolute diet diversity between the wet and dry seasons (Table 4.3 and Figure 4.3, $t = 0.76$, d.f. = 10, n.s.). Males utilized over 50 plant species during the year, though these preferences switched between individual species seasonally.

Bulls did not show any seasonal change in relative diet diversity or "evenness" when analyzed across all forage types (Table 4.4 and Figure 4.6, $t = 0.21$, d.f. = 10, n.s.). Males spent more time browsing during the dry season and less time grazing (Figure 4.8). However, for the browse categories of shrubs, trees, and seedlings combined, bulls had significantly higher J-values in the wet season than in the dry season (Figure 4.7, $t = 2.44$, d.f. = 10, $P<.05$). This indicates that bulls foraged more evenly on browse species during that time. This higher "evenness" suggests that bulls used a greater number of browse species but in smaller individual amounts. In the dry season, when browse comprised over 75% of the diet, males apparently devoted more time to a few preferred species, just as females did when browsing.

Lengths of feeding bouts on forage types

The average lengths of foraging bouts across all forage types were higher in the dry season (Table 7b). This seasonal difference was explained by the significantly higher average foraging bouts on trees and shrubs in the dry season. Like females, males showed distinctly different feeding patterns on

the grass component of the diet, when broken into early and late dry season and wet season. Foraging bouts were significantly longer ($t = 3.00$, d.f. = 7, $P<.02$) in the early dry season (mean = 7.87 minutes/bout) than in the wet season (mean = 3.43 minutes/bout). The length of foraging bouts did not differ significantly between the wet and late dry seasons ($t = 0.95$, d.f. = 8, n.s.).

Characteristics of plants in the diet

Like females, males used significantly more green grass leaves in the wet season than in the dry season ($\chi^2 = 256.6$, d.f. = 1, $P<.001$). In the wet season, 70% of the grass leaves eaten by bulls were green, whereas in the dry season this figure dropped to 6%. Green grass leaves were always preferred over dry when available. In all other forage types only green leaves were utilized.

Male elephants fed primarily on the leaves and shoots of all forage types. Roots of some shrubs, seedlings, herbs, and grasses all occurred in the diets in small amounts. Bark and branches were seen in the dry season diets but not to a significant degree.

Males browsed at different heights in different seasons. For shrubs, these preferences changed in a manner similar to that seen for females (Table 8b). Whereas, in the wet season, males predominantly fed on the 0 - 1m height class, in the dry season, foraging at other heights increased. This change in the distribution of feeding heights reflected a preference for the 0 - 1m class during periods when new growth was stimulated by

rainfall. Many shrubs sent out extensive, coppicing shoots at the onset of the rains. This was particularly apparent following hot fires or damage to mainstems by elephants, wildebeest and others. During the dry season, when sprouts were no longer available, elephants expanded their foraging to include higher levels. For trees, the data were not extensive enough to establish height preferences in each season, however, the general pattern was similar to that found for shrub use.

Although males can feed more easily at greater heights than females, the distribution of their feeding heights, in the Mara, was the same. This was probably due to a scarcity of preferred forage species in the classes above 2m, yet still within their reach. Males did utilize forage at greater heights than females when it was available and occasionally pushed trees over to get at leaves in the tree crowns. Fallen trees within the riverine forests and in the open, Acacia woodlands demonstrated the extent of this behaviour.

Discussion

Mara elephants followed the same general foraging patterns observed in many African elephant populations (Nicholson 1954, Buss and Wing 1970, Napier-Bax and Sheldrick 1963, Laws and Parker 1968, Field 1971, Leuthold and Sale 1973, Wyatt and Eltringham 1974, Laws et al. 1975, Thomson 1975, Guy 1976, Field and Ross 1976, Leuthold 1977a & b, Tieszen et al. 1979, Barnes 1982, Weyerhaeuser 1982, Hansen et al. 1985). Males and females showed similar seasonal diet changes. Both sexes

concentrated on grasses and herbs in the rainy season and browse species in the dry season. Males browsed more than females, while female diets contained more herbaceous matter than males throughout the year. These seasonal changes in elephant diets are most likely a direct reflection of both the relative quantities of preferred forage and the ability of elephants to track crude protein levels.

Effects of food quality

Shrubs were used throughout the year by both sexes but comprised a higher proportion of diets of females in the wet season. There was no evidence to support Barnes' (1982) finding that females ate significantly more woody components (twigs and branches) than leafy ones (leaves and shoots) in the dry season. However, woody forage did not comprise a large component of elephant diets in any season in the Mara. This may have been a reflection of the local scarcity of preferred woody forage.

In accordance with recent optimal foraging theory, elephants, as generalist herbivores, should select forage in a manner which maximizes their net energy intake (Belovsky 1986). The additional costs of acquisition and assimilation of certain forage containing debilitating toxin loads must be worked into this overall equation (Rhoades 1979, 1983). Olivier (1978) and Barnes (1982) speculated that seasonal changes in elephant diets may be both controlled and constrained by secondary compound levels in the available forage. While grasses may have structural defenses, such as silica, which create digestion problems for some grazers (Olivier 1978, McNaughton et al.

1985), they present no problem for elephants. Furthermore, toxin levels in grasses are negligible and not generally considered a constraint on elephant diet choice (Olivier 1978, Barnes 1982).

However, Mbi (1978), Milton (1979), Coley (1980), Oates et al. (1980), Macauley and Fox (1980) and Bryant et al. (1985) found that the vulnerable plant parts of a variety of trees and shrubs species, such as young shoots, stems, and leaves (which seasonally comprise a large portion of elephant diets) contain higher amounts of terpenoids and total phenols (quantitative toxins), than older leaves and woody materials. These findings contradict those of Feeny (1970, 1976), McKey (1974, 1979), and Rhoades and Cates (1976) who found that older, more mature foliage of perennial trees and shrubs contained greater quantitative chemical loads than new growth. These same investigators did speculate, however, that young leaves may contain higher concentrations of qualitative toxins, such as alkaloids and cyanogenic glycosides and therefore still be well-defended from herbivory. If we assume that the former findings apply in elephant forage species, then the observations that elephants ate less browse and had shortened feeding bouts on browse species in the wet season, when new growth was abundant, lends support to the hypothesis that elephants forage in a manner aimed at minimizing their toxic intake. However, if we assume the latter findings to be true in this case, then we must look for other explanations for the observed diet choices. But Coley (1980) pointed out that the latter, more classical views of plant defense strategies, were largely developed for

temperate systems and needed to be re-examined, particularly in tropical systems, where opposite patterns have tended to be the case. As most work on plant-herbivore coevolution has been conducted in the neotropics and the temperate zones, more work is required on patterns of plant defense among African species, which have evolved with a broad range of herbivores for millions of years.

Olivier (1978) argued that the digestive system of elephants renders them more sensitive to plant toxins than sympatric ruminants and that this influences their diet choice. While it may be true that elephants are sensitive to plant toxins, it is also the case that they have very high absolute daily energy requirements (Sikes 1971, Laws et al. 1975). In order to meet these needs during times of food shortage, elephant diets may be chosen primarily to maximize energy intake and secondarily to minimize toxin ingestion. To achieve this, elephants may diversify their diets and, thus, avoid a buildup of toxins from defended plants while still meeting their energy needs. Although toxins may act secondarily to interfere with digestive processes and energy assimilation, it is unlikely that elephants are seriously affected by toxicity levels in the diet. Elephants are, however, affected by declining food quality and quantity. When the availability of suitable forage falls below subsistence levels, elephants initially show a decline in overall body condition (Albl 1971, Guy 1976, Barnes 1982), in acute cases, they may even starve to death (Corfield 1973), while in chronic situations they may show declining reproductive rates, deferred sexual maturity, lengthened interbirth

intervals, and increased calf mortality (Laws et al. 1975, Laws 1981b, Weyerhaeuser 1982).

Masai Mara elephants tended to pick the most nutritious species first (grasses following the rains and browse species in the dry season), and resorted to poorer quality forage only as the former became unavailable. In general, elephant foraging patterns appeared to be aimed more at maximizing energy intake than minimizing toxin loads.

Effects of the wildebeest migration

The Masai Mara Game Reserve is the northernmost extension of the Serengeti-Mara ecosystem where, every dry season, over a million migratory wildebeest take up residence. These migrants remove over 90% of the standing crop during their stay (Figure 4.9). Immediately following cessation of the rains and prior to the arrival of the wildebeest, both sexes of elephants showed an obvious preference for grasses. At this time, the newly germinated grasses were very abundant and at the peak of their digestible protein levels (Figure 4.10). However, upon the arrival of the wildebeest, a distinct change in diet choice occurred. Elephants immediately decreased their feeding on grass and they stopped feeding on grass altogether in the latter stages of the wildebeest occupancy, despite the production of new grass following intermittent local storms. Wildebeest kept the grasses grazed down to lawn height (McNaughton 1984). At this height grasses may have become difficult for elephants to eat.

This change in feeding patterns probably reflected a

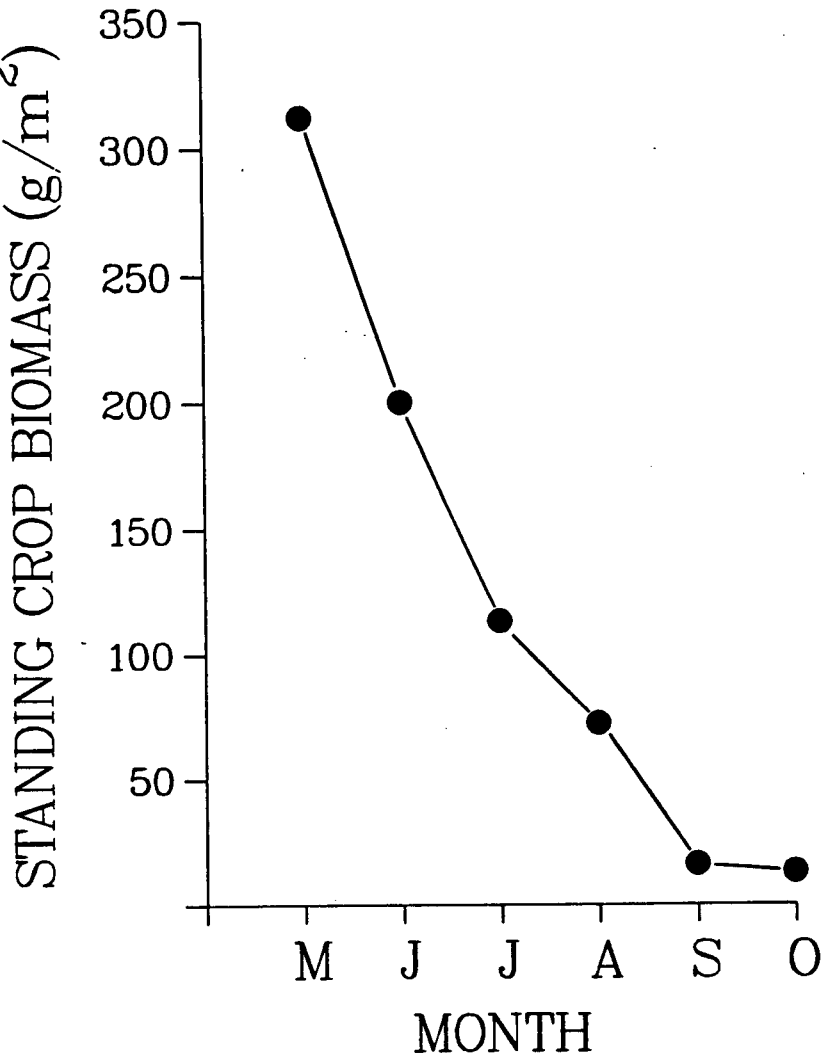

Figure 4.9. Standing crop biomass through the dry season (during the time the migratory wildebeest are present in the study area).

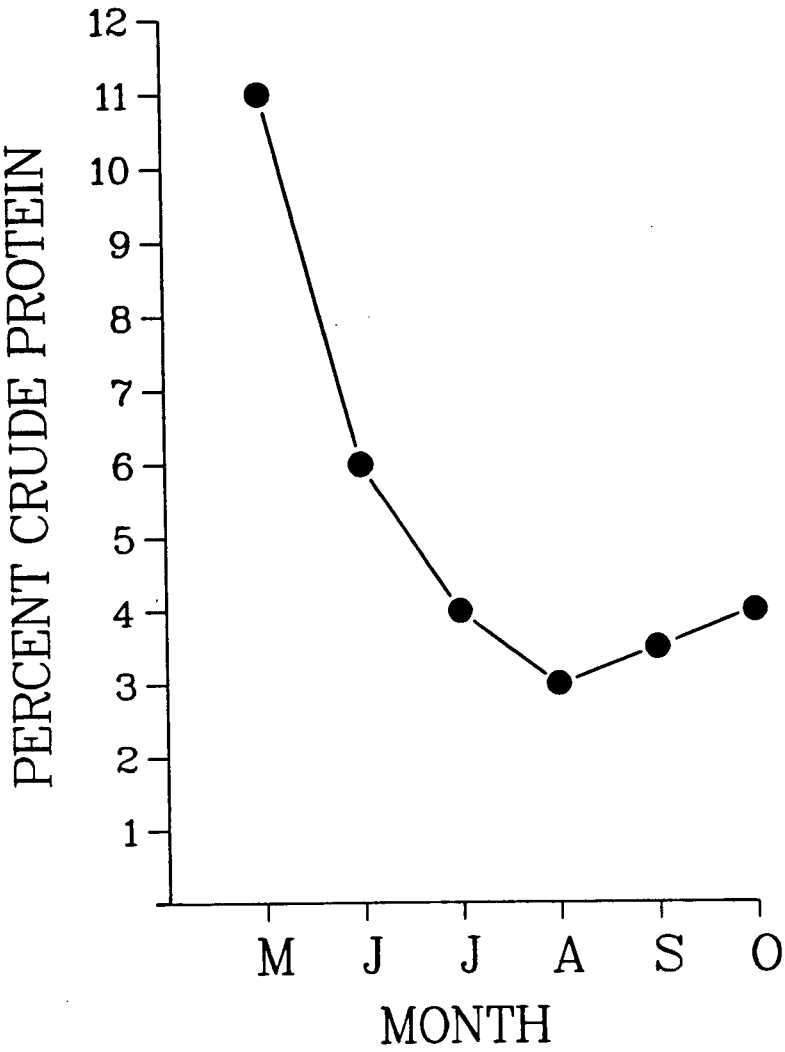

Figure 4.10. Percent crude protein of long grasses over the course of the dry season (redrawn from Sinclair 1975).

decline in both grass quantity and quality. Woody species remain relatively higher in crude protein than herbaceous species as the dry season progresses. Pellew (1981) reported that some preferred browse species, such as Acacia gerrardii, A. senegal, and Commiphora trothae, maintained crude protein levels above 13% even in older leaves. Dougall (1963) and Dougall et al. (1964) found even higher values for the mature leaves of Acacia brevispica (17%), Boscia angustifolia (33%), and Solanum incanum (30%) which were also used by Mara elephants in the dry season. The grasses eaten by elephants, such as Themeda triandra and Cynodon dactylon drop as low as 5% and 8% crude protein during the dry season (Dougall 1963, Dougall and Glover 1964, Field 1971, Sinclair 1975). By the height of the dry season, elephants spent the majority of their feeding time on the available browse species (Figure 4.11).

Throughout Africa elephants are considered the primary agents of habitat change (Laws 1970, Thomson 1975). Although Field (1971) suggested that giraffe may compete with elephant under certain circumstances, no other species is known to alter habitats as significantly, or to compete with elephants for grazing resources. The evidence provided above, however, suggests that the sheer numbers of migratory wildebeest, coming into the Mara each year, so alter the habitat during their annual stay that they come into direct competition with elephants late in the dry season. Although elephant browsing activity increases significantly during any period of low rainfall (Figure 4.8), competition with the wildebeest may exacerbate this pattern and result in elephants placing even

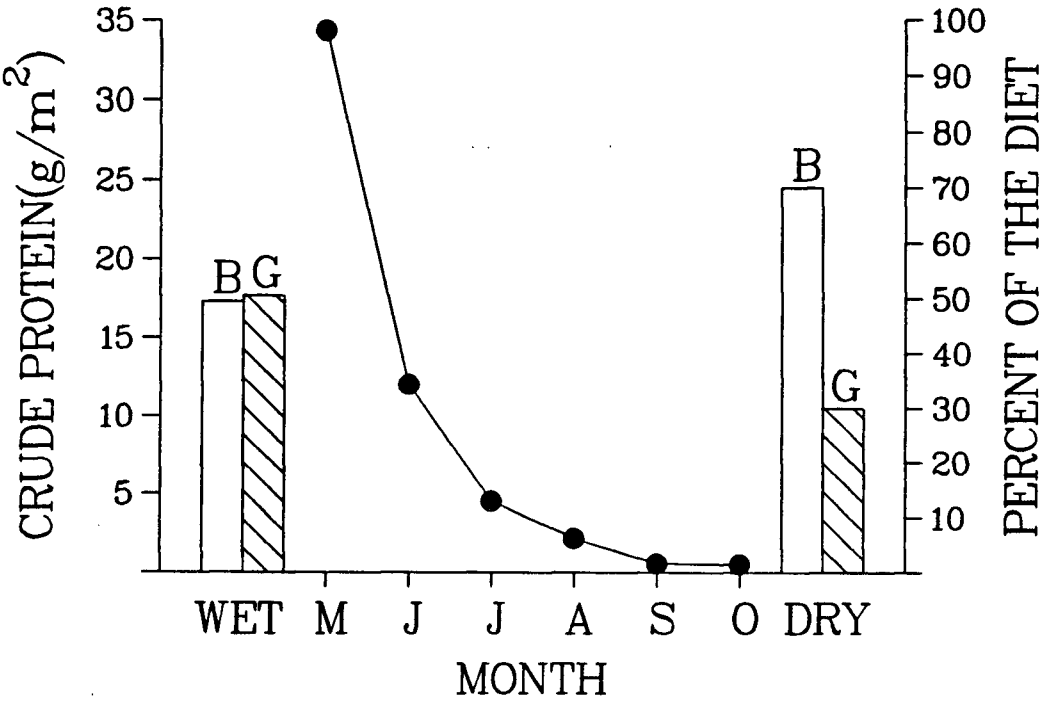

Figure 4.11. Grams crude protein per m^2 of long grasses during the dry season (left axis, line graph) and a percentage breakdown of elephant diets between grazing (G) and browsing (B) in the wet and dry seasons (right axis, bar graphs).

greater pressure on available browse species in the dry season. Croze (1974a) studied the feeding behaviour of bull elephants in an area of the central Serengeti where wildebeest were not present in the dry season. He found that bulls spent approximately 70% of their time in the Acacia woodlands and 30% of their time in vegetation along permanent water sources. Between the two habitats, browsing took up 34% of the elephants' feeding time. This is in contrast to elephants in the Mara who spent 70% of their foraging time on browse during the dry season.

Effects of seasonal change

Female elephants seemed to be more sensitive to environmental changes than their male counterparts. Cow elephants are either pregnant or lactating throughout most of their adult lives and, therefore, their energy demands are high relative to males. Female foraging patterns differed from males in ways which may reflect these energetic differences. Throughout the year, females maintained a higher absolute diet diversity than males and this difference became even greater in the dry season. This expansion in female diet choice was consistent with the prediction from optimal foraging theory that foragers should expand their diets to include less-preferred items when more desirable items become less available (Schoener 1971, Pyke 1984). Males showed no parallel seasonal change in diet diversity. With lower relative energetic requirements males may have been able to meet their needs by increasing their bulk intake rate on a few species during energy-limited times,

rather than by diversifying their diets. Olivier (as cited by Barnes 1982) speculated that due to their smaller body size females must be even more cautious of toxin content than bulls. This proposed difference in sensitivity to toxins could partially explain why females elephants diversified their diets and reduced the risk of dangerous toxin levels in any single species.

Relative diet diversity or dietary "evenness" did not change seasonally in bulls or cows when all forage types were compared. Elephant foraging time was distributed similarly among all species of grasses, herbs, shrubs, trees, and seedlings throughout the year. However, an analysis of browse species only showed significant differences between sexes and between seasons. Males fed more evenly than females in the wet season whereas females showed no seasonal change. These findings suggest that males distributed their time more evenly among more browse species during the wet season. Greater diet "evenness" in the wet season may have been largely due to the simultaneous sprouting peak of a variety of seedlings following the onset of the rains. This flush of new growth allowed bulls to distribute their foraging time among a broad range of nutritious browse items. Barnes (1982) reported these same seasonal patterns of diet evenness for bull elephants but had no comparable data for cows.

It was assumed that the length of foraging bouts was positively correlated to the absolute amount of forage consumed, though the quantitative expression of this relationship is currently being investigated by Lindsay (in prep.). Bulls and

cows did not differ significantly from one another in the length of their foraging bouts throughout the year. In the dry season, both sexes had significantly longer bouts when analyzed across all forage types. Presumably, once a good forage type was found, elephants fed for a longer time before switching to a new type. These longer foraging bouts in the dry season were accounted for by differences in the use of individual forage types by bulls and cows. Females spent significantly longer bouts on herbs, trees and seedlings, while males increased the length of foraging bouts on shrubs and trees. This is similar to Barnes' (1982) observations on the browsing patterns of bulls season in Ruaha National Park, Tanzania. Both sexes had significantly longer feeding bouts on grasses in the early dry season than in the late dry season or wet seasons. This seasonal difference in foraging bouts on grasses has been interpreted as a reflection of the elephants' preference for high grass quality and quantity immediately following the rains, just prior to the arrival of the wildebeest migration (see above).

The characteristics of food plants used by elephants remained consistent throughout the year. Cows and bulls ate all forage types in their green leaf condition, when available. Leaves and shoots were always eaten more than other plant parts, such as twigs, bark, or branches. Some use of roots and bark occurred in the dry season. This same pattern was seen by Field (1971), Field and Ross (1976), Guy (1976), Olivier (1978), Barnes (1982), and Ishwaran (1983) in elephants from different localities. Field (1971) explains this as the result of

elephants constantly seeking the highest available crude protein levels in their forage.

Effects of woodland disappearance

Elephants fed primarily in the 0 - 1m height range. Although elephants expanded their diets to include other height classes during the dry season, their feeding below one meter accounted for an annual mean of 80% of the browse diets. Because seedlings were often consumed at a rate of over 400 per hour, the effects were noticeable when entire herds began "weeding" out seedlings in open grasslands. In all other forage types, feeding took place exclusively in the 0 - 1m height range. These findings are consistent with those of Brooks (1957), Buss (1961), Wing and Buss (1970), Field and Ross (1976), Guy (1976), and Weyerhaeuser (1985) but contrary to those of Croze (1974b) for elephants of the central Serengeti woodlands in the early 1970's. Croze found that elephants fed largely in proportion to availability for all size classes except those under one meter, which were rarely eaten. Either elephant food preferences have changed for reasons which are not clear or this high use of forage under one meter is a direct result of the change in relative availability of forage in other, possibly more preferred, height classes. Either way, this differential use of seedlings may account for a significant proportion of the lost recruitment potential in local tree populations today.

We know that major changes in woodland communities have taken place over the past 25 years. These include a loss of

tree cover in the larger height classes throughout the Mara Game Reserve. Some areas have experienced as much as a 95% relative loss since 1950 (Chapter 2). This decline was largely the result of fire and elephant impacts on the trees in the past, and their continued negative influence on seedling regeneration, today (Chapter 5). These impacts were exacerbated by other factors, such as wildebeest and small, mammalian browsers (Belsky 1984).

While elephants are certainly one of the primary biological factors in woodland changes, Mara elephant densities (approximately 0.75 - 1.00/km^2) are low relative to other parks and reserves in Africa. Tanzania's Lake Manyara National Park supports densities up to 6.00/km^2 (Weyerhaeuser 1982), while Kenya's Amboseli National Park has local densities up to 10.00/km^2 (Western and Lindsay 1985). Few obvious signs of elephant activity meet the eyes of casual observers in today's Masai Mara Game Reserve. Standing trees are not uniformly bark-stripped or toppled, elephants are exerting a more subtle influence. The present day role of Masai Mara elephants in woodland dynamics is not so much one of destroyer as one of inhibitor (Chapter 5).

The relative contribution of elephants to the loss of adult trees or the inhibition of woodland regeneration may be highly dependent on local weather conditions. Dry years, like 1984, lead to increased browsing on woody plant species because of the elephants' dependence on browse during dry periods. The innate ability of elephants to switch to grasses when browse species have been virtually eliminated, makes them a unique, and

potentially more detrimental herbivore than those strict browsers, like giraffes, whose population dynamics are more closely linked to browse availability (Field 1971, Norton-Griffiths 1979, Pellew 1983). Although elephant populations might eventually respond to woodland habitat loss through decreased reproductive rates as suggested by Laws et al. (1975) it may be too late to save affected tree populations. And, even if the woodlands could survive until a decline in elephant numbers occurs, other browsers, fires, and the migratory wildebeest, might effectively inhibit woodland regeneration.

Summary

The feeding ecology of free-ranging elephants in the Masai Mara Game Reserve was studied over a two and a half year period by direct observation. The study investigated the seasonal use of grasses, shrubs, herbs, seedlings, and adult trees by both male and female elephants, with an emphasis on the overall impacts of elephants on the remaining woodlands and thickets.

Both male and female elephants concentrated on grasses and herbs in the wet season and woody species in the dry. Males consistently browsed more than females, while females used more herbaceous forage. Elephant diets changed upon the arrival of the migratory wildebeest herds, switching from grazing to browsing as the standing crop of grass was rapidly reduced by the migrants. Females maintained a higher absolute diet diversity than males throughout the year. This difference was most pronounced in the dry season. Males distributed their foraging time more evenly among the available browse species

during the wet season than during the dry, whereas females showed no seasonal change. However, at the height of the dry season, a few favoured browse species were fed upon disproportionately by both sexes. Both sexes had longer foraging bouts in the dry season indicating that once a good forage type was found, elephant fed longer before switching to a new type. Elephants concentrated their feeding activity in the 0 - 1m height class and almost exclusively ate the green leaves and shoots of all forage types.

Elephant impacts on woody vegetation in the Mara increased in the dry season. These impacts were further exacerbated by the arrival of the migratory wildebeest who removed almost all available grass leaving no alternative forage for the elephants. As well, the elephants currently have restricted access to their former dry season dispersal areas which are now experiencing agricultural development, intensive livestock grazing, and severe poaching activity. As a result, elephants are currently a primary factor in the inhibition of woodland regeneration in the Mara Game Reserve.

CHAPTER 5. THE EFFECTS OF ELEPHANTS, FIRE, WILDEBEEST AND BROWSERS ON THE ACACIA WOODLANDS

Introduction

The loss of woodlands in the Masai Mara Game Reserve of Kenya over the past 30 years has left the area an open grassland. These woodlands formerly provided both food and protection for many species of wildlife. Today, there is little woody material available to browsing species and much of the cover afforded other species has dwindled away (Glover and Trump 1970, Dublin 1984, Lamprey 1985). The potential for regeneration of these woodlands is of interest from both an ecological and a management perspective. Regeneration seems to be limited by existing biological conditions in the Reserve.

The recovery of these woodlands is now dependent on the ability of seedlings to establish themselves and grow to maturity. It has been hypothesized that this process is currently being inhibited by a combination of several biological factors; each one affecting the woodlands in different ways at different times. Based on past work, Belsky (1984) summarized these agents of mortality and inhibition as fire, elephants, and giraffe. She added the effects of small browsing mammals and wildebeest to this list but did not quantify their relative impacts on woodlands. Although research has been done on the effects of these factors on mature trees and their influence on woodland dynamics in local areas of the Serengeti National Park (Glover 1965, Lamprey *et al*. 1967, Croze 1974a & b, Norton-Griffiths 1979, Pellew 1983), no quantitative information was

available on the process of seedling establishment and its role in woodland regeneration in the Mara today.

The experiments in this study were designed to separate and analyze the relative effects of fire, elephants, and wildebeest on seedling populations. Using experimental evidence, this chapter examines the hypotheses that these factors, acting alone or in combination, are effectively inhibiting seedling establishment and the recovery of Acacia woodlands in the Masai Mara Game Reserve.

Background Information

A strong correlation has been established between fire and woodland loss in the Serengeti-Mara ecosystem (Norton-Griffiths 1979, Lamprey 1985, Dublin, Chapter 2). Throughout Africa fire has long been recognized as a primary factor in tree mortality and the inhibition of seedling growth (Charter and Keay 1960, Buechner and Dawkins 1961, Glover 1965, 1968, Seif El Din and Obeid 1971, Spinage and Guinness 1972, Harrington and Ross 1974, Thomson 1975, Brookman-Amissah et al. 1980, Trollope 1982a, Sabiiti 1986). For these reasons, fire has been widely used as a tool to combat bush encroachment and protect domestic grazing lands (West 1958, Thomas and Pratt 1967, Pratt and Knight 1971, Strang 1973, 1974, Trollope 1972, 1982b). However, in natural ecosystems, like the Serengeti-Mara, ecologists and managers have looked for ways to minimize the detrimental effects of fire on woodlands and grasslands.

Norton-Griffiths (1979) estimated that over a ten-year

period (1962-1972) the canopy cover of woodlands in the northern Serengeti had declined by 26% on average and up to 50% in the northernmost areas. He attributed these losses primarily to the effects of increases in the frequency and severity of fires. However, he did not conclude that fire alone was responsible for the loss of canopy cover. In other areas within the system, he reported an overall woodland loss of 7% over this same time period. These losses were attributed to an increase in local elephant densities and the subsequent impact of their browsing activities on individual woodland stands.

Croze (1974a & b) described in greater detail the role of elephants in the dynamics of the central Serengeti woodlands. He estimated the loss of mature trees to elephants at a rate of 2.5% per year on average, with local losses as high as 6.0% per year. Based upon the age structure of trees in his study area, he concluded that under these conditions, elephants did not pose a severe threat to the future of woodlands. Glover (1965), Lamprey et al. (1967), and Herlocker (1976a) disagreed, arguing that elephant related damage was more extensive and woodland re-establishment more limited. These studies concentrated primarily on the impact of elephants on mature trees in a restricted area of the system and less on the effect of elephants on seedling survivorship in general.

Over the past 20 years, the Serengeti's migratory wildebeest population has increased by a factor of five (Sinclair and Norton-Griffiths 1979). Norton-Griffiths (1979) speculated that the increase of these generalized grazers would reduce the standing crop of grass thereby reducing fire severity

and enhancing seedling survivorship. However, wildebeest have other directly detrimental effects on the woody vegetation. Wildebeest damage seedlings in significant numbers through their trampling, inadvertent browsing, and sparring activities during the rut. These effects are predicted to be most pronounced in the northern Serengeti and Mara woodlands where the wildebeest have the most extended contact with woody species during their annual dry season migration.

Pellew (1981, 1983), working in the central Serengeti woodlands, investigated the role which giraffes played in local woodland dynamics. He concluded that the rate of growth of trees from one size-class into the next was heavily dependent on the extent of browsing by giraffe. This browsing retarded the growth of trees and prolonged their period of fire-susceptibility. The overall effect merely compounded the impacts of fire and elephants on woodland regeneration. In the Masai Mara Game Reserve, the effects of giraffe are minimal. The existing woodland communities are not favourable for giraffes due to the loss of trees in the height classes they prefer. These losses exceed those found by Norton-Griffiths (1979) in the northern Serengeti (Dublin, Chapter 2). Consequently, many giraffes have emigrated to other areas and there has been a consequent decrease in their population numbers within the Reserve (Lamprey 1985, K.R.E.M.U. unpubl. data).

Woodland regeneration in the Mara is, nonetheless, in serious jeopardy. Elephants currently reside year-round in unprecedented numbers, fires continue to burn, and there are the added trampling, thrashing, and browsing effects of an increased

wildebeest population which visits the area for three to four months each year.

Methods

Five study sites were established within the Acacia gerrardii woodland communities. Sites were selected for homogeneity of composition, height distributions and density of seedlings between sites. One-way ANOVAS were conducted on transformed (see below) heights and stem numbers of each of the five sites when the study began. There was no significant difference amongst any of the five sites on either height or number of stems (heights: $F = 2.04$, n.s.; stems: $F = 1.86$, n.s.). Also, sites were described in terms of the densities and frequency distributions of Acacias in the different height classes measured (Table 5.1, Figure 5.1). These distributions show a size structure which is heavily biased towards the under 1m height class, with other height classes comprising only a small proportion of all trees and occurring in very low numbers.

Each site was divided into three separate treatment plots: (a) burned and browsed, (b) browsed only and (c) neither burned nor browsed. Treatments (a) and (b) were conducted in 25 x 100m plots. Treatment (c) plots were 15 x 15m fenced exclosures. The latter excluded all large browsing mammals. Grazers had free access to treatments (a) and (b) but not (c). Each treatment plot was surrounded by a 10m firebreak to guard against invasion by wildfires.

Table 5.1. Seedling densities per hectare by height class. Mean densities (± one s.d.) are also presented.

	HEIGHT CLASS (m)			
SITE NO.	0-1	1-2	2-3	3+
1	850	25	38	36
2	982	17	20	32
3	1105	0	29	24
4	720	19	0	32
5	595	0	51	37
Mean Density:	850 ± 202	12 ± 11	29 ± 17	32 ± 5

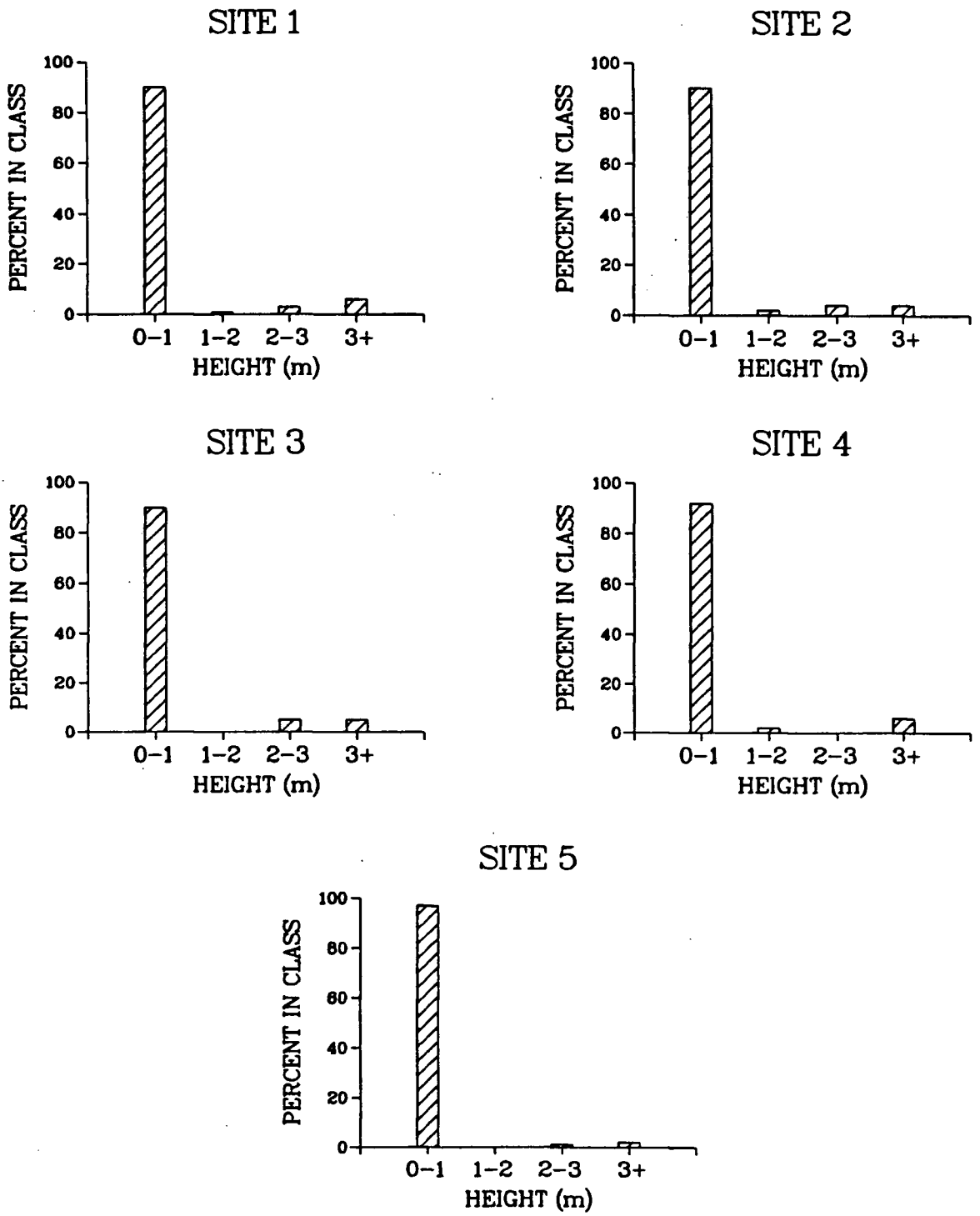

Figure 5.1. Height distributions of Acacia gerrardii in five sample sites.

Measuring the Effects of Browsing

The term "seedling" is used throughout the text for all Acacias less than 1m, as it was impossible to distinguish without destructive sampling those which were growing from seed versus those sprouting from rootstocks. However, excavations of many such seedlings, in adjacent areas, revealed that most were coppicing shoots. Due to this process of coppicing, studies of the population dynamics of African trees in many fire-derived savanna systems have been based on height classes rather than age distributions (Glover 1965, Vesey-Fitzgerald 1973, Spinage and Guinness 1972, Leuthold 1977b, Belsky 1984, Lamprey 1985, Sabiiti 1986, Jachmann and Bell 1985).

All plots were established in June of 1982 and measured every six months until May of 1985. Within each plot all seedlings and trees were individually tagged and accurately mapped to insure finding them again following treatments. Sampling periods for both the burning and browsing treatments were as follows: May-June (pre-wildebeest) and November-December (post-wildebeest). A year into the study, the treatment (c) exclosure plots were divided in half, with the grass clipped every three months on one side and left unclipped on the other. The clipping treatment most closely simulated the grazing effects experienced by plants in the burned and browsed (a) and browsed only (b) treatment plots and, therefore, was the most realistic control. This manipulation was also performed to investigate the possible competitive inhibition of seedling growth by neighbouring grasses. It should be noted that this manipulation only addressed the potential for above ground

competition. The study of competition between plants below ground for water or other resources was not within the scope of this research.

Initially, the longest stem of each plant was measured and tagged. In each following sample period the height of the marked stem, total number of stems, and condition of every plant were measured. Condition referred to any signs of browsing by elephants and other species plus the effects of trampling and thrashing by migratory wildebeest on leaves and stems of marked plants. In the majority of cases, the factor responsible for stem removal or damage could be readily distinguished. When a marked stem had died but the individual seedling was still alive, the cause of stem death was recorded and the longest remaining live stem was then tagged with the original identification number. Those plants missing altogether were initially noted as "missing" in that sampling period and later classified as "dead" if they did not reappear by the end of the study. The fate of each "missing" individual was determined by inspection when possible. Plants which resprouted in subsequent sampling periods, referred to as "regenerates", were retagged with their original identification numbers. All individuals were followed over a minimum of six months and a maximum of three years. New seedlings were tagged as they were found.

Measuring the Effects of Burning

In the first year, burning experiments were conducted in October, at the end of the dry season. The migratory wildebeest arrived in the study area each year in late June or early July

and in some areas removed up to 95% of the standing crop of grass before leaving in early October. Therefore burning in October proved difficult because of the lack of grass fuel and all subsequent burns were conducted in the short dry season (February and March). At this time wildebeest were not present, and there was sufficient fuel for burning (see Chapter 4).

For each burn treatment the prevailing wind speed, relative humidity, air temperature, surface and below-surface temperatures during burns, fuel moisture, rate of spread and flame heights were recorded. As heavy, wood fuels were uncommon in the plots and contributed an insignificant amount to actual fuel loadings, the experimental burns were exclusively grass fires. The dominant grasses present were Themeda triandra and Pennisetum mezianum. Based on Rothermel (1972) and Sneeuwjagt and Frandsen (1977), these grass fuels were assumed to produce a heat yield of approximately 18,000 kJ per kg. Fuel loadings were estimated using a point-frame analysis calibrated from oven-dried grass clippings (McNaughton 1979). Fire intensities were calculated from Byram's (1959) formula:

$$I = Hwr$$

where I = fire intensity (kW/m), H = heat yield (kJ/kg), w = dry fuel consumed (kg/m^2), and r = rate-of-spread (m/sec).

Rothermel and Deeming (1980) recommended the use of this equation in experimental burning situations similar to those applied in this study. Fires were set between 1200 and 1500 hours and were very consistent in character both between sites

and burning seasons (Table 5.2). All fires were measured in the 1000 - 2000 kW/m or kJ/m/sec range and classified as "moderately hot" following McArthur and Cheney (1966) and Trollope (1982b).

In addition to these large-scale burning experiments, multiple-burn experiments were conducted on three groups of 100 wild seedlings. This experiment was designed to simulate the effects of repeated fires on the root reserves of established seedlings. Three different fuel loadings which had been recorded under natural conditions were used in these experiments: 150g/m^2, 300g/m^2, and 600g/m^2. These plants were watered and re-burned once they reached their original heights. All plants were burned ten times.

Seed germination experiments were conducted under different burning conditions to simulate the effects of wildfires on seeds in the surface layer of the soil (0 - 2cm). Acacia gerrardii seeds were collected from mature trees in the Mara and sorted to remove any damaged or insect-infested specimens. From these seeds, five sets of ten groups (with 200 seeds in each) were randomly selected and subjected to one of five different fuel loadings: 200 g/m^2, 400 g/m^2, 600 g/m^2, 800 g/m^2, and 1000 g/m^2. This distribution of fuel loadings was considered to be representative of the entire range of field conditions found in the Mara. Seeds were sown into the top 2cm of soil on cleared, one square metre plots. Fuel loadings on these plots were then set at one of the five experimental loadings. A control group of seeds not exposed to burning and the five different treatment groups were then put in petri dishes and kept moist. Germination rates were recorded on a daily basis. A one-way

Table 5.2. Characteristics of large-scale experimental burns.

Fuel loads	=	200 - 400 g/m^2
Fuel moisture	<	35%
Air temperature	=	27°C - 30°C
Relative humidity	<	30%
Wind speed	<	10 km/hr
Fire intensity	=	1000 - 2000 kW/m

ANOVA was performed on these data to measure the effects of fuel loadings on seed germination.

Data Analysis

Square roots of all plant heights, logarithmic transformations of all stem numbers, and arcsine transformations of all percentage data (i. e. percent of stems removed) were performed to allow the use of parametric statistical analyses (Zar 1984).

The problem of "pseudoreplication" in data analysis (Hurlbert 1984) was addressed. I concluded that individual marked seedlings within burned and browsed (a) and browsed only (b) treatment plots could not be considered independent observations because of the nature of the feeding and movement patterns of elephant, wildebeest, and other browsers. If an animal entered an experimental plot and ate or damaged one seedling, the probability of a neighbouring seedling being similarly affected would increase. For this reason, all measurements were averaged within each of the plots in the five sites and all ANOVAS on seedling measurements from large-scale treatment plots were weighted by sample size. ANOVAS were performed on MINITAB (Ryan et al. 1985) for small, balanced data sets and BMDP (Dixon 1985) for weighted, mixed effects models.

Results

Large-scale Field Experiments

Mortality of Trees and Seedlings

For the purpose of calculating mature tree mortality rates, three hundred trees greater than 3m high were randomly selected throughout the Reserve, marked and their fates followed throughout the study. Mature trees suffered mortality rates of 7% (n = 300, s.e.= 1.5%) per year due to elephant damage and another 1% (n = 300, s.e.= 0.6%) from other natural causes. However, under extreme conditions, like the drought of 1984, the mortality rates of trees were much higher in localized areas. For example, in October of 1984, a herd of approximately 6 bull elephants visited a 2 sq. km. of 753 mature Acacia stand. Within 24 hours they had killed or fatally damaged 256 (34%) of the trees and another 166 (22%) of the trees had many broken branches. Other stands experienced similar damage during this very dry period.

Mortality rates of seedlings were calculated for each of the five study sites. Estimates of the percent of seedlings killed were based on the averages and standard deviations amongst the five sites. Within these experimental sites, 4% (s.e. = 0.5%) of the 6000 seedlings marked initially in treatment plots (a) and (b) were killed by elephants, 1% (s.e. = 0.6%) by wildebeest trampling and thrashing, and another 1% (s.e. = 0.3%) through other natural causes. In the burned and browsed treatment plots (a), fire killed an additional 4% (s.e.

= 0.8%) of all marked seedlings each year. Total seedling mortality rates averaged 10% (s.e. = 1.2%) per year. This annual mortality greatly exceeded the estimated rate of seedling replacement of 2% (s.e. = 0.6%) per annum (approx. 17 new seedlings per ha/yr) across the five experimental sites.

Seedling Inhibition: the effects of fire and animals

The greatest effect of fire, elephants, other browsers, and wildebeest trampling was the inhibition of growth in seedlings under 1m in height (Figure 5.2). In each sampling period, 30% - 60% of all stems marked in the previous period were removed in unburned plots and in burned plots 90 - 100% of marked stems were removed by a combination of fire, elephants, wildebeest and other browsers between sampling periods. Although individual seedlings were not killed, their growth was severely inhibited by this extensive utilization and they were effectively held below 1m through the combined effects of fire, wildebeest, elephants and other browsers.

The fraction of stems removed by elephants, wildebeest, and other browsers combined was analyzed across the five study sites for the wet and dry season in burned and browsed, browsed only, and neither burned nor browsed treatment plots using a weighted, three-way, mixed effects ANOVA. Season, site, and treatment effects were all significant (Table 5.3). Stem loss was significantly greater in the dry season than the wet, and was greater on burned than unburned plots (Tukey's multiple comparison at the 5% significance level). Two of the five sites showed significantly greater losses than the other three.

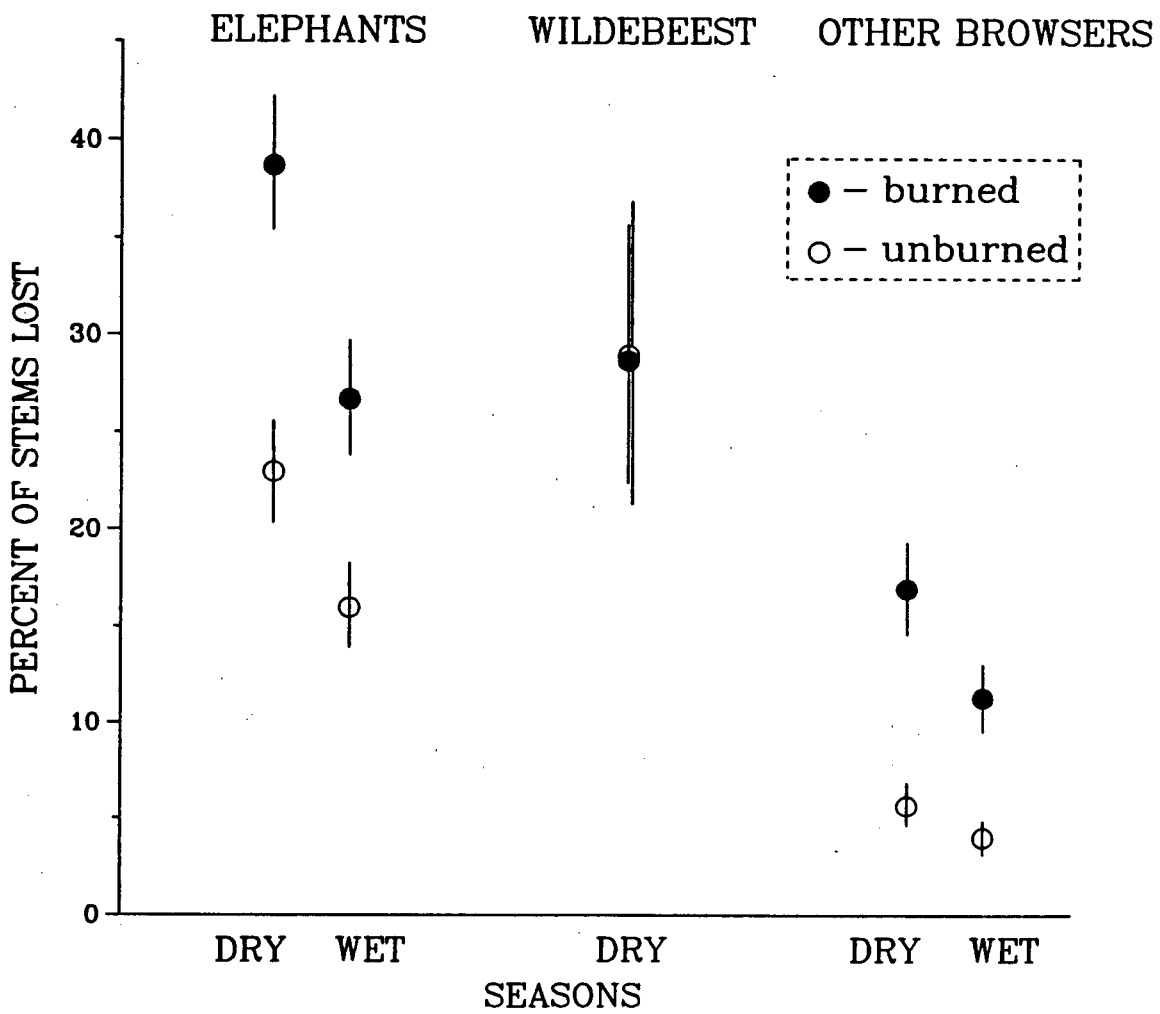

Figure 5.2. Percent of marked stems removed in each season by elephants, wildebeest, and other browsers (± one s.e. showing the variability between sites).

Table 5.3. ANOVA results for the fraction of stems removed by: (a) all causes of mortality combined; (b) elephant-related mortality only; and (c) wildebeest-related mortality only across seasons, sites, and treatments. A weighted three-way mixed effects ANOVA model was used (site was considered a random effect and the others were fixed). F-ratios are reported below, ** = P<.01, *** = P<.001.

EFFECT	D.F.	ALL CAUSES COMBINED	ELEPHANT ONLY	WILDEBEEST ONLY
SEASON	1	74.30***	63.60***	---
SITE	4	4.76**	n.s.	138.61***
TREATMENT	2	118.41***	965.58***	n.s.
REMAINDER	22	---	---	---

A weighted two-way ANOVA was performed separately on wildebeest-related stem loss (Table 5.3). Only dry season data were analyzed because the wildebeest are not present in the wet season. Migratory wildebeest removed on average 29% of all marked stems, in all plots combined, during their annual three to four month dry-season residency in the three study years. These stems were primarily killed by unintentional browsing, thrashing by rutting males and trampling by concentrated herds of migrants. The range of stem removal by wildebeest was 10 - 85% over three years on the five treatment sites. Stem losses were not significantly higher in burned than unburned plots but there was a significant site effect owing to the highly localized nature of damage by wildebeest. Whereas seedlings in some locations were only lightly damaged, seedlings in other areas were virtually all damaged. These differences may be accounted for by the movement patterns of migratory wildebeest. In the dry season, wildebeest follow local thunderstorms and then concentrate in areas of recent rainfall for three to four days.

The percent of stems removed by elephants alone was analyzed across seasons, sites, and treatments with a weighted three-way ANOVA (Table 5.3). Elephants showed two important patterns of stem use. First, they removed a significantly higher proportion of resprouting stems on burned plots than unburned plots (Tukey's multiple comparison at the 5% significance level). Elephants removed an average of 33% of all marked stems every six months in burned plots and 20% in unburned plots (Figure 5.2). Secondly, they removed

significantly more stems in the dry season than in the wet season (Table 5.3, season effect, P<.001). No significant site effect was found. Other browsers, such as impala (Aepyceros melampus), Grant's (Gazella granti) and Thomson's (Gazella thomsoni) gazelles, dikdik (Madoqua kirkii), giraffe (Giraffa camelopardalis), and rhinoceros (Diceros bicornis) removed an average of 14% burned plots and 5% unburned plots between seasons. Elephants removed more stems than other browsers on both burned and unburned plots during both the wet and dry season.

A weighted two-way ANOVA was performed on the fraction of stems browsed, trampled, or not damaged in burned and unburned plots across each of the 5 study sites (Table 5.4). Both site and treatment effects were significant. Overall, 38% of seedlings in unburned plots had no visible browsing damage versus 16% in burned plots (Figure 5.3). A second analysis on browse damage, only, showed no significant site differences but highly significant differences between burned and unburned plots. Browsing was significantly higher on burned plots than unburned plots (at the 5% significance level). While only 57% of the unburned seedlings were browsed, 78% of those in burned plots had been browsed to some extent. This preference was probably due to a qualitative difference between resprouting, burned seedlings and unburned seedlings. Of those seedlings which had been browsed the majority had damage to both the leaves and stems.

A third analysis for trampling damage, alone, showed no significant difference between treatments in the percent of

Table 5.4. ANOVA results for the fraction of stems damaged by: (a) all causes combined; (b) browsing damage only; and (c) trampling damage only across sites and treatments. A weighted two-way mixed effects ANOVA model was used (site was considered a random effect and treatment fixed). F-ratios are reported below, ** = P<.005, *** = P<.001.

EFFECT	D.F.	ALL CAUSES COMBINED	BROWSING ONLY	TRAMPLING ONLY
SITE	4	33.08**	n.s.	54.62***
TREATMENT	1	13615.13***	9459.93***	n.s.
REMAINDER	4	---	---	---

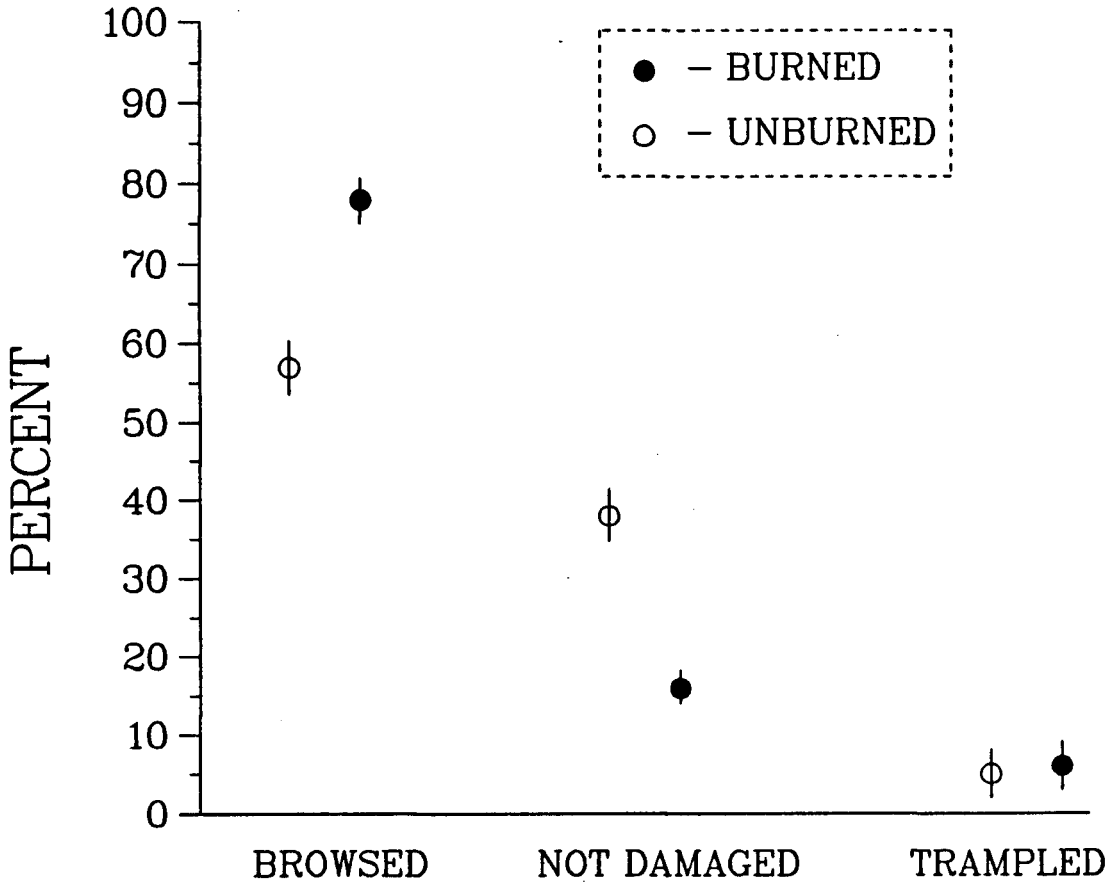

Figure 5.3. Percent of marked stems browsed, not damaged and trampled over the entire study period (± one s.e. showing the variability between sites).

individuals trampled (5% on unburned plots and 6% on burned plots). There was, however, a sigificant site effect. A multiple comparison test showed that two out of the five sites had a significantly higher percentage of stems trampled than the other three (at the 5% significance level). This is probably explained by the highly localized patterns of wildebeest impacts described above.

Although relatively few seedlings were actually killed each year, many were repeatedly browsed to ground level, resprouting at a later date. This process was termed "reversal" and these seedlings were called "regenerates". The cause of their disappearance was recorded whenever possible. Removals by elephant, fire, and wildebeest were easily distinguished from one another. The most interesting detail of these removals was the period of time required for resprouting (Figure 5.4). The majority (over 90%) of the plants removed by wildebeest or fire, that did resprout, returned within six months. Those removed by elephants, however, experienced much greater delays in recovery. Only 31% resprouted within 6 months, another 54% took a year, 9% took 18 months, and the remaining 7% required over 2 years to regrow. Therefore, not only did elephants remove the greatest proportion of seedlings at ground level but these seedlings took much longer to recover.

Seedling Growth: stem numbers and heights

Figure 5.5 shows the change in stem heights over the entire study period averaged over all sites for each treatment. A weighted two-way ANOVA model was used to examine stem heights

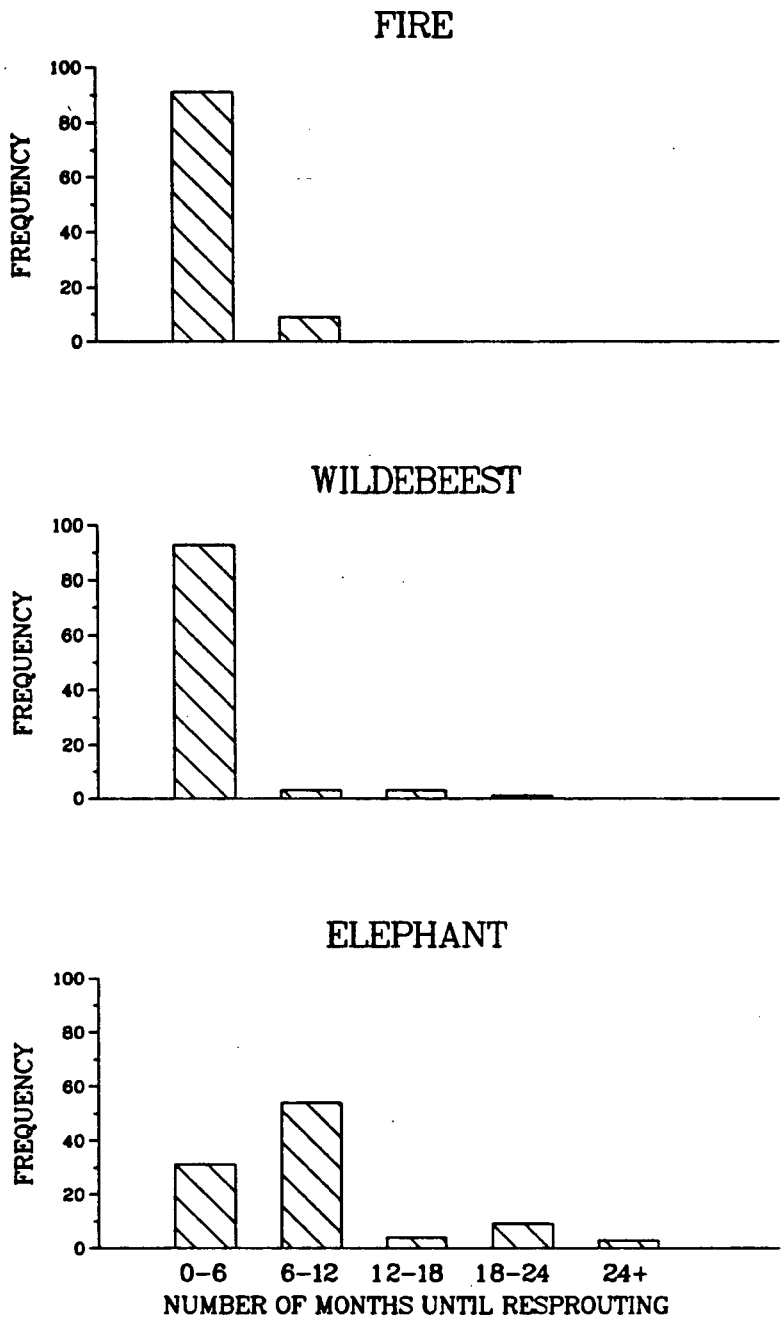

Figure 5.4. Frequency distribution of return times for resprouting "regenerates" originally removed by elephants, wildebeest, and fire.

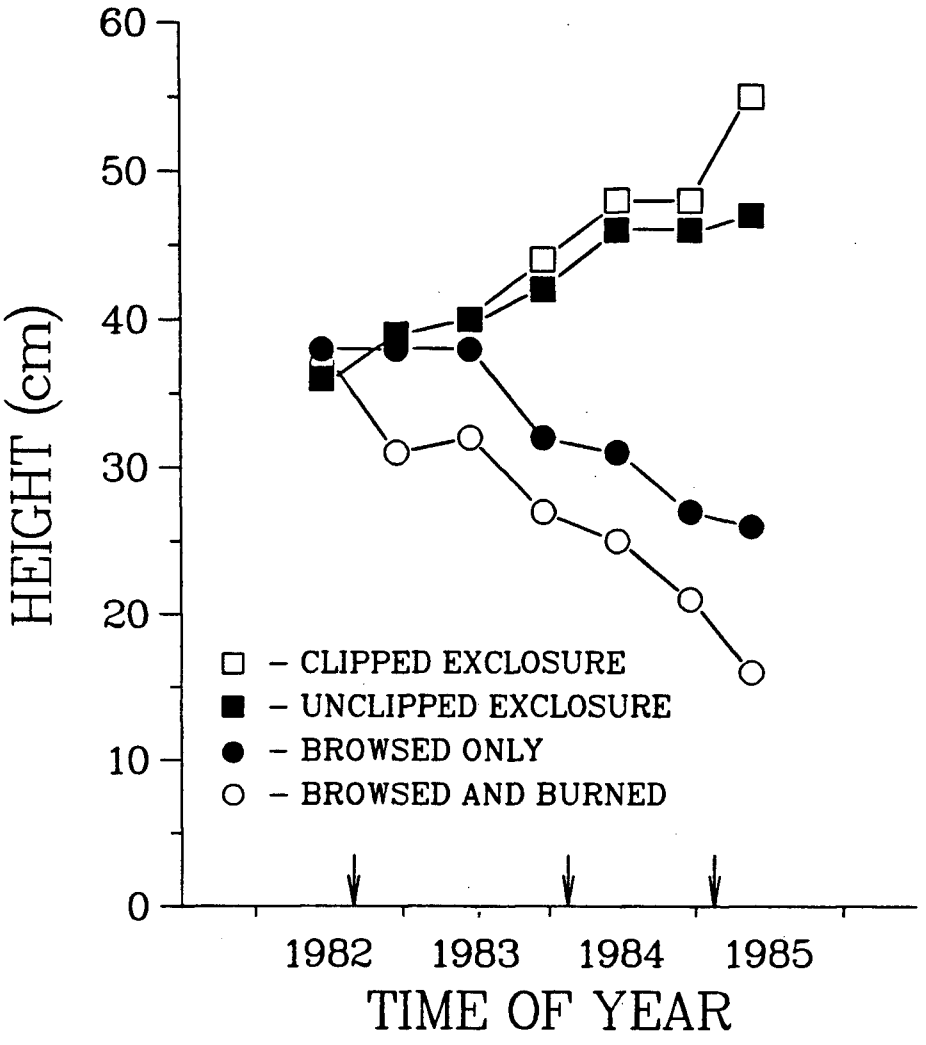

Figure 5.5. Change in the average heights of marked stems over the study period. Arrows indicate experimental burns.

amongst sites and treatments at the beginning of the study. No significant differences were found in stem heights between sites ($F = 1.96$, n.s.) or treatment plots ($F = 3.01$, n.s.).

A weighted two-way ANOVA was performed to examine the overall differences in changes in stem heights between burned and browsed plots (a), browsed only plots (b), and an average of the clipped and unclipped halves of exclosure plots (c) at the end of the study. No significant differences were found between sites ($F = 1.66$, n.s.), however, significant differences in the change in stem heights were found between treatments ($F = 588.59$, $P<.001$). Tukey's multiple comparison tests showed that the seedlings which were neither burned nor browsed grew significantly more than those which were browsed only and those which were browsed and burned (at the 5% significance level). In both the burned and browsed (a) and browsed only (b) treatment plots stem heights declined throughout the study. However, stem heights in the browsed only treatment plots did not decline as much as those in the browsed and burned treatment plots (at the 5% significance level). Stems which were browsed only declined from 38cm, on average, to 26cm, whereas those which were burned and browsed dropped from 37.5cm to 16cm over three years. In contrast, seedlings in exclosures grew between 10cm and 15cm per year.

The graph of mean stem heights over time (Figure 5.5) suggested that within the neither burned nor browsed treatment (c) those seedlings in the clipped half grew even more than those in the unclipped half. So, in a further analysis I divided treatment (c) into two separate treatments - clipped and

unclipped. I then performed a weighted two-way ANOVA on the change in stem heights between study sites in four treatment plots: burned and browsed, browsed only, clipped with no burning or browsing and unclipped with no burning or browsing. Although no differences were found between sites ($F = 1.89$, n.s.), there was still a significant treatment effect ($F = 39.61$, $P<.01$) even with the reduced sample size resulting from the separation of clipped and unclipped treatments.

The change in stem heights was significantly greater in clipped than unclipped plots and each of these treatments showed significantly more growth than the other two treatments which both showed stem height declines (Tukey's multiple comparison tests at the 5% significance level). Although both the clipped and unclipped plots started from an average height of 36cm, the clipped half grew to 55cm on average, while the unclipped half grew to only 47cm by the end of the study. The removal of grass appears to enhance seedling growth, but the negative effects of burning and browsing appear to swamp this effect in unprotected plots.

No significant differences in the average number of stems per plant were found amongst sites ($F = 3.11$, n.s.) or treatments ($F = 2.49$, n.s.) at the beginning of this study (Figure 5.6). A weighted two-way ANOVA on changes in stem numbers over the entire study still showed no significant site effect ($F = 3.93$, n.s.). However, changes in the average number of stems per plant did vary by treatment ($F = 410.85$, $P<.001$). In exclosure plots, there was no apparent change in the average number of stems per plant in either the clipped or unclipped

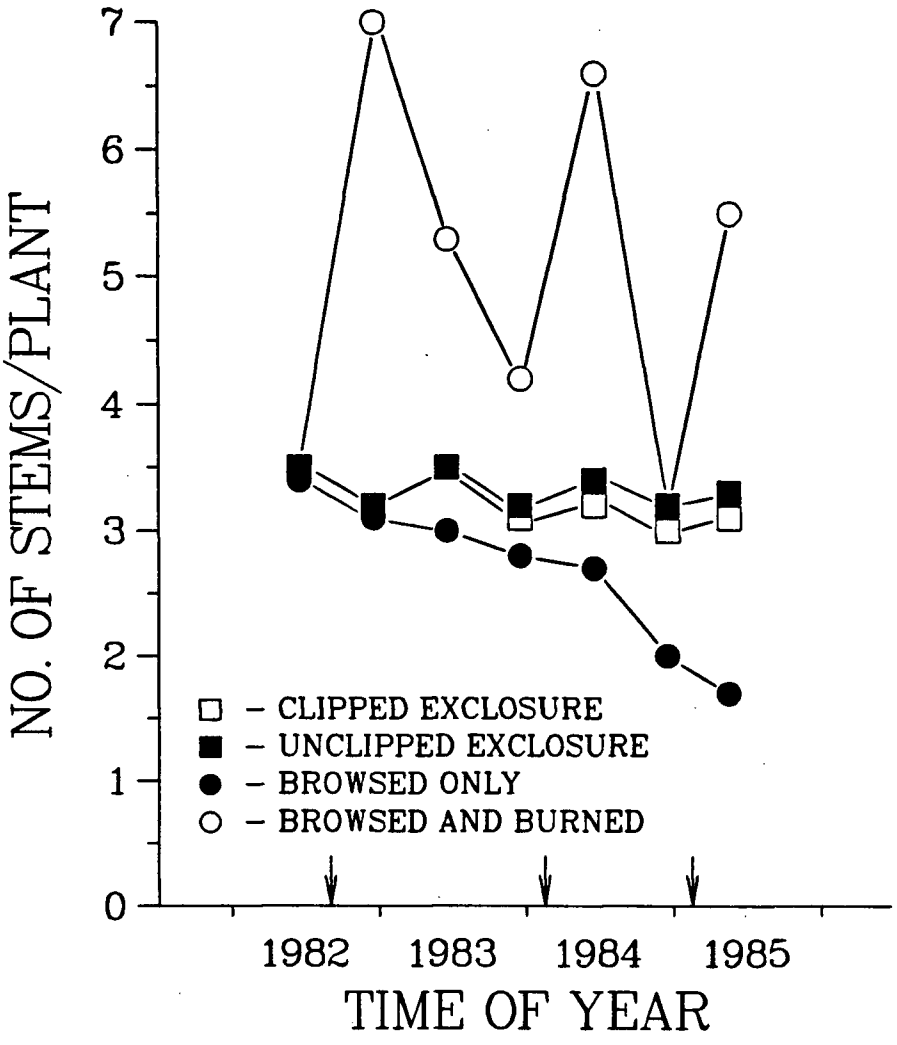

Figure 5.6. Change in the average number of stems per marked seedling over the study period. Arrows indicate experimental burns.

sides. Those plots which were browsed but not burned showed a steady decline in average stem numbers per individual from 3.6 to 1.7. Tukey's multiple comparison tests revealed that this loss of stems on browsed plots was significantly greater than either exclosures or burned and browsed plots (at the 5% significance level). By the end of the study, the average number of stems per plant was significantly greater in burned and browsed plots (5.5 stems/plant) than in exclosure plots (3.5 stems/plant) which were neither burned nor browsed (at the 5% significance level). While burning experiments apparently stimulated an immediate increase in stem numbers, stem numbers declined rapidly due to browsing in the time periods between burns but rose again following each subsequent burn (Figure 5.6).

Multiple-burn Experiments

Figure 5.7 shows the pattern of seedling mortality in the multiple-burn experiments. The percent of plants surviving are plotted against the number of burning trials for each treatment group. Plants in the lightest burning treatment (150g/m^2) showed very high survivorship with only eight plants being lost over the entire period. Those in the second burning treatment (300g/m^2) had over 80% survivorship until the seventh fire when survivorship dropped rapidly, leaving only 10% of the plants by the end of the study. The most severe treatment (600g/m^2) showed a similar pattern of survivorship, but heavy losses occurred earlier in the sequence of treatments: by the fifth burn survivorship had fallen below 60% and by the final burn

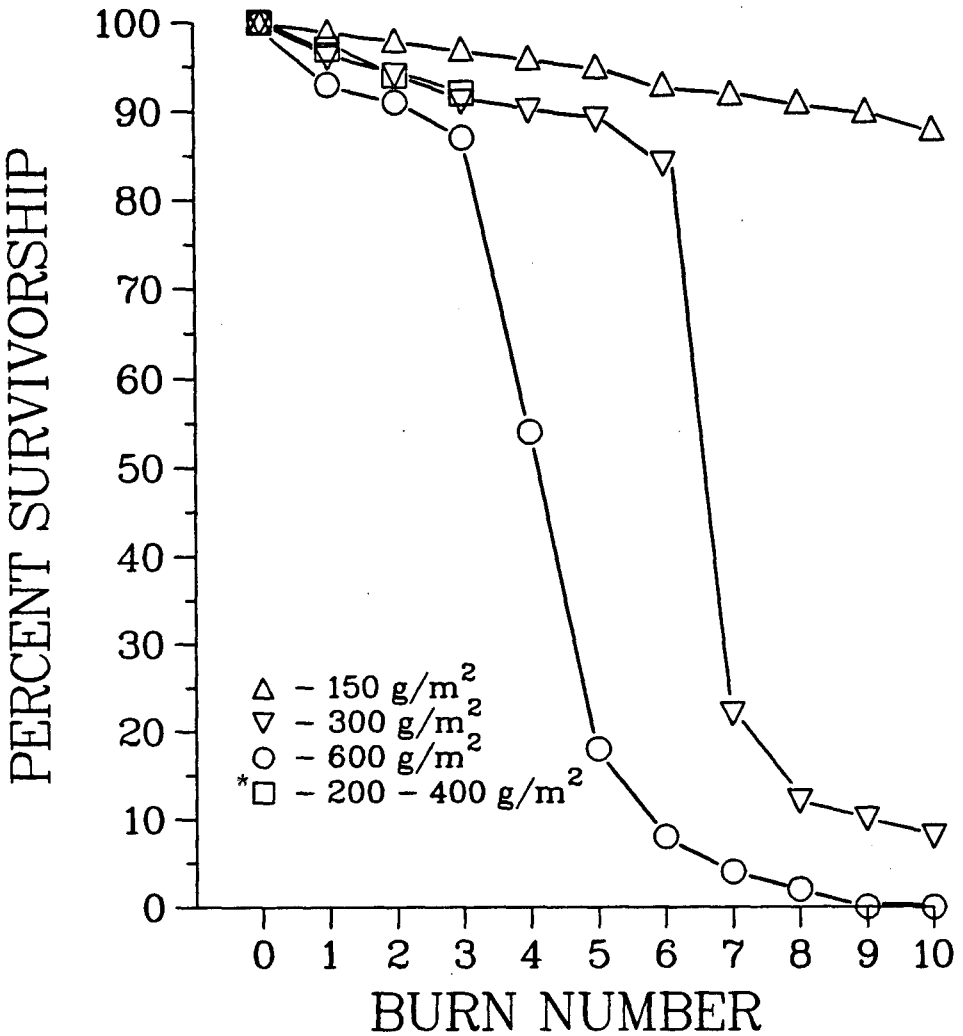

Figure 5.7. Seedling survivorship for multiple-burn experiments under three burning treatments.

Note : * = seedling survivorship for three, sequential, large-scale experimental burns where fuel loadings were 200 - 400 g/m^2.

there were no survivors at all. Figure 5.7 also shows survivorship from the large-scale burn experiments which had fuel loads between the first and second treatment levels. The survivorship patterns were in line with those produced by the first three trials of the multiple-burn experiments.

Seed Germination Experiments

The fire-treated seed experiments demonstrated a highly significant effect of fuel loadings on germination rates (Figure 5.8, $F = 1175.5$, $P<.001$). Germination rates were higher (mean = 64%) in those seeds exposed to 400 g/m^2 than in those exposed to the cooler temperatures experienced at 200 g/m^2 (mean = 29%), or the hotter temperatures at 600 g/m^2 (mean = 40%). All three of these treatments produced higher germination rates than those of control seeds (mean = 18%). The rate of successful germination declined as fuel loadings rose to 800 and 1000 g/m^2.

Discussion

If woodland regeneration were strictly dependent on existing seedling densities, the recovery of Mara woodlands would be assured. Seedling densities throughout the Reserve are still high but may be steadily declining under continued pressure from trampling by wildebeest, browsing by elephants and others, and wildfires. While Croze (1974b) concluded that *Acacia* woodlands in the Serengeti could withstand elephant predation, and Norton-Griffiths (1979) predicted that the

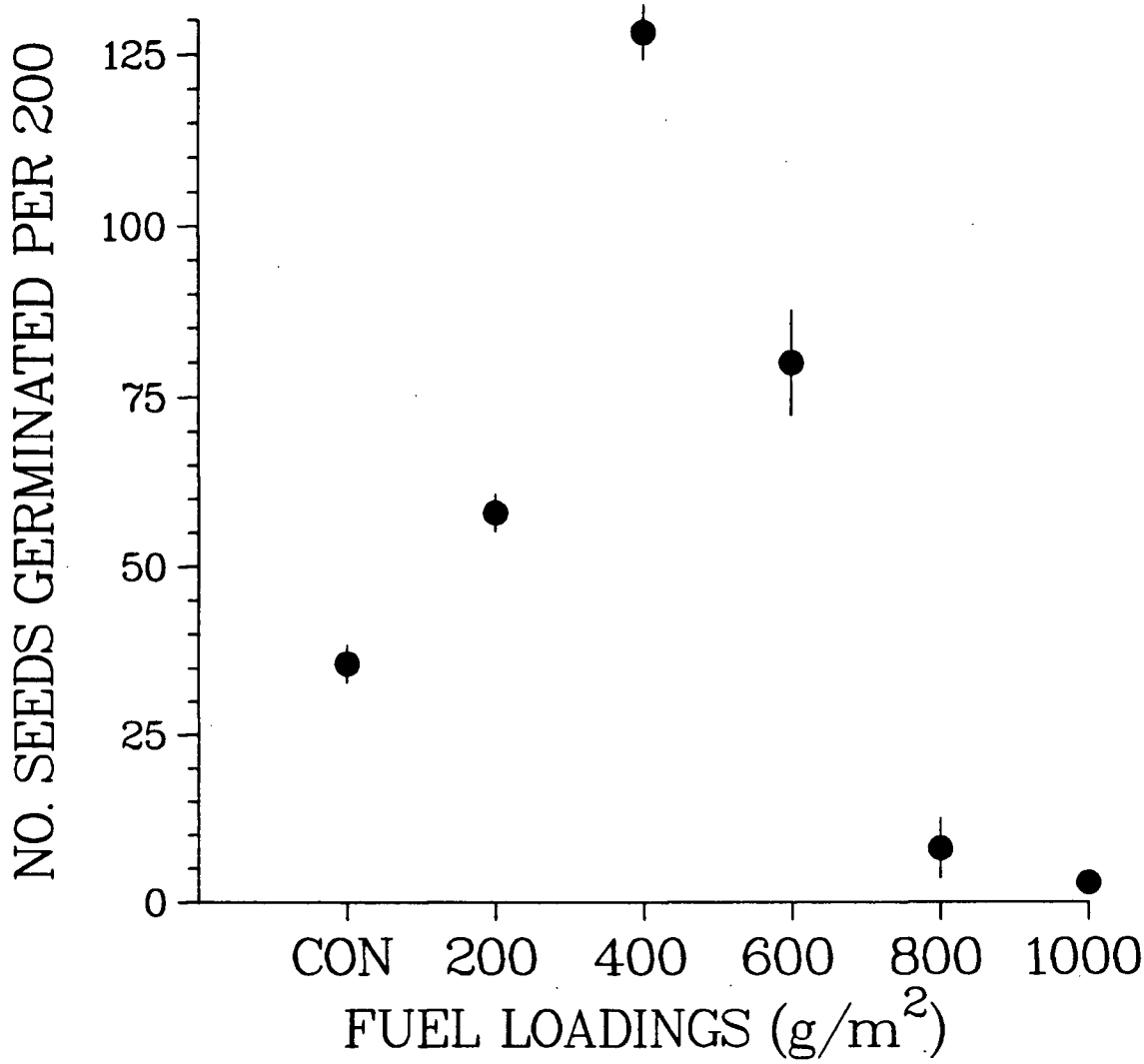

Figure 5.8. The average number of seeds germinating in ten sets (200 seeds each) under each of five different fuel loading treatments (± one s.d.). Fuel loadings of 200, 400, and 600 g/m^2 all stimulated germination beyond control levels.

increase which has occurred in wildebeest numbers would lead to a reduction in fires and a greater chance of woodland recovery, this recovery has not occurred yet in the Mara. Woodland regeneration is severely inhibited by the combined effects of elephants, fire, and wildebeest (Chapter 6).

Elephants

Under good growing conditions, trees in the Mara may require 15 - 20 years to reach 3m, at which they are no longer vulnerable to all but the most severe fires. Until they reach this height they experience damage from browsing, trampling and fire and even above this height they are still influenced by elephants and giraffe (Croze 1974a & b, Pellew 1983). Based on work by Croze (1974b) and Pellew (1983), Norton-Griffiths (1979) and Belsky (1984) assumed that elephants "largely ignored" trees under 1m and, therefore, had little affect on seedling survivorship in the Serengeti. In contrast, results from this study demonstrate that elephant browsing is currently a primary factor in seedling mortality and the inhibition of seedling growth in the Mara.

There are several possible explanations for this difference in findings. First, Croze (1974a & b) concluded that Serengeti elephants in the late 1960s and early 1970s browsed trees in approximate proportion to their height availabilities, but avoided trees under 1m. Trees above 1m were abundant, comprising up to 60% of the total population in the Acacia woodlands studied (Lamprey et al. 1967, Glover 1968, Croze

1974b, and Norton-Griffiths 1979). In the Mara there has been a major change in the height distribution of trees following a progressive loss of the taller classes (Dublin 1984, Chapter 2). Unlike the height distribution of trees in the 1960s, the current height structure of the Mara woodlands is heavily biased towards the 0 - 1m height class (Figure 5.9). Dublin (Chapter 4) showed that over 80% of the browse diets of elephants in the Mara came from trees less than 1m, which is in proportion to the current frequency distribution of tree heights in Acacia woodland stands. Therefore, the observed difference in the feeding behaviour of Mara elephants may have resulted from this change in the population structure of trees.

Secondly, elephants browsing on seedlings may mistakenly appear to be feeding on nearby grasses. Seedlings occur in their highest densities in open grassland areas of the Mara. From a distance, it is possible to mistake their feeding on seedlings for grazing on grasses. I determined forage selection by elephants in the Mara through direct, close-up observations of individual animals (Dublin, Chapter 4), whereas earlier studies often determined the forage preferences of elephants through their impact on vegetation and their distribution among habitats. These latter, indirect methods can be misleading. When elephants forage on seedlings, there is no obvious sign left after the seedling is completely removed. The patterns of elephant foraging recorded in the Mara are consistent with findings from other elephant populations. Studies by Brooks (1957), Buss (1961), Field and Ross (1976), Guy (1976), Jachmann and Bell (1985), Okula and Sise (1986), and Weyerhaeuser (1985)

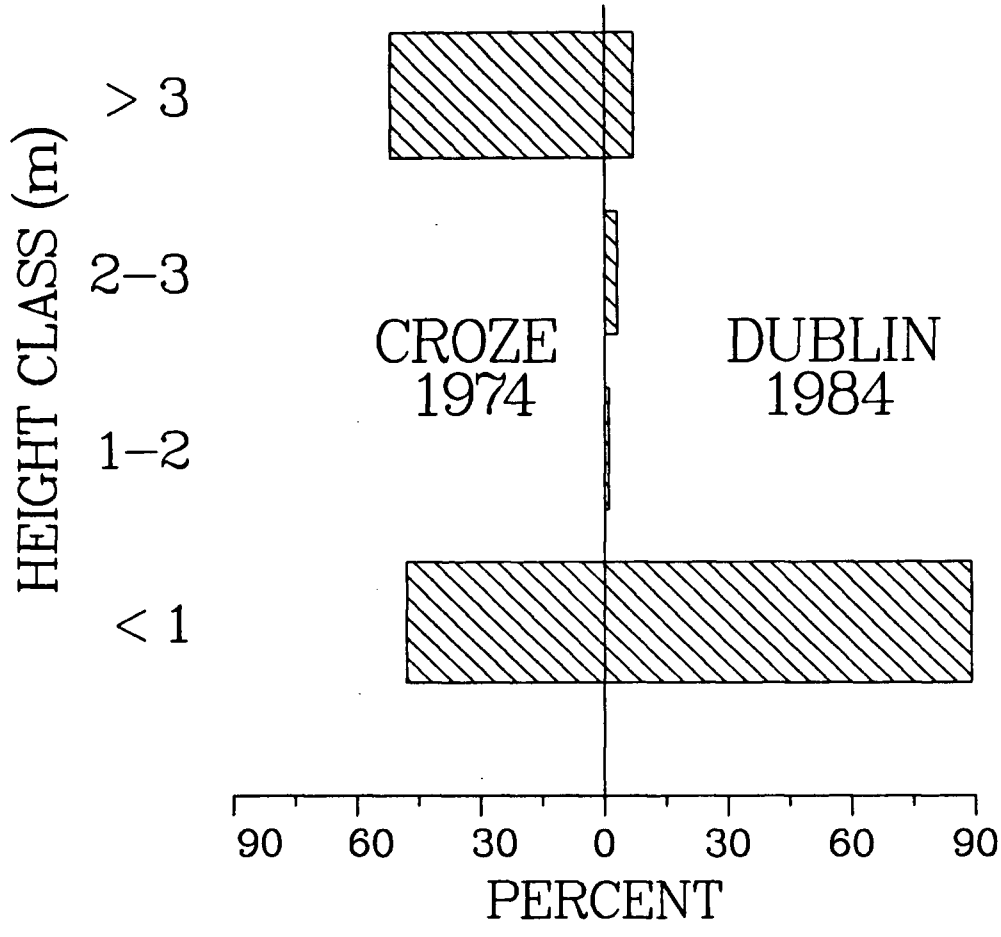

Figure 5.9. Distribution by height class for Acacias in the Seronera woodlands (Croze 1974b) and in the Mara woodlands (Dublin 1984).

all reported that elephants utilized regenerating seedlings where they were available. It is, therefore, possible that earlier studies of elephant feeding in the Serengeti simply failed to notice the extent to which elephants utilized seedlings.

Elephants were the most important cause in reducing seedling height back to ground level each year. This effect was consistently higher in the burned plots. Although a large proportion of these seedlings did eventually resprout, those taken by elephants took much longer to come back than those removed by fire or wildebeest. This suggests that elephants did more extensive damage to the plants than did fire or trampling effects (and hence the plants required a longer recovery period). During this period of recovery from elephant browsing, seedlings were exposed for a longer time to other factors affecting survivorship and establishment.

The impact of elephants on the regeneration of woodlands in the Mara is further exacerbated by the current distribution of local elephant populations. The northern Serengeti, just to the south of the Mara, is an extensive area of prime elephant habitat. In the 1960s and 1970s this area supported a large number of elephants which seasonally travelled north to the Mara (Watson and Bell 1969, Watson et al. 1969, Dublin and Douglas-Hamilton, in press) but were not resident all year. Today, elephants are being driven out of the northern Serengeti by intensive poaching pressure. Because of this influx from the south and increasing human settlement on the Reserve boundaries, the seasonal migration of elephants out of the Mara has been cut

off almost entirely. Currently, elephants are heavily concentrated within the Reserve (Figure 5.10) and over 1000 elephants are in residence year-round. If poaching in the northern Serengeti could be curbed, elephants might move back into that area, thereby temporarily easing the browsing pressure on woodlands in the Mara.

Fire

Fire has played an important role in the decline of woodlands and the inhibition of regeneration in the Serengeti-Mara (Dublin 1984, Chapter 2) and in many other areas of Africa (Buechner and Dawkins 1961, Thomas and Pratt 1967, Glover 1968, Pellew 1983, Trollope 1982a, 1984). But the impact of fire has changed in the Mara over the past 5 - 10 years. Since the mid-1970s a greater number of the migratory wildebeest (whose population numbers close to 1.5 million) have been spending the dry season in the Mara. Over the course of their 3 - 4 month residence, the wildebeest remove a significant proportion of the standing crop of dry grass (Dublin Chapter 4). Whereas, in the past, hot dry season fires burned annually, destroying woody vegetation, today they are not as damaging when they do occur. Most fires in the Mara now take place during the short dry season in February and March. At this time of the year the wildebeest are not present and resident herbivores are not abundant enough to remove a significant portion of the grass fuels. However, the short rains of November-December do not produce the same high grass biomass as the long rains and,

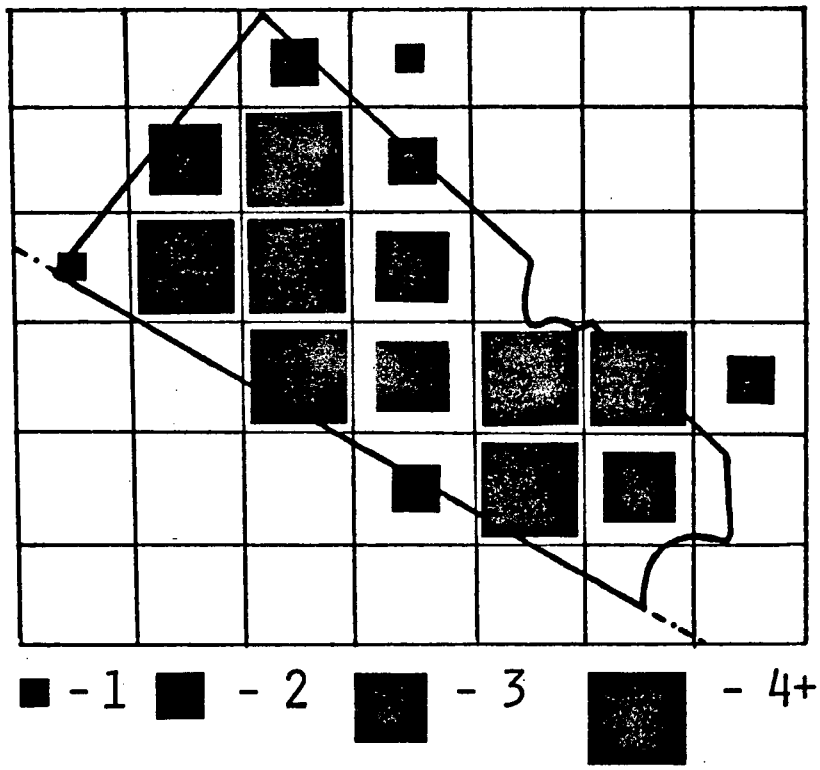

Figure 5.10. Elephant occupance within the Mara Game Reserve from 12 aerial surveys flown by the Kenya Rangelands Ecological Monitoring Unit (K.R.E.M.U.) between 1980 and 1983. The blocks represent the number of flights in which elephants were seen in each of the 10km x 10km grid squares.

Note : The surveys were flown over a much larger area (approx. 6,400 sq.km.), however, the only elephants seen were in or close to the Reserve, as shown.

therefore, short dry season fires are not as damaging as fires in the late dry season.

The large-scale experimental burns mimicked the characteristics of these wildfires well. Although these "moderately hot" grass fires resulted in almost 100% topkill of Acacia gerrardii seedlings, total seedling mortality was only 3 - 5%. The patterns of fire impact discussed here apply to a wide variety of less abundant tree species in the Mara. Presently, successful regeneration in the Mara seems limited to fire-resistant species such as Acacia gerrardii (Glover and Trump 1970, Pratt and Knight 1971, Spinage and Guinness 1972, Herlocker 1976a & b). Acacia gerrardii seedlings in the Mara showed a history of repeated burnings as indicated by their large rootstocks. Fire, in fact, stimulated the regrowth of multiple new stems which were then gradually reduced by browsers and repeated burns. Resprouting seemed to be limited primarily by water and the majority of seedlings reappeared shortly after the next rains. Coppicing is, in fact, the most commonly reported response to burning of woody species in Africa (Pienaar 1959, Kennan 1971, Pratt and Knight 1971, Trollope 1982a, Sabiiti 1986). Strang (1974) reported that eleven years of regular hot fires had not reduced the number of woody plants but merely led to coppicing and delayed woodland development. But, can this pattern of burning and resprouting go on indefinitely?

To answer this question, the multiple-burn experiments were designed to simulate the effects of repeated burns on seedlings. The process of seedling recovery was sped up in these experiments through artificial watering and, therefore, the

results may have exaggerated the rates of mortality caused by annual wildfires. However, even from a conservative perspective, the results suggest that root reserves are finite and that repeated burns would result in an eventual disappearance of trees under 3m. If wildebeest populations declined to their former low numbers (Sinclair 1979) and they no longer migrated to the Mara to remove the dry grass standing crop (Maddock 1979), hot dry season wildfires could again become a common occurrence - once or even twice each season. This would presumably accelerate the process of woodland decline which is already taking place (Norton-Griffiths 1979, Dublin, Chapter 2).

The effects of wildfires on seeds in the soil bed may also reduce the potential for woodland recovery. Story (1952), Harker (1959), Sabiiti (1986), and Sabiiti and Wein (in press) reported that exposure to fires stimulated the germination of some species of Acacia seeds. However, Trollope (1982a) argued that this was not necessarily so and that stimulation of germination may only be true when burns are followed by favourable moisture conditions. Experimental findings in the Mara suggest that germination rates may be a function of the actual intensity of the fire to which seeds are exposed. At temperatures recorded on the soil surface during average burns (400 g/m^2), seeds were stimulated to germinate well beyond control levels. The germination rates of those seeds exposed to somewhat cooler burns (200 g/m^2) also exceeded controls. However, hotter burns significantly retarded the germination rates of Acacia gerrardii seeds compared to the controls. Such

fuel loadings and fire intensities are found under natural conditions in the Mara.

The Mara woodlands currently contain a very small proportion of mature, seed-producing trees. Although the length of life for seeds already within the soil is unknown, it is probably not indefinite. The only other seeds available are those carried by transient herbivores, like elephants, from outside the Reserve and deposited within. Under current conditions, this requires not only long-distance movements by carriers but also travel to areas inhabited by local pastoralists or poachers. The limited seed source in the Mara may eventually limit the regeneration potential of existing woodlands; the role of hot fires in reducing germination rates of seeds in the soil further exacerbates this problem.

In the Brachystegia woodlands of Malawi, Bell and Jachmann (1984) found that elephants actually avoided burned areas. From this they concluded that fire could be an effective tool in manipulating elephant distributions and reducing the impact of their browsing on woodlands. However, in this study, elephants browsed even more intensively on burned plots. This was most likely because newly resprouting seedlings were high in protein (Dougall et al. 1964, Pellew 1981) and browse of all kinds was in short supply in the Mara.

The results from my controlled, multiple-burn experiments (Figure 5.7) suggest that even under current burning conditions (fuel loading of 200 - 400g/m^2), root reserves are probably being depleted by short dry season fires. This, coupled with continued browsing by elephants, diminishes the likelihood of

woodland recovery. A change in both burning and browsing regimes will be necessary if the current trend towards open grasslands is to be slowed or halted (see Chapter 6).

Wildebeest

Though the combination of elephants and fire appears to be effectively inhibiting the recovery of *Acacia* woodlands in the Mara, there is a third important factor. The role of wildebeest in removing the standing crop and thus limiting the intensity of fires has been discussed above. Wildebeest, however, have a second, less obvious role in woodland dynamics. Under present day conditions, the sheer numbers of wildebeest inhabiting the Mara Reserve during the dry season are having a significant impact on the woody vegetation through trampling and feeding. When the wildebeest first enter the Mara, just following the cessation of the long rains, the grasses are tall and green. The wildebeest move through these areas, grazing as they go. Inadvertently, they bite off many stems of regenerating seedlings which are hidden in the tall grass, and they trample others. When they finally leave the Mara their grazing grounds are transformed into a dry wasteland, with little sign of live seedlings.

In addition to these trampling and accidental browsing effects, male wildebeest have a further impact on the woody vegetation. The Serengeti wildebeest are at the end of their rutting period when they first arrive in the Mara, and resident wildebeest (from the Mara Reserve and Loita Plains area) are

still in the peak of their breeding season. Like many other rutting ungulates, male wildebeest spar with seedlings and small trees in addition to other males. Though this damage is most prevalent in the 1-2m height class (which is underrepresented in the Mara) it is obvious in trees under 1m, as well. Belsky (1984) reported that young bull wildebeest broke tops and branches of Acacias in the range of 30-150cm. Such thrashing of seedlings may reduce the vigour of the plants but is not as significant a mortality factor as trampling and browsing which kill large numbers of stems in the Mara each year.

Other Browsers

In addition to elephants, the Mara still provides sufficient habitat for a rich diversity of other browsing mammals. Among these are impala, dikdik, some giraffe, a few rhinoceroses and seasonally even the Thomson's and Grant's gazelles have been shown to feed on woody species (Tieszen et al. 1979, pers. comm.). As Belsky (1984) suggested, these species probably were not major agents of mortality, but they did have a measureable impact on seedlings. As this study has shown, each year the majority of seedlings were reduced to ground level by several browsing species. This inhibition of growth by browsing is a significant factor in the failure of seedlings in the Mara to ever reach 1m let alone grow beyond it.

Summary

The number of mature trees in the Mara has been reduced over the past 30 years. The remaining mature trees are now being lost at a rate of over 8% per year. The future of these disappearing woodlands is dependent on the potential for replacement from regenerating seedlings.

In the Mara, the growth potential of seedlings and coppicing rootstocks is being severely inhibited. In this study, 4% of all seedlings were killed annually by elephants, 4% by fire, 1% by wildebeest trampling and thrashing and another 1% through other natural causes. Seedlings experienced the greatest impacts from elephants and other browsers in the dry season. Wildebeest, elephants, and other browsers removed up to 60% of all surviving stems in unburned plots and an even greater proportion in burned plots. While wildebeest impacts were similar under both treatments, elephants and other browsers showed a distinct preference for seedlings in burned plots. Browsing effects on seedlings varied accordingly and were significantly higher in burned plots than in unburned plots. The majority of seedlings removed at ground level by wildebeest or fire resprouted within six months. Those taken by elephants, however, experienced much greater delays in recovery. This suggests that elephants did more severe damage to the plants than did fire or wildebeest.

Seedlings exposed to browsing animals showed significant decreases in height over the study but were significantly taller than those seedlings which had been burned and browsed. Those seedlings which were browsed but not burned showed a steady

decline in stem numbers. However, burning, coupled with browsing, stimulated an increase in the stem numbers of marked seedlings. In exclosure plots, where seedlings were neither burned nor browsed, they grew a maximum of 10 - 15cm per year while the average number of stems remained more or less the same.

Multiple-burn experiments demonstrated that seedling survivorship was inversely related to the level of fire intensity. Seedling survivorship remained high after repeated cool burns (fuel loads up to 150g/m^2) but dropped significantly after repeated hot burns (fuel loads > 300g/m^2). Seed germination rates were stimulated beyond control levels by fires of 200 - 600g/m^2 but declined at higher fuel loadings.

Under current conditions, it is unlikely that mature trees will eventually be replaced and that woodlands in the Mara will expand or even persist. A significant change in one or more of the prevailing inhibitory factors must take place for woodlands within the Reserve to successfully regenerate.

CHAPTER 6. DYNAMICS OF THE MARA WOODLANDS: PAST, PRESENT, AND FUTURE

Introduction

The role of elephants in woodland declines has stimulated much controversy among ecologists and managers over the years. In the majority of cases elephants have been cited as the primary cause of woodland losses in parks and reserves throughout Africa (Eggeling 1947, Buechner and Dawkins 1961, Brooks and Buss 1962, Pienaar et al. 1966, Wing and Buss 1970, Laws 1970, Field 1971, Spence and Angus 1971, Harrington and Ross 1974, Laws et al. 1975, Thomson 1975, Guy 1976, Barnes 1982, Weyerhaeuser 1985). The Serengeti-Mara woodlands presented no exception to this case (Glover 1965, 1968, Lamprey et al. 1967, Russell 1968, Glover and Trump 1970).

By the 1960s, researchers and Park managers in the Serengeti were already deeply involved in the controversy. Tsavo National Park, in neighbouring Kenya, had become a focal point for the study of "elephant problems" (Glover and Sheldrick 1964, Laws 1969, 1970, Myers 1973, Parker 1983) and the question of controlled cropping of elephant populations was much in the forefront. Throughout southern Africa, park managers and ecologists had already begun cropping elephants in an attempt to halt woodland losses (Pienaar et al. 1966, van Wyk and Fairall 1969, Pienaar 1969). And, today, culling is still advocated and practiced in a number of countries (Bell 1983, Cumming 1983, de Vos et al. 1983, Owen-Smith 1983, Pienaar 1983). In few of these cases, if any, has it ever been fully established that

elephants are, in fact, the primary agent driving the observed trends from dense woodland to open grasslands.

My study of the decline and dynamics of the Masai Mara woodlands provided an opportunity to address this issue in a deductive manner. Two questions were central to this study. First, what factor(s) were responsible for the woodland declines over the past 30 years? And, second, what factor(s) are currently preventing any significant recovery of woodlands in the Reserve?

Under the first question, the "1960s elephant" hypothesis suggests that elephants, alone, were responsible for the observed declines through their impacts on mature trees. This hypothesis predicts that the rates of elephant damage measured in the early 1960s, during the period of the most extreme declines (Lamprey et al. 1967, Croze 1974a & b), had been sufficient to account for the observed losses. Alternatively, the "1960s fire" hypothesis states that fire, alone, through its effect on trees and seedlings under 3m, reduced recruitment rates to the point where they could not offset adult tree mortality rates. The fire hypothesis predicts that burning rates measured in the early 1960s (Sinclair 1975, Norton-Griffiths 1979), had been capable of causing the documented loss of woodlands in the northern Serengeti and Mara.

In answer to the second question, the "1980s fire" hypothesis states that fire, alone, through its repeated effect on seedlings and small trees is capable of inhibiting woodland regeneration. The hypothesis predicts that the present day rates of burning, within the Reserve boundaries, could halt the

recovery of the Mara woodlands and produce the patterns seen today. Using the rates of browsing by elephants that I recorded in the Mara over the past four years, the "1980s elephant" hypothesis argues that elephants alone, through their effects on both seedlings and fully mature trees, are preventing the regeneration of the Mara woodlands. From recent census work, I established that elephant numbers were at unprecedented highs in the Mara, due to poaching in other areas of their range, and that the Mara is now experiencing heavy browsing by elephants on a year-round basis. I predicted that, taking into consideration the observed effect of elephants both on the seedling class (trees under 1m) and those which have escaped the effects of fire (over 3m), the woodlands will not be able to recover with the current numbers of resident elephants.

In addition to these four primary hypotheses, I also investigated the individual and synergistic effects of wildebeest and browsers (other than elephants) at their estimated levels in each time scenario.

To investigate the plausibility of these different hypotheses, I have developed a model which incorporates a number of measureable factors involved in both past and present woodland dynamics. The model is designed to examine the above hypotheses under a variety of conditions. Combinations of burning rates, elephant browsing rates, wildebeest trampling and thrashing effects, and the impact of resident browsers, as determined from actual measurements in the field, are used in the model and results are then compared with predictions.

The Model

1. The Assumptions

This model is a first attempt at simulating a complicated and dynamic natural system in which many factors operate simultaneously. For this reason, this initial effort is necessarily simplistic but, nonetheless, informative in its limited way. In designing a qualitative model of this type it is necessary to make a number of assumptions about the conditions under which the model can be expected to be accurate. The stated assumptions should be both biologically realistic and conservative.

The factors affecting woodland dynamics in the Mara and included within the model are the annual rates of: a) elephant impact on seedlings and mature, adult trees, b) burning, c) the damage due to the trampling, thrashing and inadvertent browsing by the migratory wildebeest, and d) browsing by resident browsers other than elephants.

A. Elephants

Elephants affect trees of all heights found in the Acacia woodlands of the Mara. The rates of browsing by elephants are treated as proportional to elephant population sizes (as determined from aerial total counts). In answering the initial question about the causes of woodland declines in the 1960s and 1970s, I have assumed that elephants fed according to the

patterns stated by Croze (1974a & b) and that they largely ignored seedlings under 1m during the time when larger trees were more abundant. In answering the second question about current woodland dynamics, I have determined browsing rates from direct observations of elephant feeding behaviour and from the measured effects elephants have had on marked trees of all height classes.

B. Fire

Fire affects all trees less than 3m high. The burning rate used in the present calculations is determined by the percentage of area burned over time (Norton-Griffiths 1979), which is assumed to be equivalent to the percentage of trees burned (when trees are uniformly distributed). It is also assumed that burning rates are correlated not only with fuel loadings but also with the number of people resident nearby. This assumption is made because most fires in this part of Africa are believed to be lit by humans and not started by lightning. I assumed, therefore, that at the turn of the century, although there were few wildebeest and there were probably sufficient fuel loadings to support severe fires, relatively few fires occurred because human populations in the area were very small.

C. Wildebeest

In the Mara, wildebeest significantly affect only those trees under 1m. The rates of mortality and stem loss on seedlings due to wildebeest were considered to be negligible during the period of rapid woodland loss in the 1960s. During this period, wildebeest numbers were still low following their recovery from rinderpest, and their annual migratory movements did not take them to the Mara in significant numbers (Pennycuick 1975, Maddock 1979). Wildebeest were assumed to have a measureable impact on woodland dynamics only when they had reached their current population size of around 1.5 million animals. The majority of these animals visit the Mara during the dry season each year.

D. Resident Browsers (other than elephants)

Like wildebeest, browsers in the Mara are assumed to affect only those trees under 1m. Giraffe numbers are relatively low in the Mara, probably due to a shortage of desirable forage. So, this means that the smaller species, such as impala, dikdik, and Grant's gazelles, at some times of the year, are the primary browsers involved in the woodland dynamics. Recent aerial censuses (Sinclair and Dublin, unpublished data) as compared with earlier census work (Sinclair and Norton-Griffiths 1979) indicate that resident browser population sizes have not changed significantly over the past 15 - 20 years. Therefore, I have assumed that browsing rates by animals other than elephants were

the same in the 1960s as my measurements have shown them to be in the Mara today.

Only fire and elephants are considered to be agents of both mortality and reversion of trees into smaller height classes, whereas, wildebeest act as reversion and inhibition agents (Norton-Griffiths 1979, Pellew 1983), and browsers act only as inhibition agents (see Appendix A).

2. Constants and Variables

The tree population used in the model is described by several constants. These constants (Table 6.1) are derived from the results of Lamprey et al. (1967), Glover (1968), Croze (1974a & b), Herlocker (1976a), Norton-Griffiths (1979), and Pellew (1981, 1983), in addition to my own data. Tree densities were converted to a 10 hectare basis for the purpose of analysis.

Seven variables are built into the model (Table 6.2). Six of these variables are expressed as "mortality", "reversion", or "inhibition" rates. Mortality rates refer to the percentage of seedlings or mature, adult trees which are killed annually by a given factor. "Reversal" rates refer to the proportion of seedlings which are browsed or trampled back to ground level but later resprout and "inhibition" rates pertain to the percentage of seedlings which repeatedly have stems removed though still maintain some stems above ground level. The seventh variable, burning rate, is derived from the proportion of woodland area burned each year and assumed to be equal to the percent of trees

Table 6.1. Constants which are built into the model.

FOR ALL PLANTS:

1) Seedling densities: 850/ha

2) Adult tree (>3m) densities: 32/ha

3) New seedlings: 17/ha/year

4) Growth of seedlings: 15cm/year

5) Fire escapement height: 3m

6) Natural mortality rate of adult trees and seedlings: 1%/year

FOR BURNED PLANTS:

1) Number of plants under 1m which are killed by fire: 5%

2) Number of plants in the 0-1m class which revert to the 0-1m class: 95%

3) Number of plants in the 1-2m class which revert to the 0-1m class: 90%

4) Number of plants in the 2-3m class which revert to the 0-1m class: 5%

5) Number of plants in the 2-3m class which revert to the 1-2m class: 29%

Table 6.2. The parameters varied in the model.

1) Burning rate
2) Elephant mortality rate on seedlings
3) Elephant reversal rate on seedlings
4) Wildebeest inhibition rate on seedlings
5) Wildebeest reversal rate on seedlings
6) Browser inhibition rate on seedlings
7) Mortality rate of mature, adult trees

exposed to fires annually. In examining the four working hypotheses, the input values of these seven variables are set at actual values reported from field studies in the Serengeti woodlands during the 1960s or from my own studies in the Mara in the 1980s. Predictions are made from each hypothesis for each time scenario (i. e. the 1960s and the 1980s) and then considered using the pertinent value of each variable for the appropriate time period.

3. Test Conditions

For the purpose of answering my two central questions, I established two data sets, one for the 1960s and one for the 1980s (Table 6.3). Predictions were generated from the "elephant and "fire" hypotheses put forth to explain the woodland losses in the 1960s and the current inhibition of woodland recovery. To isolate the individual effects of fire, elephants, and other factors, all other rates were held constant, while the factor of interest was varied within realistic ranges. To determine the synergistic effects of these factors on woodland dynamics, the effects of other browsers and wildebeest were added to those of elephants and fire.

Recruitment rate (R) is the ratio of trees entering the height class taller than 3m to mature trees dying. If R is greater than unity then the tree population is growing. For the figures, the natural log of R is used so that the threshold value is zero. When ln(R) is greater than 0, adult recruitment is exceeding adult mortality and the tree population is growing,

Table 6.3. The test conditions for the 1960s and 1980s which were used in the simulation model.

THE 1960s

450	approximate elephant population size
62.0%	burning rate
2.5%	overall elephant-related adult tree mortality
6.0%	localized elephant-related adult tree mortality
1.0%	other natural mortality of adult trees
26.0%	browser inhibition rate on seedlings

THE 1980s

1100	approximate elephant population size
5.0%	burning rate
7.0%	elephant-related adult tree mortality
4.0%	elephant mortality rate on seedlings
1.0%	other natural mortality of adult trees
8.0%	elephant reversal rate on seedlings
1.0%	wildebeest reversal rate on seedlings
29.0%	wildebeest inhibition rate on seedlings
26.0%	browser inhibition rate on seedlings

and vice versa.

Results

Woodland Declines in the 1960s

The values of variables in the 1960s scenario were set using data collected in the Serengeti National Park during that time. It was assumed that during this period elephants largely ignored seedlings under 1m. However, two levels of adult tree mortality by elephants were used in these calculations. First, I used the mortality rates reported by Lamprey *et al.* (1967) and Croze (1974b), for severely affected local areas of the central Serengeti woodlands, (approx. 6%). Second, Croze's more conservative estimates for the overall rate of elephant-related tree mortality of 2.5% were run through the model. Burning rates were also set according to those measured at the time. Although Norton-Griffiths (1979) reported a 75 - 100% burning rate in the area bordering the Mara during this period, the more conservative average of 62% burning throughout the tall grasslands was used (Sinclair 1975). Browsing rates, by species other than elephants, were set at 26% per year and wildebeest were considered to have no impact at this time.

If elephants, alone, were responsible for the decline in the woodlands ("1960s elephant" hypothesis), and if all other factors were set at zero, then an overall recruitment value ln(R) of less than 0 should occur. Table 6.4 shows that at adult mortality rates of 3.5% per year (2.5% due to elephants,

Table 6.4. The ln(Recruitment rates) for fire, elephants, and browsers acting alone in the 1960s scenario. Those values less than zero indicate woodland loss, whereas those values greater than zero indicate woodland increase.

FACTOR	ln(Recruitment rate)
Fire	-2.91
Elephants (at 2.5% elephant-related adult tree mortality)	2.74
Elephants (at 6.0% elephant-related adult tree mortality)	2.05
Browsers	2.46

plus, 1.0% due to natural causes), the ln(R) value equals 2.74. At the highest reported adult mortality rates of 7.0% (6.0% due to elephants, plus, 1.0% due to other natural causes) the ln(R) value was still greater than 0, at 2.05, contrary to that predicted by the elephant hypothesis.

If fire, alone, caused the woodland declines of the 1960s ("1960s fire" hypothesis), and if all other factors were held at zero, then the recruitment value (ln(R)) should be less than 0. Table 6.4 shows the ln(R) value to be -2.91 under these conditions, in agreement with the fire hypothesis.

Browsers, alone, were unable to reduce the ln(R) value below zero (Table 6.4). Figure 6.1 shows the ln(R) values for different population sizes of elephants (as a percentage of current elephant numbers in the Mara) without other browsers or wildebeest, with other browsers but no wildebeest, and coupled with other browsers and wildebeest. At Croze's (1974b) estimate for overall elephant-related tree mortality (2.5%/year) in addition to other natural mortality (1.0%/year) and other browsers, ln(R) was 1.16 (Figure 6.1). Even when elephant-related tree mortality rates were set at their highest reported levels (6.0%/year), ln(R) was still above zero (0.47).

The addition of browsing effects to those of fire, alone, only made the ln(R) value more negative (Figure 6.2). When fire, elephants, and browsers are all acting together and adult mortality rates are set at 7.0%/year (6.0% due to elephants, plus 1.0% due to other natural causes), the ln(R) value was -8.23. When adult tree mortality rates were set at 3.5%/year (2.5% due to elephants, plus 1.0% due to other natural causes),

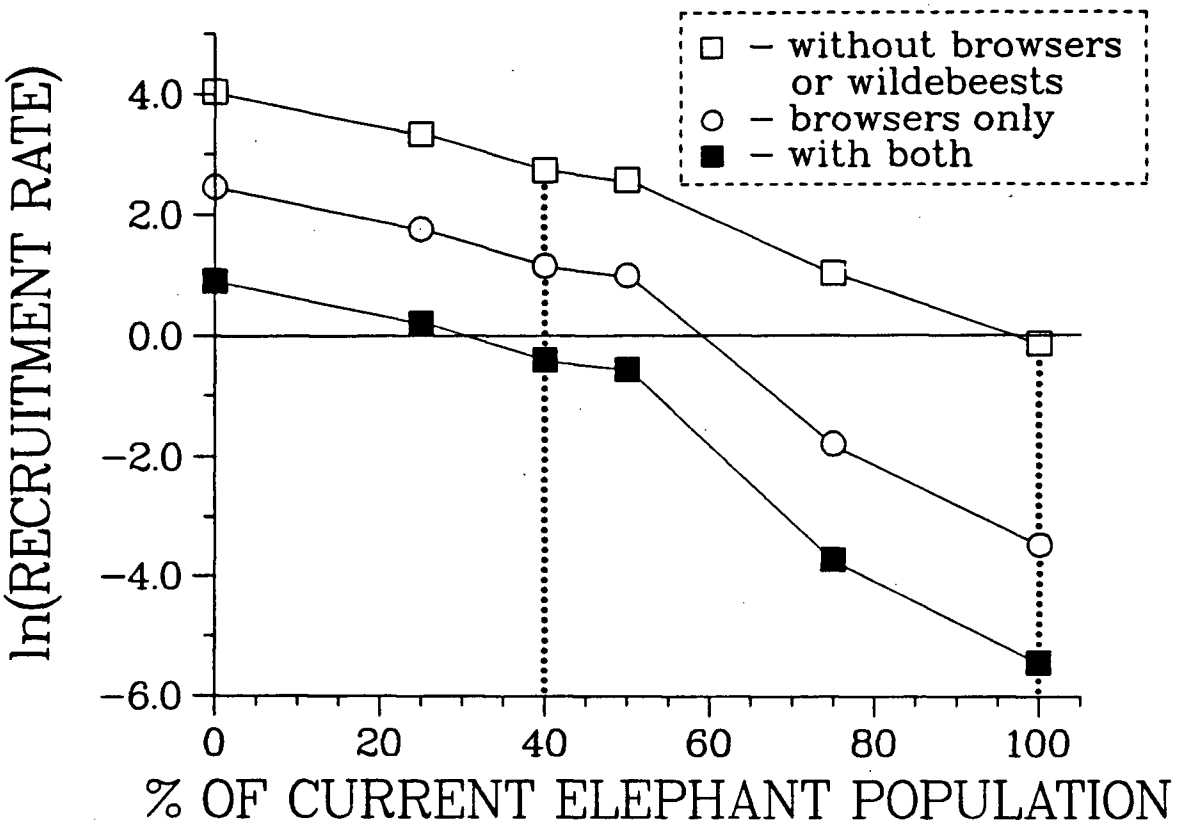

Figure 6.1. The natural log of recruitment rates (R) for varying elephant populations: a) without wildebeest or browsers; b) with browsers but no wildebeest; and c) with both wildebeest and browsers. Those values less than zero indicate woodland loss, while those values greater than zero indicate woodland increases.

Note : The dotted line at 40% represents elephant population sizes of the 1960s. The dotted line at 100% represents the current elephant population size in the Mara. Burning rates are held at zero.

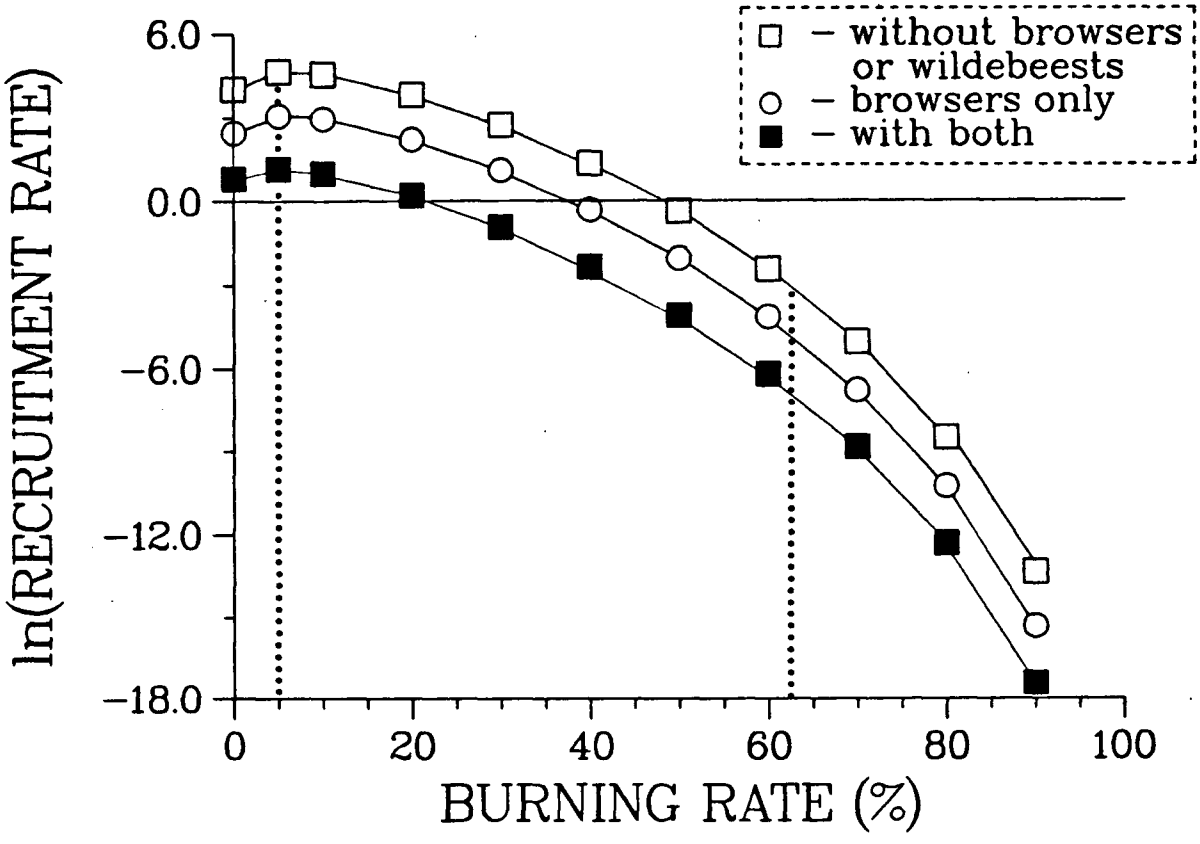

Figure 6.2. The natural log of recruitment rates (R) for varying burning rates: a) without wildebeest or browsers; b) with browsers but no wildebeest; and c) with both wildebeest and browsers. Those values less than zero indicate woodland loss, while those values greater than zero indicate woodland increases.

Note : The dotted line at 62% represents the burning rates of the 1960s. The dotted line at 5% represents the current burning rates in the Mara. Elephant impacts are held at zero.

the ln(R) was -7.95. This latter case most accurately describes the actual 1960s scenario when significant woodland losses occurred (Chapter 2).

Woodland Dynamics in the 1980s

All variable values under the 1980s scenario were set from those recorded in the course of this study. Burning rates have been very much reduced in recent years, since the wildebeest have moved to the Mara in large numbers during the dry season. For the purposes of this modelling exercise, I have set current day burning rates at 5% per year. Elephants are at their highest recorded population numbers, over 2.4 times those counted in the late 1960s and early 1970s for the Mara (Stewart and Talbot 1962, Talbot and Stewart 1964, Dublin and Douglas-Hamilton, in press). Adult tree mortality rates were set at 8.0% (7.0% due to elephants and 1.0% due to natural causes). Browsing rates were the same as those used in the 1960s scenario as recent census data and that of Talbot and Stewart (1964) and Stelfox et al. (1986) shows little change in the population sizes of these species. The most important additional factor in the current day situation is that of the migratory wildebeest. Their impacts have been incorporated in this model.

The "1980s fire" hypothesis states that fire, alone, is responsible for the inhibition of woodland recovery. If fire is responsible, then at today's burning rates, with all other factors being held at zero, the ln(R) value should be less than 0. Table 6.5 and Figure 6.2 show that the current ln(R) value for fire, acting alone, is 4.66, a number considerably greater

Table 6.5. The ln(Recruitment rates) for fire, elephants, browsers, and wildebeest acting alone in the 1980s scenario. Those values less than zero indicate woodland loss, whereas those value greater than zero indicate woodland increase.

FACTOR	ln(Recruitment rate)
Fire	4.66
Elephants (at 7.0% elephant-related adult tree mortality)	-0.14
Browsers	2.46
Wildebeest	2.58

than zero. Fire, therefore, is not the main inhibitor of seedling regeneration.

The "1980s elephant" hypothesis states that elephants, in the absence of any other factors, can prevent the expansion of the Mara woodlands. In this case, elephant impact, alone, should result in a ln(R) value of less than 0. Under these conditions, the ln(R) value was, in fact, -0.14 (Table 6.5 and Figure 6.1). Therefore, elephants are capable of preventing seedling regeneration under current conditions but not to a great degree.

Neither browsers nor wildebeest, when considered in the absence of all other factors, reduced the ln(R) to a negative value (Table 6.5). Even when wildebeest and browsers are added to the current burning effects, ln(R) values still remain positive (Figure 6.2). Obviously, the addition of wildebeest and other browsers to the effects of elephants drives ln(R) values even further below zero (Figure 6.1). Under current conditions for elephants, fire, wildebeest, and other browsers, combined, the ln(R) value equals -5.64, indicating that the woodlands are still declining.

Woodland Dynamics in the 1890s

To challenge the model under a variety of plausible conditions, I went back and reconstructed the conditions of the late 1890s and early 1900s to see what pattern of woodland growth would be generated, assuming that woodland dynamics were operating in similar ways then as they are today. It is

important to note that there are limitations which accompany this assumption. Test conditions were set as accurately as possible from my historical reconstruction of the period (Chapter 2), however, there were no actual records available for rainfall, burning rates, or animal numbers.

Following the great rinderpest epidemic, wildebeest and human numbers had been reduced to negligible amounts. Likewise, poaching had greatly reduced the elephant population to the point where no elephants were reported by hunters for several decades following the turn of the century. Fires were presumed to be minimal due to the low human populations in areas nearby. And, I assumed that the browsing impact was not significantly different from that of today (though this could be an overestimation of their impact if rinderpest had also reduced their numbers). If rinderpest did affect browsers and reduce their numbers, then my calculation may overestimate the combined effects of all four factors during this period and, therefore, underestimate tree recruitment rates. Natural mortality of adult trees was considered to be 1.0%.

To examine this scenario, the burning rate was set at 5%/year, elephant and wildebeest effects were set at zero, and the impacts of other browsers set at the current rate of 26% per year. Under turn of the century conditions, the ln(R) value was well above zero (3.08), indicating an increase in woodland populations. This is consistent with the pattern of woodland expansion which took place between the late 1890s and the 1940s.

Escapement Rates of Trees under Different Scenarios

In addition to looking at recruitment rates into the adult height class, I also looked at the rates of recruitment into a variety of height classes prior to reaching the 3m class. I refer to these as escapement rates and they are presented in Figure 6.3 as log10 of the number escaping from each height class relative to 100,000 starting at the zero height class. To make these rates comparable to survival rates by age, I have assumed that plants reach the 15cm class in approximately one year, the 1m height class in 6 years, the 2m class in 11 years, and the 3m class in 15 years. I have considered three different scenarios in the calculations presented in Figure 6.3: 1) the conditions at the turn of the century, 2) the conditions of the 1960s, and 3) those conditions existing in the Mara today. The turn of the century period showed the greatest escapement rates into all height classes, whereas the conditions of the 1960s (except for escapement into the 15cm and 1m classes) were the lowest. This is consistent with the patterns of woodland growth and decline reported for these two time periods.

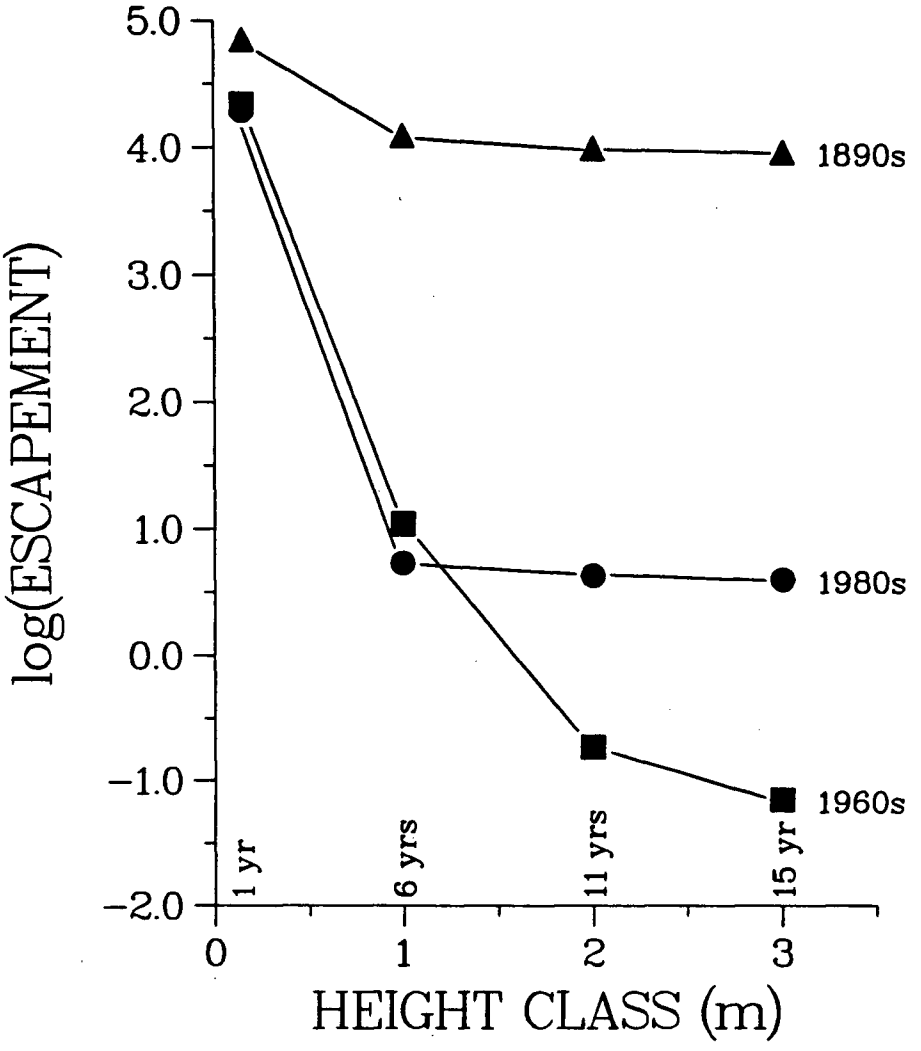

Figure 6.3. Escapement values for Acacia gerrardii to 0.15m, 1.0m, 2.0m, and 3.0m height classes plotted as the log(a cohort of 100,000 individuals in the starting population). I assume that 0.15m is achieved at 1 year, 1.0m at 6 years, 2.0m at 11 years, and 3.0m at approximately 15 years. Three different time scenarios are presented.

Discussion

The 1960s and 1970s

The hypothesis that elephants, alone, were responsible for the observed woodland losses in the 1960s and 1970s seems unlikely. Even under the most extreme conditions of elephant-related tree mortality, elephants were not able to reduce recruitment rates below mortality rates (Table 6.4). However, fire alone was easily able to hold recruitment rates well below mortality rates even at burning rates which were conservative (62% per year) for that period of time (Norton-Griffiths 1979). Therefore, I could not reject the explanation that fire was responsible for the woodland declines. Browsers served only to lower recruitment rates but were not capable of reducing woodlands on their own.

These findings support the contention of Croze (1974b), Norton-Griffiths (1979) and others that elephants were not responsible for the loss of woodland canopy cover in the northern Serengeti and Mara region. Despite their sometimes significant effects on local tree stands, elephants were not capable of moving the woodlands into a phase of decline on their own. Although elephant populations were increasing within the Serengeti and Mara boundaries during this period (Stewart and Talbot 1962, Talbot and Stewart 1964, Watson and Bell 1969, Dublin and Douglas-Hamilton, in press), they cannot fairly be blamed for the loss.

These results support the argument that under the prevailing burning conditions of the time, fire, alone, was able

to halt the succession of woodlands and produce the observed trend towards open grasslands. Rainfall during this period was uncommonly high, promoting unusually high grass productivity throughout the area. In addition, wildebeest populations were still being held below carrying capacity by the viral disease, rinderpest, and, therefore, they did not reduce the grass fuels significantly each dry season (Sinclair 1979). Consequently, the early 1960s was a period of frequent and severe fires in the northern Serengeti and Mara (Langridge et al. 1970, Dublin, Chapter 2).

Current Dynamics

Though conditions in the Mara are currently very different from those recorded 20 years ago, the woodlands continue to decline (Dublin Chapter 2), and at present there is no sign of recovery. In answer to the question of what factor(s) are preventing woodland regeneration, the hypothesis that fire, alone, is inhibiting woodland recovery seems implausible (Table 6.5). Recruitment rates under current burning rates exceed adult mortality rates. However, the same cannot be said for the effects of elephants in the Mara. Given the rates of elephant impact measured in the Mara during the early 1980s, the hypothesis that elephants, alone, are preventing woodland recovery seems likely. Elephants are holding recruitment rates below those necessary to balance adult mortality rates (Table 6.5). With the addition of browsers and the migratory wildebeest, woodlands are decreasing at an even more rapid rate

(Figure 6.1). Wildebeest and other browsers together, or coupled with current burning rates (Figure 6.2), still cannot drive recruitment rates below mortality in the absence of elephants.

Due to the present high rate of grass offtake by the migratory wildebeest (Chapter 4), fuel loadings in the Mara are no longer sufficient to support hot burns by the end of the dry season. Today burning is largely restricted to the short dry season, when fuel loads are lower, moisture content is higher, and fires are less damaging when they do occur. If these conditions persist, then fire cannot be considered a major concern in the inhibition of woodland recovery. However, if there were a significant change in wildebeest numbers, fire could once again become a major element in the control of woody regeneration.

Elephants, alone, now appear to be able to hold down woodland populations in the Mara. Poaching activity in the Serengeti and the settlement of most land surrounding the Reserve have led to a change in the patterns of elephant distribution and numbers in the past few years (Dublin and Douglas-Hamilton, in press). Today the Mara is utilized all year-round by approximately 1,000 elephants, over twice the numbers recorded in the 1960s. These elephants rely heavily on the available browse material, particularly during the dry season (Chapters 3 & 4). Because there is a scarcity of trees in the larger height classes, elephants now concentrate their browsing efforts on the "weeding" out of seedlings (Chapter 4 & 5). Croze (1974b) reported that in the 1960s and early 1970s

elephants in the Serengeti largely ignored these seedlings but today trees under 1m comprise a significant proportion of elephant diets. Although this change may be a reflection of availability rather than preference, it has important repercussions for woodland dynamics. As Norton-Griffiths (1979) concluded, the Serengeti-Mara woodlands seem to be far more sensitive to impacts on regenerating seedlings than to those on mature trees. Furthermore, Caughley's (1976) "stable limit cycle" hypothesis of woodland recovery cannot work unless seedlings have a safe refuge from elephant browsing. Seedlings in the Mara today have no such immunity.

In the case of the Mara woodlands, elephants were not capable of initiating the woodland declines reported two decades ago. However, once the adult tree densities had been reduced by the previous perturbation (i. e. increased burning rates following a reduction in wildebeest numbers and the increased frequency of man-made fires) elephants did accelerate the rate of decline. Today, elephants are holding the Mara ecosystem in a grassland phase. This pattern suggests that the Mara has two locally stable states (in the sense of Holling (1973)), predominantly woodland or grassland, and that an external factor such as fire is necessary to move the system between these two states. Elephants apparently cannot move the system from one state to another, but once it is in the grassland phase, elephants can hold it there.

The Future

These findings stimulate some interesting questions about the future of the Mara woodlands:

1) Would the woodlands stabilize if elephant numbers declined due to poaching or other factors?

A simple graph of the interaction of fire and elephants helps to answer this question (Figure 6.4). The scenarios represented by this graph include browsing at current levels but have not included the impacts of wildebeest. Even if we postulated a total decline of elephants, woodland recovery rates will be highly dependent on the rate of burning each year. Given present burning rates of 5% per year, the elephant population in the Mara would have to be 50% lower than their current numbers to achieve a balance of tree recruitment and mortality. To attain an increase in woodlands would require a further reduction in elephant numbers even if burning rates remained low. Realistically, dry season burning rates will not increase if wildebeest numbers remain high.

2) What would happen if a virulent strain of rinderpest returned to the system and reduced wildebeest numbers to pre-1960s levels?

At the turn of the century conditions were, in fact, similar to this scenario; wildebeest and elephant numbers were low and woodlands increased. However, there was one notable difference, fire probably had a limited role in the early 1900s because human populations in the area had also been reduced.

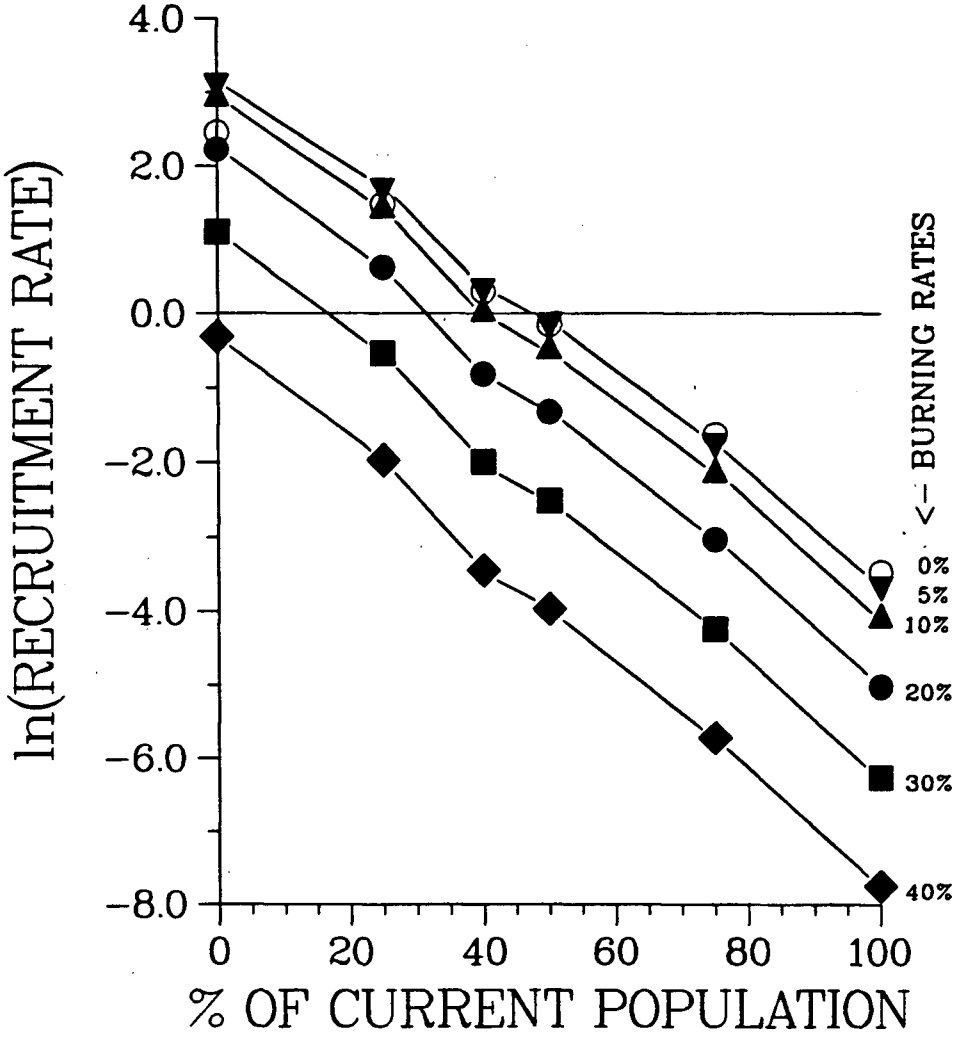

Figure 6.4. The natural log of recruitment rates (R) for both varying elephant population sizes and burning rates. In all cases, the impacts of wildebeest are held at zero and those of other browsers are held at their current rate. Burning rates are indicated on the right, vertical axis. Those values less than zero indicate woodland loss, while those values greater than zero indicate woodland increases.

Today, the area adjacent to the Mara is densely populated on a year-round basis (Lamprey 1985). These pastoralist peoples have always used fire as a tool in the cultivation of pasture land for their livestock. The main factor limiting the spread of fires set by man today is the amount of fuel available to burn. Therefore, if wildebeest numbers were reduced today burning rates might well return to those of the 1960s (above 60% per year) and fire would, once again, become an important factor in woodland dynamics. It would then become important to ask:

3) At what burning rate would we achieve a balance between recruitment and mortality rates if elephants and wildebeest were reduced?

Figure 6.4 allows us to answer this question by looking at the combined effects of varying levels of fire and elephant impacts. Even if elephants were totally eliminated from the Reserve, the woodlands would not begin recovery unless burning rates were held at less than 40% per year. This seems an unlikely possibility. Given the amount of grass produced in a normal year in the Mara (Chapter 4) burning rates of over 75% (Norton-Griffiths 1979) would be expected in the absence of significant wildebeest offtake. If elephant numbers in the Mara returned to their 1960s levels (approx. 40% of the current population size), woodlands could only be sustained under a 10% annual burning rate, an even less likely possibility.

For tree recruitment to exceed mortality when wildebeest are held at their current levels, simulations revealed that elephant numbers had to be reduced by 40% or more, even with

burning rates held at zero. Not only is it unreasonable to assume that fire could be totally eliminated from this ecosystem but, given the precarious status of elephants in many parts of Africa today (Douglas-Hamilton 1979), population reductions of this magnitude are not a desirable alternative.

Management Implications

Under present day conditions, the Mara seems to be locked into a grassland phase. Nothing short of dramatic reductions in elephant numbers combined with the control of burning seem able to reverse this trend. Fire may be maintained at low levels if wildebeest numbers remain high but how can we alleviate the impacts of elephants without having physically to remove them?

Currently, the northern Serengeti, which borders the Mara Reserve, is virtually devoid of elephants, although areas of suitable habitat exist. It is poaching, alone, which keeps the elephants from freely utilizing this area which has historically held large numbers (Watson and Bell 1969, Watson et al. 1969). The resulting concentration of elephants into the Mara is not desirable but could be relieved if Serengeti Park authorities could be helped to stop the poaching efforts which plague the north. In this age of extensive elephant poaching throughout Africa (Douglas-Hamilton 1983), cropping elephants for unnecessary reasons is unacceptable. When there is habitat available for them to roam freely, is it not our responsibility to secure it for them?

History has repeatedly shown that the Serengeti-Mara is by

no means a stable system. Perturbations, both natural and man-made, play a major role in the dynamics of this area (Sinclair & Norton-Griffiths 1979). For this reason, it is essential that trends in vegetation and animal populations in the Mara be closely monitored over time so that changes can be documented as they occur. From a management perspective, it is far better to track changes as they take place rather than confront the outcome when changes go unnoticed. Managers should always view change as integral and, thus, an essential consideration in planning for the future. Whether the Mara should remain an open grassland, whether it should be consciously managed to allow woodland recovery or whether it should be allowed to proceed along its own course without intervention is a decision for local authorities.

Political pressures and economic realities will be central to the future of the Mara. Conservation goals for the Reserve now rest with the Kenyan government. It will be their responsibility to formulate management plans which will address the needs of both the local peoples and the wildlife. To help them with this task, scientists must provide the necessary information on which they can base their decisions. The findings presented here may have important implications for management of the Mara in future.

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APPENDIX A. THE WOODLAND DYNAMICS MODEL

This appendix provides the parameter definitions and mathematical expressions incorporated in the woodland dynamics model of Chapter 6. Each equation expresses a particular proportion or number which is used in further calculations. Therefore, it is important to define the terminology used in the word descriptions of each mathematical expression in order to follow the logic of the model. The program was written in "awk" and run on a Vax 11/750 computer.

Animals and fire have three different effects on seedlings: "killing", "reversing", and "inhibiting". "Killed" refers to seedlings or trees which are removed and do not return. "Reversed" refers to those seedlings totally reduced to ground level but resprouting at some later date. "Inhibited" describes those seedlings which lose some but not all stems and are effectively kept in the height class below 1m. Only elephants and fire act as mortality agents. Fire, wildebeest, elephants and other browsers can all act as reversion agents, whereas, only wildebeest and browsers (which may include elephants under some scenarios) act as agents of inhibition.

Recruitment rate (R) is the proportion of trees entering the adult height class (3m) to the number of adult trees dying each year. The data are presented as the natural log (ln) of R-values.

Definitions of the parameters entered into the model:

$1 = proportion of seedlings and trees burned

$2 = proportion of seedlings "reversed" by

wildebeest

$3 = proportion of seedlings "killed" by elephants

$4 = proportion of seedlings "reversed" by elephants

$5 = proportion of seedlings "inhibited" by elephants plus other browsers

$6 = no. of adult trees "killed" by elephants and other natural causes

$7 = proportion of seedlings "inhibited" by wildebeest

Word descriptions of equations in the model:

q5 = no. of seedling entering the population annually

q6 = no. of seedlings regenerating after "reversal" by fire

q7 = proportion of seedlings regenerating after "reversal" by wildebeest

q71 = no. of seedlings regenerating after "reversal" by wildebeest

q8 = no. of seedlings regenerating after "reversal" by elephants

q9 = starting number of regenerating seedlings

q91 = no. surviving fire, elephant, and wildebeest effects

q10 = no. of seedlings "inhibited" by browsers

q101 = no. of seedlings "inhibited" by wildebeest

q11 = no. of recruits in first height class (<15cm)

q12 = no. escaping fire (F)

q13 = no. escaping (F) and wildebeest "reversal" (W)

q14 = no. escaping F, W, and elephant "killing" and "reversal" (E)

q15 = no. escaping F, W, E, and other browsers (B)

q151 = no. escaping F, W, E, and B = no. escaping at year 1

q16 = proportion escaping after year 1

q17 = no. escaping at year 6

q18 = no. escaping at year 7

q19 = proportion escaping at year 7

q20 = no. escaping at year 11

q21 = no. escaping at year 12

q22 = proportion escaping at year 12

q23 = no. escaping at year 15

q24 = recruitment rate (R)

q25 = natural log of R

Mathematical expressions incorporated in the model:

```
  q5 = 170.
  q6 = 0.95*$1*8500
  q7 = $2*(1-$1)
 q71 = q7*8500
  q8 = $4*8500
  q9 = (q5+q6+q71+q8)
 q91 = q9*(1-$1)*(1-$3-$4)*(1-q7)
```

```
 q10 = q91*$5
q101 = q91*(1-$5)*$7
 q11 = q9+q10+101
 q12 = (q11*(1-$1))+(0.05*$1*q11)
 q13 = (1-q7)*q12
 q14 = (1-$3-$4)*q13
 q15 = (1-$5)*q14
q151 = (1-$7)*q15
 q16 = q151/q11
 q36 = log10(100000*q16)
 q17 = q151*(exp(5*log(q16)))
 q37 = log10(100000*(q17/q11))
 q18 = (q17*(1-$1))+(q17*$1*0.1)
 q19 = q18/q17
 q20 = q18*(exp(4*log(q19)))
 q47 = log10(100000*(q20/q11))
 q21 = (q20*(1-$1))+(q20*$1*0.66)
 q22 = q21/q20
 q23 = q21*(exp(3*log(q22)))
 q57 = log10(100000*(q23/q11))
 q24 = q23/$6
 q25 = ln(q24)
```