

THE ECOLOGY OF A TRUNCATED ECOSYSTEM

THE ATHI-KAPITI PLAINS

Thesis submitted for the degree of

Doctor of Philosophy

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by

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DECLARATION

I, Helen Wanjiru Gichohi, declare that this thesis is my original work and has not been presented for a degree in any other University.

Signature  Date 12th February 1996.

We, Dr. D. Harper, of the Zoology Department, University of Leicester

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and Dr. D. Western of Kenya Wildlife Service (KWS)

Signature  Date 12 FEB 96

declare that this thesis has been submitted for examination with our approval as University Supervisors.

The Ecology of a Truncated Ecosystem - The Athi-Kapiti Plains
Helen W. Gichohi

ABSTRACT

Many ecosystems in Kenya are undergoing severe alteration due to landuse changes and associated human impacts. In one such large ecosystem, the Athi-Kapiti plains to the south of the city of Nairobi (and including Nairobi National Park), relatively healthy populations and migrations of large herbivores have been maintained despite increasing concentrations of domestic stock, settled agriculture amongst former pastoralists and increasing industrialization.

This study measured the factors that control the vegetation structure and the dynamics of the large herbivore communities. The effects of rainfall on vegetation quality, quantity and species composition was measured inside and outside exclosures, so that the effects of large herbivore grazing could be isolated. The distribution and movement patterns were established by aerial, ground and dung counts. Interactions between the herbivores and vegetation were studied by measuring patterns of vegetation use, species composition, chemical analyses for vegetation quality and dung quality.

The results show that the quality of vegetation and its biomass reflect the gradient of total rainfall across the Athi-Kapiti plains. Biomass accumulation rates in the exclosures were directly proportional to rainfall. Vegetation biomass and quality changed seasonally and with this, the distribution and utilization patterns by large herbivores. In general, vegetation quality and biomass were highest during the wet months and lowest during the dry regardless of grazing intensity. However, during both seasons, the heavily grazed areas had the highest quality vegetation. The plains in the south experienced heavy grazing in the wet season compared to Nairobi National Park. The impact of heavy grazing in the wet season was to increase plant diversity and produce shorter, more prostrate growth forms of plants.

Wildebeest and zebra migrated down the rainfall gradient from Nairobi National Park to the plains in the wet season and up the gradient on their return to the park in the dry season. Small ungulates tended to remain on the plains during the dry season while the large bulk feeders (e.g buffalo) remained in the park. The vegetation selection patterns shown by these herbivores were distinct: large grazers were negatively correlated with quality in contrast to small herbivores, which were strongly positively correlated. Medium sized grazers showed a positive relationship with vegetation quality but in the wet season only.

Variation in dung protein between the various species also illustrated the differences in the quality of diet selected by the large herbivores in the ecosystem. Browser dung had the highest crude-protein content followed by small, medium and large grazers in that order. The data revealed significant declines in dung protein with increasing body weight. Zebra, the only non-ruminant in the group, was the only exception to the quality body weight trends.

The conclusions drawn from the study show that despite being a highly altered ecosystem the large herbivore movements and diet selectivity patterns still follow rainfall and food quality pulses. This information can be used to make recommendations for the conservation of parts of the ecosystem which are critical to the migrations and the continued survival of this important wildlife population.

DEDICATION

To my family for giving me space and time needed to research and write a thesis. I appreciate the sacrifice you have made. To the many wives and mothers who have the aptitude and a burning desire to pursue a higher degree but are prevented by their many roles and the demands placed on their time. I now know that it takes a special family and special support!

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LIST OF ABBREVIATIONS

ACC	- African Conservation Centre
ADF	- Acid Detergent Fibre
CP	- Crude Protein
DCA	- Detrended Correspondence Analysis
DMD	- Dry Matter Digestibility
DRSRS	- Department of Resources Surveys and Remote Sensing
EANHS	- East African Natural History Society
EPZ	- Export Processing Zone
GIS	- Geographical Information Systems
KREMU	- Kenya Rangeland Ecological Monitoring Unit
KWS	- Kenya Wildlife Service
LSD	- Least Significant Differences
MCF	- Malignant Catarrh Fever
MR/GC ratio	- Metabolic rate to Gut capacity ratio
NDF	- Neutral Detergent Fibre
NNP	- Nairobi National Park
PCQ	- Point-Centre Quarter
WCI	- Wildlife Conservation International

CHAPTER 1

THE THEORIES OF COMMUNITY STRUCTURE IN RELATION TO MANAGEMENT OF LARGE HERBIVORES

1.1 Introduction

The Athi-Kapiti ecosystem occupies approximately 2400 km² to the south of Nairobi and includes the Nairobi National Park (hereafter NNP or the Park) in its northern end. It is a savanna ecosystem that once had the second largest migrating population of wildebeest and zebra in Kenya (Fig. 1.1). In addition to these large herds of wildlife, over 75% of this ecosystem also holds a large number of livestock. Pressures of human population growth, settlement, changing lifestyles and other human-induced changes have reduced the ecosystem as well as the ranging patterns of wildlife, but most of the wildlife is sufficiently intact for a study on large mammal communities. Many studies have been conducted in different East African ecosystems in order to explain large mammal distribution patterns for example (Lamprey, 1963; Western, 1973; Cobb, 1976; Norton-Griffiths, 1979; Walker and Noy-Mier, 1982; McNaughton, 1983) and to understand the factors that regulate their populations. Particular emphasis was placed on food (Sinclair, 1974; Western and Lindsay, 1984), rainfall and water availability (Coe *et al.*, 1976; Western, 1975) and competition (Dublin *et al.*, 1990; Sinclair, 1985; Sinclair and Norton-Griffiths, 1982).

Feeding patterns of some of the major species groups of the Athi-Kapiti ecosystem such as zebra (Owaga, 1975), Coke's hartebeest (Stanley-Price, 1974) as well as eland in Nairobi National Park (Hillman, 1979) have been studied. The interactions and structure of the ungulate community in the whole ecosystem has however not been adequately quantified and described. A better understanding of the large herbivore community of the Athi-Kapiti ecosystem is essential, especially in the light of its deteriorating conservation prospects due to changing land use patterns. Presently the only protected part of this ecosystem is NNP. It constitutes a very small part of the ecosystem and only covers the dry season feeding range. Information on the nutritional and spatial requirements of wildlife in this system can be used to argue a case for creation of corridors to a defined wet season dispersal area, or the conservation of an even further truncated ecosystem that will take account of the wet season needs as well.

1.2 Community structure

The term community is generally applied to assemblages of plants and animals found living together with some degree of permanence, and which also interact with one

another (Whittaker, 1975; Greig-Smith, 1986). The same combination of organisms tend to recur on different sites under similar environmental conditions and, given knowledge of the physical characteristics of the environment, geographical location and history of an area, it is in principle possible to predict what organisms will be found there (Greig-Smith, 1986). Each species of the many millions that inhabit the earth has different requirements for existence and characteristic variations in abundance in space and time. Each place on earth is distinctive, and is inhabited by a particular assemblage of species. The goal of community ecology is to understand the patterns in natural systems, to explain them by discerning the causal processes that underlie these patterns and processes (Brown and Maurer, 1989).

1.2.1 Theories and ideas on organization of communities

Different theories have been proposed to explain the factors governing ecological communities. The most prominent, the equilibrium theory presumes that systems are at or close to equilibrium, that they are ecologically saturated, resource limited and governed by biotic interactions especially competition (Cody, 1974a,b; Schoener, 1974b; Pianka, 1976). The theory assumes a certain constancy in the relative abundance of species, guilds and functional groups in a community. Stochastic extrinsic events play a relatively minor role and in a changing environment, the equilibrium community will track changing conditions with a minimum time lag (Gee and Giller, 1987). In general, equilibrium models tend to obscure important relationships between intrinsic and extrinsic processes in communities (Brown, 1988). The opponents of the equilibrium theory have in turn sought explanation for species diversity in chance, history (Hubbell and Forster, 1986) and variability (Chesson and Case, 1986). They define non-equilibrium communities as those that have varying and largely unpredictable structure. Biotic interactions are likely to be transitory and the evidence of their presence masked by direct and delayed responses to environmental factors. Stochastic extrinsic factors are likely to dominate the organisation of such communities. A slightly varied view of the non-equilibrium view emphasises deterministic or regular extrinsic factors e.g. the variable environment view of Wiens (1977).

The spatial and temporal scales of community investigations determine the range of patterns and processes that may be detected, and therefore the level of understanding and explanation that can be achieved. They also influence our perceptions of the nature of the community. It seems probable that the point occupied by the community on the equilibrium/non-equilibrium continuum depends on the scale of time on which it is being viewed (Gee and Giller, 1987).

1.2.2 Patterns in community structure

Many properties of communities are considered as possible evidence of community structure. These include species abundance relations (May, 1975), correlations between body size and abundance (Schoener and Janzen, 1968), food web patterns (Cohen, 1978; Yodzis, 1980; Pimm, 1982), geographical trends such as latitudinal gradients (Whittaker, 1975), patterns of geographical configurations (Brown and Maurer, 1989), life history traits and species diversity (Fischer, 1960; Pianka, 1966). In the last three decades however, ecologists have realised that explaining the enormous diversity and complexity of the natural world has only had limited success due to problems of scale, measurements of these patterns and trends in the real world as well as the interpretation of the patterns observed.

Amidst this complexity, ecologists have found what seems to be repeatable patterns such as ecomorphological relationships, diet niche relationships and patterns of habitat occupancy as well as the occurrence of limited subsets of species from the potential regional resource pool. These patterns observed among communities suggest that there are underlying factors or processes that constrain and structure ecological communities. The structure, production and dynamics of any ecosystem is determined by historical events (Ricklefs, 1987), proximally by both the extrinsic physical and biotic environment and intrinsic interactions among the species themselves (Brown, 1987; McNaughton and Georgiadis, 1986).

Other factors such as predation are also important. In many communities, however, competition and predation can work in concert to regulate a community (Vance, 1978). Moreover, the importance of competitors as opposed to predators and physical factors can oscillate seasonally (Koch, 1974) or vary from one ecosystem to another.

1.3 Physical controls on community structure

In a savanna grassland community the distribution of animals is often indirectly related to physical variables such as rainfall, temperature, soil type and geomorphology through their effects on vegetation type, its distribution and productivity. They also partly determine the quality of the vegetation. The combination of these factors also contributes to habitat heterogeneity by influencing the balance between trees and grasses. This can enhance species richness by simply providing a larger number of food types that are useable by potentially competing species.

1.3.1 Rainfall

Rainfall is a crucial factor in terrestrial ecosystems. It influences vegetation type and, therefore, indirectly secondary production. Primary production is related to rainfall in habitats ranging from deserts to moist savannas (Whittaker, 1975). The higher the rainfall, the greater the primary production. Secondary production of herbivores also increases as a function of rainfall across a wide range of habitats, for both wildlife and livestock (Watson, 1972; Coe *et al.*, 1976; East, 1984). The conclusions from large scale mammal surveys in the African savannas suggest that some robust and relatively simple rules govern herbivore biomass, production and turnover rates, richness, size frequency distribution and dominance along a resource gradient from arid to moist savannas (Coe *et al.*, 1976; Cumming, 1982; Western, 1989). Rainfall influences structure and productivity of grasslands and determines both food supply and availability of water to herbivores. Rainfall seasonality is important in determining the quality, quantity and distribution of vegetation in both time and space.

1.3.2 Soils

In addition to rainfall and vegetation, herbivore biomass is also related to geomorphology and soil type, basic geology and soil fertility (McNaughton and Georgiadis, 1986). East (1984) found that the correlation between biomass density and rainfall was positive for 19 of 23 herbivore species on highly fertile soils. Soil nutrient availability modifies the relationships between biomass and water availability, and secondly it influences composition of biomass and determines the quantities and vegetation types as well as the size classes of animals (Bell, 1982; Huntley, 1982). The quality of soil is inversely related to rainfall (Young, 1976). Protein production and hence soluble carbohydrates production are also strongly influenced by soil nutrient availability. McNaughton and Georgiadis (1986) showed that dystrophic savanna grasslands growing on old, heavily leached basement rocks are represented by the tall-grass landscape. The eutrophic savanna grasslands that grow on rich volcanic soils have short grass grasslands. The Amboseli ecosystem and Athi-Kapiti plains which are characterized by a high diversity of small and medium sized herbivores exemplify eutrophic grasslands (Bell, 1982; Huntley, 1982).

In general, soils derived from precambrian rock or ancient sedimentary formations contain low reserves of plant nutrients. The soils are sandy, highly weathered, heavily leached and moderately to extremely acidic. They also contain low levels of organic matter (Montgomery and Askew, 1983; Sarmiento, 1984; Tothill and Mott, 1985). In regions with annual rainfall above 700 mm these soils support dystrophic savannas. In

contrast, eutrophic soils occur in drier low rainfall regions where the effects of weathering and leaching are minimized. These soils are derived from basic rocks and alluvial deposits of volcanic ash. They are normally more alkaline, clayey and richer in organic carbon and nutrient reserves. Eutrophic savannas tend to have communities dominated by the medium sized grazers typical of African savanna parks such as wildebeest, zebra and gazelle species (McNaughton *et al.*, 1988). Bell (1982) derived a series of relationships between herbivore biomass to rainfall; one curve for volcanic soils of high fertility, one for soils of low fertility from basement rocks and another for basement rocks of the Rift Valley. The herbivore communities consisted of large bodied ungulates in higher rainfall areas, particularly elephant and buffalo where they contributed 75% or more of total animal biomass, and those in more arid grasslands where the smaller herbivores such as wildebeest and gazelles dominated the animal biomass.

1.4 Biotic controls on community structure

Community structure, initially defined by environmental variables, is often highly modified and mediated by biotic factors. Ungulates may for example regulate vegetation productivity to partially override the rainfall-driven primary production factors either by direct removal of vegetation or their influence on soil structure, nutrient status and soil moisture conditions. Large African mammals have major organizing effects upon ecosystem processes as well as structure. Where these animals are abundant their impact on vegetation physiognomy, structure, composition and quality can be profound.

There is strong evidence to suggest that large mammal ecosystems, whether dominated by wildlife or livestock, are limited by food (Coe *et al.*, 1976; Sinclair, 1975; 1979). In many grassland ecosystems availability of food to large herbivores is measured by the quality rather than the quantity. The seasonality in primary production due to rainfall results in seasons of food abundance and others of food shortages. Ungulates require on average 4-5 % of crude protein to maintain body fat. In the dry season there is a shortage of high quality herbage and quality requirements can only be obtained by selecting for the small quantity of green material available. Such resource limitation is one of the factors that causes competition among herbivores.

Competition as a major force causing the differential use of resources is believed to give rise to morphological and behavioural differences. One example of morphological differences is the variation in beak size in Darwin's finches. This allows the use of foods of different size and hardness. Behavioural differences are exemplified by divergence between species in feeding time or by feeding at different altitudes (Cody, 1974a; Pianka, 1976; Schoener, 1974a; 1982). Schoener (1983, 1985) and Connell (1983) summarized

more than 150 field experiments designed to test for the existence of the interspecific competition in natural communities. Although there were differences between the reviews (Schoener, 1985), both concluded that interspecific competition was detectable in more than half of the species studied (Tilman, 1987).

However, such competition has been hotly debated (Connell 1980) for over a quarter of a century (Schoener, 1982). The main areas of contention have been:

1. The use of observational data to infer competition. Inferences of competition have been made from niche differentiation, generally manifested in morphological and behavioural variation; for example among desert rodent communities (Brown, 1975), lizards (Schoener, 1970), Darwin's finches (Lack, 1969; Boag and Grant, 1981) and fruit pigeons (Diamond, 1975).
2. Removal experiments. Examples include experiments that show niche shifts or expansion in resource use when closely related or potentially competing populations are manipulated (Schoener, 1983).

Connell (1975) counter-argued that predation is the primary interaction structuring communities. His position was derived mainly from experiments performed in the marine intertidal region. Wiens' (1977) work on shrub-steppe birds suggested a lack of competitive-caused patterns and proposed the "variable environment view" in which competition is a sporadic, often impotent interaction. His observations suggested that shrub-steppe birds of North America were very different from birds in certain other ecosystems. Andrewartha and Birch (1954) had previously expressed similar ideas on competition and believed that the importance of competition as an agent of natural selection was minimal. In their view, climatic factors rather than biological interactions were the key.

Tilman (1987) contended that many of the experimental manipulations performed had determined the total effect of one species on another and have tended to concentrate on the phenomenon of competition rather than the mechanisms of the interactions for example (Connell, 1983; Schoener, 1983; 1986). In his view a study of competition should be mechanistic, i.e. include both the direct process by which competition occurs and information on the physiology, morphology and/or behaviour of individual species or functional groups. Thus if species compete for resources, then resource levels should be explicitly considered. Much of the confusion and disagreement may have arisen from the tendency of most scientists to generalise results obtained from working on particular organisms as already shown. Important differences between areas and between species, resources and other environmental variables are as a result ignored.

In East African savanna ecosystems the central question for many ecologists has been "Why is there peaceful coexistence of so many species that are dependent on the same resource base". For two decades, research on African ungulates has described ecological separation of savanna herbivores by habitat (Lamprey, 1963; Bell, 1970; Jarman, 1972), by species and size of animals as well as by plant parts eaten (Gwynne and Bell, 1968; Sinclair, 1977). The underlying premise was that any form of niche separation was the result of interspecific competition. Early pioneering studies by Lamprey (1963) in Tarangire Game Reserve, Tanzania showed feeding separation among herbivore species, ranging from exclusive grazers such as wildebeest and buffalo to strict browsers such as giraffe and dik-dik and between these two extremes, the mixed feeders. Lamprey (1963) further showed that feeding at different heights from the ground contributed to resource partitioning among species, as did the use of different habitats in wet and dry seasons and in the transition periods. In many studies, a high diversity of grazers co-existed with extensive overlap in the species composition of their diet (Lamprey, 1963; Hansen *et al.*, 1985). The proportion of different plant parts in ingesta has also been used as an indicator of trophic distinctions between grazers. Relatively more stem than leaf material was found in zebra diets than in wildebeest diets in the Serengeti, while fruits were more prevalent in the diet of Thomson's gazelle, especially during the dry season when fresh, short vegetation was in short supply (McNaughton and Georgiadis, 1986). Differences in feeding preference among herbivore species also emerged when food particles in gut and fecal samples were classified according to plant species (Hansen *et al.*, 1985; Hoffmann and Stewart, 1972).

Resource overlap indices have also been used as a measure of competition. In theory, the greater the overlap in the use of resources, the greater the competition coefficient - and hence - the greater the intensity of competition. But many field observations show that overlap varies seasonally (Smith *et al.*, 1978), and annually (Lister, 1980). In nearly all cases, overlap is smaller during the lean season, potentially the time of greater competition and overlap is higher when resources are plentiful.

It has been argued that during the lean times, strong directional selection resulting from interspecific competition is likely to have produced adaptations most suited to resources used relatively exclusively by the species (Lack, 1947; Schoener, 1982; 1986). During the period when resources are abundant (fat period), it may become profitable to use food types other than the ones for which the phenotype has specifically been selected (Gordon and Illius, 1989). African ungulates in areas of moderate to high rainfall concentrate on small areas during the wet season and disperse into expanded ranges during the dry season. In low rainfall areas, they commonly disperse over large areas

during the wet season and congregate in areas of higher rainfall and productivity potential during the dry season (Lamprey, 1963).

Hairston *et al.*, (1960) and Slobodkin *et al.*, (1967) had observed that green plants are normally abundant and largely intact and that herbivores are scarce, most of the time. In their view this indicated that herbivores as a whole are seldom food-limited but are instead regulated by predation. There is evidence for food limitation among some populations of herbivores e.g. Sinclair (1975; 1979), Caughley and Lawton (1981). Some plant parts are inedible due either to nutritional unacceptability or toxicity from secondary compounds (Van Valen, 1973). As a result herbivores have to select for green material that is digestible and of acceptable food quality. It has been postulated that the degree of selectivity among the various species is based on body size, gut capacity, digestive efficiencies and metabolic requirements (Demment and Van Soest, 1985). Therefore if competition is important in structuring communities (Diamond, 1978), then body size (Senft *et al.*, 1987) provides one mechanism by which herbivores can differentially use a food resource axis. In the East African savannas, a strong trend of increasing mean body weight with rainfall is reason to suppose that competition is size-related (Western, 1991).

Predation has already been referred to as a factor important in structuring communities. Four important predator species occur in many savanna ecosystems: lion, leopard, cheetah and spotted hyena. These predators make use of different sections of the biomass of potential prey. This differential use is related to habitat, hunting methods, time of hunting, the size and social organization of their prey. In the Serengeti, these factors may cause a relatively low degree of overlap in their food species and in the categories of food species eaten. In general, large predators feed on a wider array of prey than small species do. Lion can prey on large animals such as buffalo and small ones such as warthog and even rabbits and mice. Group hunting confers certain advantages to medium-sized carnivores and makes them as formidable as the largest carnivores. A good example is the hunting dogs, which can kill large animals like zebra.

The impact of predators on prey populations depends on the ratio of predator to prey, and the degree of movement of prey population. In systems with a migrating prey population, the impact of predators is limited to the time of year when prey and predator occur together. For the rest of the year predation is minimal. For resident prey populations the return of migrants usually heralds a period of reduced predation pressure by providing alternative and abundant prey. However, at low numbers predators have little impact on prey populations. Certain East African parks have low numbers of predators. In Amboseli park for example, many of the lions were poisoned during the protracted altercation between the Maasai and the government over the park (Western,

1994). A similar decline in lion numbers has been reported in Nairobi National Park. It is therefore unlikely that in these parks predators have much impact on prey populations. Where predators occur in large numbers, they may have significant impacts on prey populations. In some of the African savannas, there is some circumstantial evidence for regulation of prey populations by predators, for example resident antelopes in the Serengeti park by predators in general (Sinclair, 1985), Thomson's gazelle in Serengeti (Borner *et al.*, 1987), wildebeest by lion in Kruger Park (Smuts, 1978) and in the Ngorongoro, the presence of large numbers of hyena may be significant. In controlling large herbivore diversity (Homewood and Rogers, 1991). Sinclair (1989) however contends that conclusive evidence of predator impact is lacking. Skogland (1991) also concludes that factors related to both ungulate and predator life histories strongly lower the predators prey-catch efficiency and therefore reduce their impact.

1.5 Body size and competition

1.5.1 Gut capacity and feeding strategy:

Body size ratios among herbivores have been postulated as the mechanism for structuring communities (Demment and Van Soest, 1982; 1985). The gut capacity of mammalian herbivores increases nearly linearly with body weight ($W^{0.75}$). This relationship, coupled with the change in basal metabolism with weight produces an MR/GC ratio (Metabolic Rate to Gut Capacity Ratio) that decreases with increasing body size (Kleiber, 1961). Thus put another way, gut volume is a constant proportion of body weight (Parra, 1978; Demment, 1982) while maintenance metabolism (a prime determinant of intake) is a fractional power of body weight (Kleiber, 1975). The relationship between body size and digestive capacity can be used in conjunction with the relationship between abundance and quality of plant food to show how different sized ungulates (both ruminants and non-ruminants) can feed differentially on a food axis and thus minimise interspecific competition. The fibre composition of plant material can be used as the scaling variable for the resource axis for herbivores (Demment and Van Soest, 1985).

The availability of nutrients to herbivores is a function not only of the chemical composition of the forage, but also of the spatial distribution and abundance of the nutrients. Digestibility is related to quality of diet. All species would in theory benefit from high quality diets, but these are normally patchy and not as widely available as low quality vegetation.

Owen-Smith and Novellie (1982) used a comparative formula based on protein content, cell contents (carbohydrates and protein) and cell wall (cellulose, lignin etc.) to model ungulate diets. He found that fibre was digested more slowly than carbohydrates

and proteins. Since retention time in the gut is the most important factor in predicting intake and digestibility (Mertens, 1973), the digestibility of a forage is a function of the digestion rate acting on a particle for the duration of its retention time within the gut, i.e. passage rate. Increased body size should therefore produce higher digestibility because of longer retention times. Large herbivores can therefore extract more energy from plant material than can smaller herbivores. They can cover a larger area, ingest more food relative to their requirements, retain the material in the gut for a longer period and extract a greater fraction of energy and nutrients than the smaller animals (Brown and Maurer, 1986; Demment and Van Soest, 1982). This enables large species to feed on lower quality foods and to include a much wider array of items in the diet.

The allometry of diet tolerance explains the increase in body size with rainfall in East Africa (Western, 1991). Primary production and biomass are positively correlated to rainfall; vegetation quality is inversely proportional to biomass (Glover and Duthie, 1960; Owen-Smith, 1982). Larger herbivores are therefore at a selective advantage in moister areas (Western, 1979) and progressively accumulate along an increasing rainfall gradient as their minimum energy demands are met. Smaller herbivores on the other hand require easily digestible high energy yielding diets in order to meet their metabolic demand. Therefore they progressively disappear in higher rainfall areas as the quality of vegetation falls with increasing plant biomass. The extent of such size-related distributional patterns in the Athi-Kapiti ecosystem where there is a detectable rainfall difference gradient north-south is not yet known.

1.5.2 Digestion differences

1.5.2.1 Ruminant nutrition

The nutrition of the wild ruminant grazers is a complex process that involves herbage structure, digestive physiology, body size, animal physiology and the response of the animal to predation pressures, weather conditions as well as the social organization of the species. Their digestive system optimises the utilization of the products of gut floral fermentation, an adaptation that has opened food resources to the ruminant not as readily available to other animals. The advantages of ruminant function (selective retention and pregastric fermentation) appear to be confined to a limited size range. Ruminants are unevenly distributed across the range of herbivore body-sizes (Duncan *et al.*, 1990). They dominate in the medium body-size range in the grasslands of Africa while the non-ruminants are primarily small or very large animals (Demment and Van Soest, 1982). Such differences can be explained on the basis of differences between the digestive physiology of these groups of animals, in particular the retention time of the food in the

digestive tract, rumination, the extent of digestion of food particles and the energetic consequences of having an extra trophic level (microorganisms) between their food and themselves (Demment and Van Soest, 1982; 1985). At lower sizes, rumen fill of the selectively-retained matter becomes limiting, leading to avoidance of highly lignified foods. Thus, small ruminants tend to be specialized feeders. They are constrained to rapid passage of ingesta by their high MR/GC ratio, they must therefore find high quality foods which are rare. Small ruminants are also limited in their ability to expand their diet to more common low quality foods due both to their morphology and physiology (Van Soest 1982). Animals below 5 kg would require a digestible nutrient content in excess of 100%, a feat that is simply impossible.

On the other extreme large ruminants are also constrained by retention time. To eat a diet higher in fibre, the herbivore must increase its body size. While mathematical modelling has made clear the limitations of small size, the problem of upper limits remain. Retention times increase with body size and digestibility is in turn a function of retention time. At large body sizes a point is reached where there is no need for selective retention and indeed the herbivore may need to increase transit to optimize yield of metabolizable energy (Demment and Van Soest, 1982). The advantages of rumination therefore may decrease at large sizes. The absolute magnitude of the metabolism requirement of large herbivores and their mouth size relative to food resource also limits them to unselective feeding of high fibre diets that are difficult to ruminate. If they are able to ingest a sufficient high intake, low dietary and low extraction rate become tolerable. Many herbivorous animals primarily eat the reproductive products of plants such as fruits, seeds and berries. The artiodactyla and the perrisodactyla subsist on the structural parts of the plant such as the stem and leaves. These parts contain appreciable amounts of cellulose, hemicellulose and lignin. The two ungulate groups have entered into a form of symbiotic relationship with cellulase producing bacteria and have a fermentation chamber within the digestive tract where these bacteria can break down the cellulose. But their digestive physiology differs markedly. The artiodactyla have a rumen where food is digested by bacteria and protozoa before entering the true stomach. Perrisodactyla on the other hand have caecal digestion and microbial digestion takes place after food has passed through the stomach (Hanley and Hanley, 1982).

1.5.2.2 Ruminant and hind-gut fermentation

The evolutionary response of herbivores to dietary constraints has produced digestive systems based on the location of the fermentation site; fore-gut and hind-gut (Foose, 1978) and the existence of the rumination process. All ruminants carry on

fermentation in the foregut, and non-ruminants have caecal digestion. The major differences between these digestion sites is in the areas of nutrient absorption. In ruminants this occurs in the small intestines and in the colon of hindgut fermenters. Ruminants ruminate to improve their efficiency in dealing with cellulosic and hemicellulosic material. The comparison between foregut and hindgut fermentation shows that hindgut fermenters can obtain higher energy intakes than ruminants when compared on abundant foods of lower quality (Illius and Gordon, 1992). This is counter to the argument of Bell (1971) and Janis (1976) who assumed that hindgut fermenters are only superior on forages containing high levels of fibre. Large hindgut fermenters can obtain higher energy intakes than ruminants by faster throughput, despite less efficient nutrient extraction (Duncan *et al.*, 1990; Owen-Smith, 1988). Elephant, grazing rhinos and hippos; all non-ruminants, appear to fit this category, Foote and Lloyd (Van Soest, 1982; Foote, 1982). For these reasons, an upper limit to ruminant size is postulated at 1000 kg (Demment and Van Soest 1982, 1985).

However, where resources are limited and food intake is restricted, the more efficient digestion by the ruminants would give them an advantage. Ruminants require less food to obtain the same energy yields as the non-ruminants. Illius and Gordon (1992) suggested that the predominance of ruminants in the intermediate body weight range and their high diversity has resulted from their superiority under conditions of resource limitations and the ability of the different size of ruminants to differentially use the same resource. This physiologically driven selectivity has far reaching effects on the ecology and behaviour of herbivores (Jarman, 1974).

The model of Illius and Gordon (1992) on nutritional ecology of ungulate herbivores suggests that small hindgut fermenters which can consume a medium quality diet are likely to compete directly with larger ruminant species because the former can tolerate lower food availability. A zebra, which weighs approximately 200 kg, probably competes more directly with a buffalo for the same feeding niche than with the similar-sized wildebeest (Gwynne and Bell, 1968; Owaga, 1975; Hansen *et al.*, 1985). The coexistence of these species has been explained by their different abilities to extract nutrients from forages of different qualities (Bell, 1971; Foote, 1978; Janis, 1976).

The relationship between body size and digestive capacity can be used in conjunction with the relationship between abundance and quality of plant food to show how different sized ungulates can feed on a food axis thus minimizing interspecific competition. The size of other structures such as the incisor breadth (Gordon and Illius, 1988) can be used to show the changes between different sized ungulates along a grass height and the effects of this on the grazing succession and facilitation.

1.6 The interactions between wild herbivores and livestock

The influence of man and his stock is one of the most significant biotic factors in savanna ecosystems. Livestock were introduced into East Africa some 3000 to 4000 years ago (Marshall, 1989). They account for the greatest portion of the large herbivore biomass in much of the East African savanna (Coe *et al.*, 1976). The composition of the pastoral herds changes with increasing rainfall. Camels, goats and sheep dominate herds in the more arid zones and give way to an increasing dominance by cattle at higher levels of rainfall (Western, 1975). In the Athi-Kapiti plains, sheep, goats and cattle dominate. The fact that livestock (unlike wildlife) are not free ranging has major implications on the structure of the vegetation in the savannas and upon competitive interactions among the large herbivores. In large numbers livestock are a significant agent of vegetation removal, trampling and maintaining grazing lawns (McNaughton, 1984) which attract wildlife during the growing season. Given the enormity of their impacts on savanna habitats, their exclusion from a section of an ecosystem has a number of consequences. Both standing mass and species dominance increase in the herb layer and quality of the vegetation declines (Western and Gichohi, 1993). Tall grass may provide cover for predators resulting in increased herbivore mortality from predation, encourage the presence of parasites such as ticks and hence the prevalence of disease. In the past, livestock was a constituent part of the Nairobi National Park's herbivore biomass. Since its removal, the vegetation biomass has steadily increased (Stanley-Price, 1974), and has become more coarse and rank, and therefore of lower quality (Gichohi, 1990). This is postulated as one of the main reasons for the severe decline in small bodied ungulates in the park (Gichohi, 1990).

Negative effects of domestic stock in African rangelands however also occur. These are almost entirely due to overstocking which leads to a depletion of perennial grasses and palatable herbs, an increasing proportion of annuals and unpalatable species coupled with reduced herbaceous ground cover (Cumming, 1982).

Many studies on feeding patterns of wildlife have been confined to game parks and reserves where human activities are prohibited. Within the Athi-Kapiti plains however, the presence of livestock and human settlement should influence the balance of competitive interactions reflected in structure. Since species in a guild are thought to be in more direct competition with each other (Pianka, 1981), certain species of wildlife should be in direct competition with livestock. In certain areas, it has been shown that wildlife avoid settled areas, therefore, apart from the normal resource competition, wildlife may be displaced from resources around settlement especially during the day. This probably has important implications on wildlife community structure at the local scale.

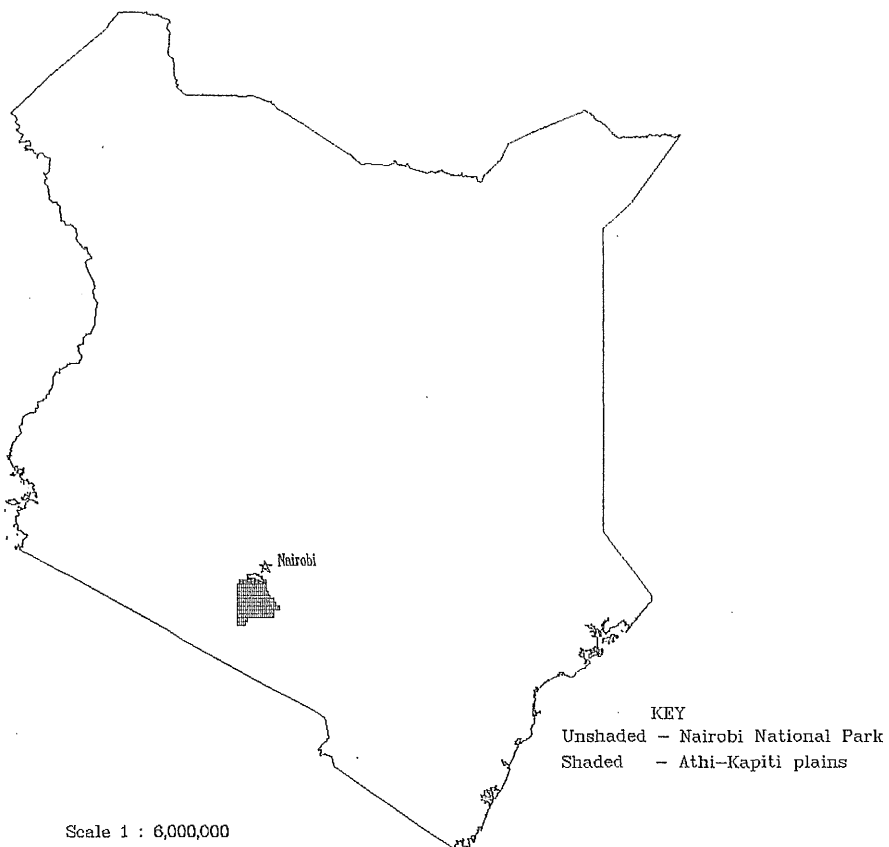
1.7 Objectives and hypothesis

The overall objective of this thesis is to understand the ecological factors controlling the large mammal community of the Athi-Kapiti system and thus to improve our scientific understanding of large scale, mixed livestock/wildlife savannah ecosystems. The insight gained will enable better management proposals for the system to be advanced. The hypotheses tested to achieve the objective during this study are as follows:-

1. To understand the consequences of the north-south precipitation gradient in the Athi-Kapiti ecosystem:
 - i) Vegetation biomass should be higher in the Park (higher rainfall) than the plains (lower rainfall),
 - ii) Vegetation quality should be lower where rainfall and biomass are higher,
 - iii) Vegetation species composition changes with rainfall gradient,
 - iv) Wildlife movement patterns should follow this gradient.
2. To understand the interaction between rainfall and grazing intensity:
 - i) Vegetation biomass should increase with rainfall despite grazing pressure,
 - ii) Vegetation species diversity should be enhanced by grazing,
 - iii) Herbivore grazing should improve quality at all rainfall levels,
 - iii) The numbers of small-bodied ungulates should progressively decline northwards along an increasing rainfall gradient as a consequence of rainfall-mediated decrease in quality,
3. To find out if there is diet selectivity among herbivores of this ecosystem:
 - i) Diet selectivity patterns should be size-related despite the presence of livestock.
4. To find out whether the ecological processes operating at the ecosystem scale also work on smaller scales:
 - i) Herbivore structure at the ecosystem level should be reflected at the level of the Park,
 - iii) Herbivore structure at the ecosystem level should be reflected at the level of human settlements.

Fig 1.1

Map of Kenya showing Nairobi National Park and the Athi-Kapiti plains



CHAPTER 2

THE STUDY AREAS

2.1 The Athi-Kapiti Plains

The Athi-Kapiti plains comprise approximately 2,200 km² of open, rolling land, bounded by the Rift Valley in the west, the City of Nairobi and Nairobi National Park in the north, the Machakos highlands in the north-east and east, and a rugged broken terrain in the south. In the west, the plains rise to approximately 1900 m, ending as the escarpment of the east side of the Rift Valley. The escarpment which runs due north-south joins the Ngong Hills at its northern end (Fig. 2.1), and with its almost vertical drop of about 300 m, it marks a drastic change in topography, climate and vegetation and is a major watershed. Surface water from this side of the plains is collected mainly by the Kitengela, Loitigoshi, Kesajui and Senya rivers and their tributaries, all of which join the Athi River.

The southern boundary of the plains between Konza and Kajiado is marked by a change in topography and vegetation from open, undulating country to an area of thick bush which drops in altitude southwards. This junction with the plains is a watershed and the area to the south is drained by a south-draining system, including the Olturoto river and its tributaries which run northwards to join the Stony Athi river and then the Athi River (Fig. 2.2).

Until the beginning of this century the plains were an ecological unit, supporting the most spectacular concentrations of wildlife in East Africa (Simon, 1962). There are many accounts of the wildlife of the Athi Plains and areas around Nairobi at the turn of the century:- "To describe what we saw in the way of game, would be put down today as exaggeration, but wherever we looked it was nothing but a moving mass of hartebeest, wildebeest, zebra and small antelope" (Preston in Trzebinski 1985). The forests of the Ngong, Karen and the Arboretum in Nairobi were also teeming with lions, rhinos, elephants and ungulates.

Subsequently, the fertile, high rainfall areas around Nairobi, the Ngong Hills, parts of Thika and Ruiru which constituted the dry season areas were taken up for agriculture and settlement. The plains to the east of the Konza - Athi River - Nairobi railway line were settled by European ranchers, leaving only the area to the west of this line for the original Maasai inhabitants to continue their traditional pastoralism. The cumulative effects of these two forms of land use over 60-70 years have been considerable, and today the remaining wildlife populations, especially of the migratory species, are almost entirely confined to the Maasai portion of the plains and few of the neighbouring ranches in

Machakos district.

The Maasai portion of the plains is currently under severe threat from changing Maasai lifestyle, increasing human population and settlement as well as growing industrialization of the Athi-River township. Industrial growth, purchases of large tracts of land and fencing has accelerated since the establishment of an Export Processing Zone (EPZ) in 1990 in the Kitengela township. The migration route to and from the Park has almost been cut-off. There is increasing agriculture with wheat and maize being grown in areas of adequate rainfall within the Maasai plains.

2.1.1 Geology, Topography and Soils

The geology of this area has been described by Baker (1954), Saggerson (1971), Matheson (1966) and Fairburn (1963). Scott *et al.*, (1971) have described the land surfaces of the Athi Plains. The Athi-Kapiti Plains are composed, essentially, of successive layers of lava from the volcanoes of the Rift Valley nearby and overlying the Basement System rocks. These rocks were laid down in the Archean Period of the Precambrian as sediments, which have been metamorphosed and locally granitized into crystalline, granitoid gneiss.

The soils of the Athi-Kapiti Plains are mostly residual weathering deposits (Fairburn, 1963), whose composition is controlled more by their situation and conditions of formation than by the present rock. Gethin-Jones and Scott (1970) show the soil of almost the whole west plains as "black clays" (grumosolic soils), consisting of a range of "black cotton" soils including the calcareous and noncalcareous variants. They are mainly derived from colluvium and occur on plains varying from sea-level to 2000 m. The dark grey-brown calcareous clay loam is the other main type of soil found over the Upper Athi Tuffs lava. Its development has been influenced by the topography and is distinguished by its derivation from lacustrine deposits (Fig. 2.3).

The influence of the topography in the formation of the soils has been mediated through its effect on water movement. On these slopes, a succession or catenary sequence of soils occurs. Where the ridges between adjacent valleys are broad and flat, and the gradient increases towards the sumps the development of the soils has been slightly different. The ridges have shallow slope and impeded drainage with typical alluvial soils. The middle and lower slopes are more freely drained and on these are found more leached soils. These are generally red or strong brown friable clays with a lateritic horizon, and may be derived from transported material (Gethin-Jones and Scott, 1970). The sumps occupy only a small area because adjacent slopes usually meet in a narrow, steep-sided river bed, often lying in a gorge. Under these conditions their soil is

well-drained, shallow and stony.

2.1.2 Drainage

There are two permanent streams on the northern edge of the Athi-Kapiti Plains, the Mbagathi and Kiserian. South of the Mbagathi and Kiserian are a number of seasonal water courses, the Kitengela, Oloolotikoshi, Senya and Olturoto. These drain the whole Athi-Kapiti sector and during wet weather carry very substantial flows of water. These rivers are also used intensively. The bulk of the Kiserian's flow is captured near source and piped to Kajiado township more than 60 km away. As a result, the Kiserian often ceases to flow below this extraction point. Water from the Mbagathi river is also heavily extracted for irrigation and household consumption in its higher reaches. Further down in the Athi-river township, it is used in industries and becomes heavily polluted beyond this point.

The Athi-Kapiti drainage is radial, and there are no natural sumps to trap and hold quantity of rainfall run-off as permanent or even semi-permanent surface water. With the exception of rocky pools which remain in some of the seasonal riverbeds, rainfall drains away rapidly. The Kiserian/Mbagathi stream present a river front of some 29 km and bring an area of approximately 435 km² (21%) of the Athi-Kapiti Plains into pastoral reach of permanent water (Fig. 2.2).

2.1.3 Climate

Rainfall on the Athi-Kapiti Plains ranges from between 400 mm and 600 mm a year in the South-east (Thompson and Sansom, 1967; Hillman, 1979) to between 600 mm and 800 mm in the North-west (Norton-Griffiths, 1977). The short rains are in the month of November to December followed by the short dry season of January to March. From December to mid-March, there is a persistent north-east wind and a low rainfall. This period is known as the "short" dry season. The "long" rains start in late March and may continue until the end of May, with April being the wettest with an average rainfall of 201 mm. This is followed by a long dry season running from June to October. Although this dry season is the longer of the two, its mean temperatures are lower, so that its effect on the vegetation and water resources may not be as severe as that of the short dry season. November is the wettest month of the year. The annual variation of rainfall is considerable (Thompson and Sansom, 1967), which is characteristic of tropical regimes. The total rainfall at Nairobi has been recorded between a minimum of 487 mm. and a maximum of 1526 mm. Rainfall variability is high on the plains, and the mean annual rainfall is 485 mm.

2.1.4 Vegetation

The Athi-Kapiti Plains have relatively homogeneous vegetation. Along the Rift rim bushland prevails, but elsewhere on the plains proper the vegetation is *Themeda* grassland, or bushed grassland in which the dominant shrub is *Acacia drepanolobium*.

In steep places there are exposures in the river beds but these are usually earth lined. Water retention is therefore poor, but the surface water is sufficient to support *Acacia kirkii* which usually lines the river valleys near the high areas around the escarpment. Riverine forests are dominated by the fever tree *Acacia xanthophloea*. In some parts of the plains, *Balanites egyptica* occurs locally.

On short grass ridges, *Sporobolus pyramidalis*, *Microchloa kunthii*, *Aristida adoensis* are frequent. Many of these species occur in areas of high use or disturbance. *Digitaria macroblephara* is also sometimes abundant.

On the extreme northern edge of the Athi-Kapiti Plains, are the Ololua forest (3.25 km²) and the Embakasi Forest (5.20 km²), both dominated by sclerophyllic species such as *Croton macrostachyus* and *Olea africana*. On the peaks and higher valleys of the Ngong Hills there are also a series of relict forest patches.

Other species of the Athi-Kapiti plains include grasses such as *Setaria phleoides*, *Ischaemum afrum*, *Pennisetum mezianum*, *Eustachys paspaloides*. Herbs include *Aspelia mossambicensis*, *Orthosiphon parvifolius*, *Senecio discifolius* and many others.

2.1.5 Animals

The large mammal fauna of the Athi-Kapiti consists of 24 species. The relative poverty compared to similar areas such as the Mara and Amboseli is due to the absence of elephant which was exterminated before 1962 (Stewart and Zaphiro, 1963), and the lack of arid zone species such as greater and lesser kudu, gerenuk and oryx.

At the turn of the century the plains ecosystem extended north-eastward from the Athi plains to the base of Ol Doinyo Sabuk (McCutcheon, 1910). However, this area was rapidly taken up with coffee and sisal plantations, and fenced ranches. Areas around Nairobi, and further beyond were cleared for agriculture and settlement and the big ungulates such as elephants and rhinos began to lose their habitat.

By 1950 at the latest the plains ecosystem had lost most of the fertile, high rainfall areas. However, it retained the Ngong Hills and the slopes south of the Mbagathi river. In the 1950s and 1960s settlement spread south, rapidly occupying this area so that by 1970 all land to the north of the Nairobi-Magadi road was detached from the system. This has continued and much land to the south of this road has been usurped by human

settlement, and the process continues. Throughout the century the ecosystem has been shrinking.

Changes in the plains ecosystem have had some considerable influence on its large mammal populations. The areas which have been lost are in the better watered parts and include all that was within Ecological Zone IV (Pratt and Gwynne, 1977) or better. The impact on the wildlife populations may therefore be large compared to the size of the area lost.

There are no early records describing large mammal use of the plains ecosystem, particularly on a seasonal basis. However, comparison with other East African ecosystems eg. the Serengeti, (Sinclair, 1979), suggests that in the dry weather, water-dependent species concentrated on permanent sources, and ranged more widely during the rains. Cowie (Anon, 1951) stressed the importance of the Ngong Hills to the plains system, which by implication suggested a westerly movement in dry seasons. Later, when the Ngong Hills were cut off from the plains, it was frequently asserted that NNP was the important dry season area for the remaining Athi-Kapiti animals (eg. Hillman, 1979).

Peterson and Casebeer (1972) showed that the distribution of wildebeest and zebra on the Athi-Kapiti plains was governed by water availability. This produced dry weather concentrations either in the north along the Kiserian and Mbagathi, or across these streams in NNP or on the cattle ranches to the east of Athi River. As soon as rain fell and water was available elsewhere on the Plains, the animals would move south towards it. Those species not dependent on the distribution of water did not make such pronounced movements.

The highest proportion of the Athi-Kapiti wildebeest recorded in the Nairobi National Park by Peterson and Casebeer (1972) was 5% at the height of the 1971 dry season (October). Zebra appeared to use the Park more, up to 30% on one occasion in March 1971 and 24% in October 1971, both dry months. Their data did not support a belief that NNP was an essential dry weather resource for Athi-Kapiti wildebeest, though it suggested that this might be the case for a substantial proportion of the zebra.

Analysis of census data for NNP from 1960 to 1990 (Gichohi - unpublished reports) showed that in the early 60s there were no substantial animal movements between Park and plains, but since the early seventies, there have been characteristic fluctuations caused by the exodus of zebra and wildebeest from NNP at the onset of the rains. For example in May 1974, the wildebeest count was 6, down from an average of 1666 in December of the previous year. By February 1976, the numbers had gone up to 3061 and by March of the same year to 10,797. This was a drought year.

The number of animals in the Athi-Kapiti system has been estimated by many

workers Stewart and Zaphiro (1963), Casebeer and Mbai (1974), Stanley-Price (1974), Hillman and Hillman (1977), Hillman (1979) and Croze (1978), and summarised by Hillman (1979) for the period 1973-1975. One characteristic has been the large fluctuation in numbers. In the last three decades there have been heavy mortalities brought about by drought and poaching followed by rapid recoveries. The position is different today and all indications point to a declining population.

Population estimates as recently as 1987 were 21,152 wildebeest, 16,142 zebra, 15,434 Thomson's gazelle and 10,829 Grant's gazelle (KREMU counts, 1987). With diminishing space and increased human settlement a continued downward trend is likely.

2.2 Nairobi National Park

Nairobi National Park, established in 1946, covers an area of 114 km² approximately 10 km South of the City of Nairobi, Kenya, at about 2° 18' south and 36° 50' east. It is one of the most remarkable parks of its size anywhere in the world in that over two dozen big game species which occupy this area are separated from the modern metropolis of Nairobi by only a fence. The southern boundary is open to the Athi Kapiti plains and allows considerable movement of large ungulate species between the two areas. The Kitengela Conservation Area which is located to the immediate south of NNP together with the rest of the Athi-Kapiti Plains form a dispersal area covering about 2,500 km² for many ungulate species (Foster and Kearney, 1967).

Most of the NNP is savanna grassland with a dry climate (Lusigi, 1977). The mean annual rainfall for 1955 to 1985 (Kenya Meteorological Department Report, 1985) is about 850 mm falling mainly in two seasons (long rains from late March to May and short rains from late October to December) but with large variations from year to year.

Rainfall within the ecosystem approximately follows an altitude gradient with the south receiving less annual rainfall than the north (Hillman, 1979). This rainfall gradient has been suggested as the main reason for the park being a dry season concentration area for animals (Lusigi, 1977).

The drainage in the NNP consists of many intermittent streams (Scott, 1963). Permanent water supply comes from Mbagathi river but artificial dams have been built to augment the natural supply for the animals during the dry season. These dams also lure animals for tourist viewing. Dry periods may normally total six months. When rains fail and the dry season exceeds six months, drought occurs. There has been a general trend during the last fifty years for drought periods to lengthen which have had devastating results on the faunal and floral communities of the park. The most serious drought periods which caused the death of many animals were in 1960-61 (Foster and Coe, 1968),

1968-69, 1973-74 (Lusigi, 1977) and 1984-85 (Komba, 1985).

The Park ecosystem is divisible into three topographic zones. The upland area to the west and the north-west is approximately 1,700 to 1,800 m above sea level, the central undulating plains about 1,600 m above sea level (Lusigi, 1977) and the gently rolling plains in the south east at even lower altitude.

The soils in this area have been described in detail by Heriz-Smith (1962) and mainly consist of the "black to dark clays", the "shallow-yellow brown to yellow red friable clays" overlaying a laterite of rock and alluvial soils. The black to dark grey clays, commonly known as black cotton soils are the most important in this area. They go to depths of up to 4 m and are sticky when wet and hard; massive and difficult to break when dry.

2.2.1 Vegetation

Verdcourt (1962) has described the vegetation in this area. The Park consists of a wide range of habitats which vary from forests to grasslands, rocky gorges and rolling plains. The major vegetation types are *Acacia drepanolobium* grasslands, open grasslands, forests, swamps and bushlands.

The *Acacia drepanolobium* grasslands occur on flat ridges and very gentle upper slopes lying on deep cracking black cotton soils. The dominant woody species is dwarf *Acacia drepanolobium* while the dominant grasses are *Setaria phleoides*, *Themeda triandra* and *Ischaemum afrum*. *Aspelia mossambicensis* also occurs here, and is frequent in some places. The woodlands are less extensive, and some areas more open than in the past. There have been changes in the density and size frequency distribution of the *Acacia* woodlands in the areas that have been frequently burnt.

Open grasslands generally occur on the black cotton and grey soils and on flat or gently undulating plains. *Themeda triandra* and *Pennisetum mezianum* are abundant. Scattered *Acacia mellifera* and *Balanites* occur. *Digitaria macroblephara* is frequently abundant with *Cynodon dactylon* and *Harpachne schimperi*, *Becium obovatum* and *Abutilon* sp. occasional. These types of grassland occur widely over the park.

The north western end of the park is covered by a semi-deciduous forest lying on humic soils (Stanley-Price, 1974). The dominant species of trees include *Croton megalocarpus*, *Brachyleana hutchinsii*, *Olea africana*, *Calendendron capense* and *Schrebera alata*. Understorey shrubs include *Rhus natalensis*, *Croton dichogamus* and *Psiadia arabica*. The forest is interspersed with glades.

The bushlands occur in the valleys, gorges and on slopes. Red lateritic soils underlie this vegetation type. Species on the upper slopes include *Lippia javanica*, *Nasae*

lythroides, *Phyllanthus sapialis*, *Hibiscus flavifolius* and *Hibiscus aponeurus*.

Further down the catena, the dominant species include *Psiadia arabica*, *Croton dichogamus*, *Grewia similis*, *Hibiscus flavifolius* and a shrubby form of *Olea africana* (Hillman, 1979). At the bottom of the catena there are strips of open grassland on wider valleys followed by thicket on the edge of the drainage channel. *T. triandra* is the dominant grass on these grasslands. The thickets are formed by *Acacia brevispica*, *Phyllanthus sepialis*, with large *Acacia kirkii* trees and *A. xanthophloea* where standing water is present.

2.2.2 Wildlife movements into and out of the Nairobi National Park

Cowie (Anon, 1951) suggested that the Ngong forest was essential to the Nairobi National Park as a reservoir of animals and for migrations. Subsequently Stewart and Stewart (1963), Hillman and Hillman (1977), Croze (1978) and Hillman (1979) have all maintained that the Nairobi National Park was a part of the Athi-Kapiti ecosystem. The inference has been that it was the dry weather resource for the game herbivores from the Athi-Kapiti plains. However, the term "Athi-Kapiti ecosystem" has nowhere been defined other than in very general terms. From a historical perspective, the open grassland and their attendant herds once stretched nearly as far north as Ol Doinyo-Sabuk and at that time what is now Nairobi National Park would have been less important. Between 1914 and 1946 when it was made a park, the value of the area may have been significantly diminished because of the human activity that took place there. The western side was for example used as a military camp and other parts of it as shooting range during the second world war. It was also ravaged by thousands of cattle owned by Somalis (Cowie, 1961). Once it was made a sanctuary, free from competing livestock and with many dams, it would have become more attractive to wild animals.

Even so it is unlikely that the Nairobi Park was biologically of any great significance to the Athi-Kapiti herds as long as the Ngong Hills and their footslopes were available to them. De Beaton (1949) recorded animal movements from the Nairobi Park west towards the hills as well as south.

The importance of the Nairobi National Park to the Athi-Kapiti game herds rose once the Ngong slopes were settled by people. However this value must have been limited by its size (out of a total of 114 km² less than 80 km² are grasslands useable by grazers such as wildebeest, kongoni and zebra).

In summary:-

1. What is now the Nairobi Park was originally only a small part of the plains system which existed in 1900, and within this it is unlikely to have had then any critical

ecological importance.

2. For a period of 32 years prior to its gazettelement as a National Park, it was so disturbed by human activity that it is unlikely to have held as much wildlife.
3. Since 1946 it has been restructured by man, and today is largely the product of this development,
4. Its importance as a resource for the Athi-Kapiti plains herds is likely to have risen in proportion to the progressive loss of other land once available to them.

There are thus grounds for suspecting the validity of claims that Nairobi Park is integral to the ecology of the Athi-Kapiti to the south. Peterson and Casebeer's (1972) data show that during their counts and reconnaissances not more than 5% of the total Athi-Kapiti-Nairobi Park wildebeest were ever in the Nairobi Park, even in a dry season, and that not more than 30% of the zebra used it.

Large herbivores that are still sufficiently numerous in the park include the zebra (*Equus burchellii*), Grant's gazelle (*Gazelle granti*), Thomson's gazelle (*Gazelle thomsonii*), Impala (*Aepyceros melampus*), waterbuck (*Kobus defassa*), eland (*Taurotragus oryx*), kongoni (*Alcephalus busephalus*), wildebeest (*Connochoetes taurinus*), giraffe (*Giraffa camelopardalis*) and the African buffalo (*Cyncerus caffer*). The park has over 80 recorded mammal species (Williams, 1972) which include small numbers of three species in the vulnerable category of the Red Data Book (Noel, 1966), the leopard (*Panthera pardus*), cheetah (*Acynonyx jubatus*) and black rhinoceros (*Diceros bicornis*). The Park is also credited with approximately 500 species of birds.

Fig 2.1

General map of the Athi-Kapiti Study Area

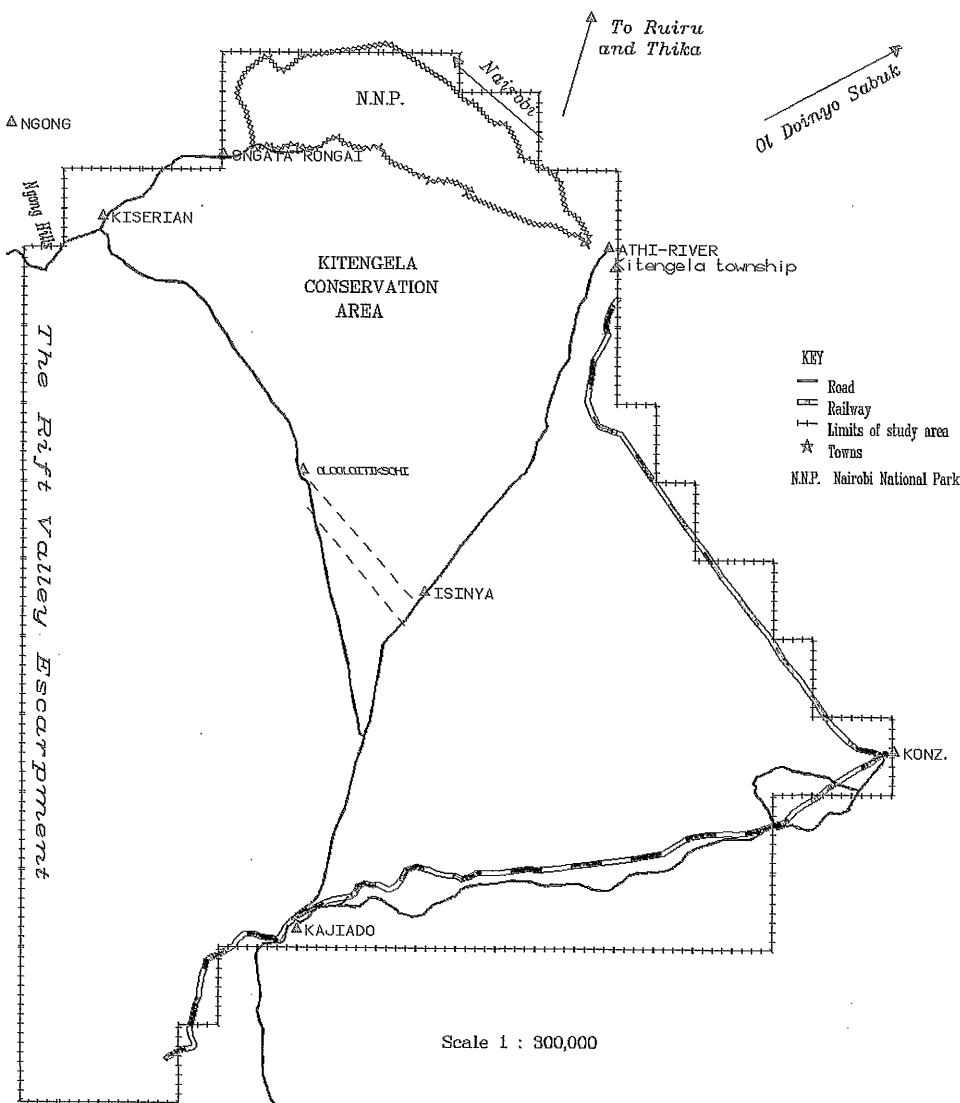


Fig 2.2
Map of the Athi-Kapiti plains
The main drainage system

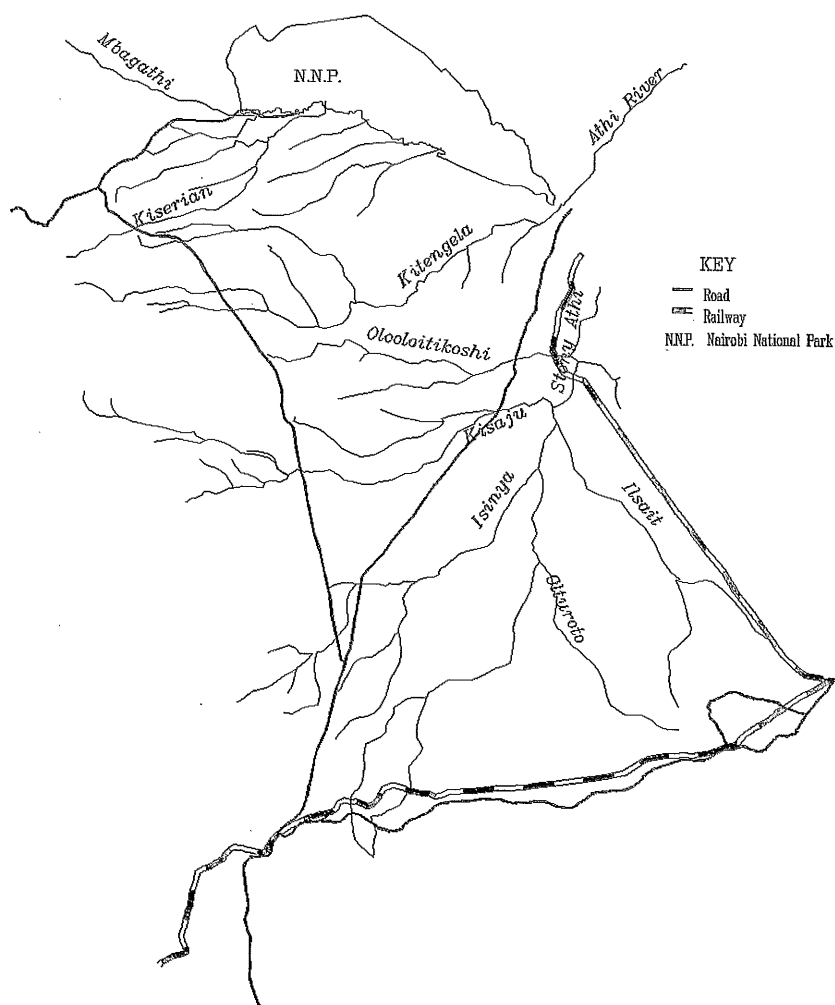
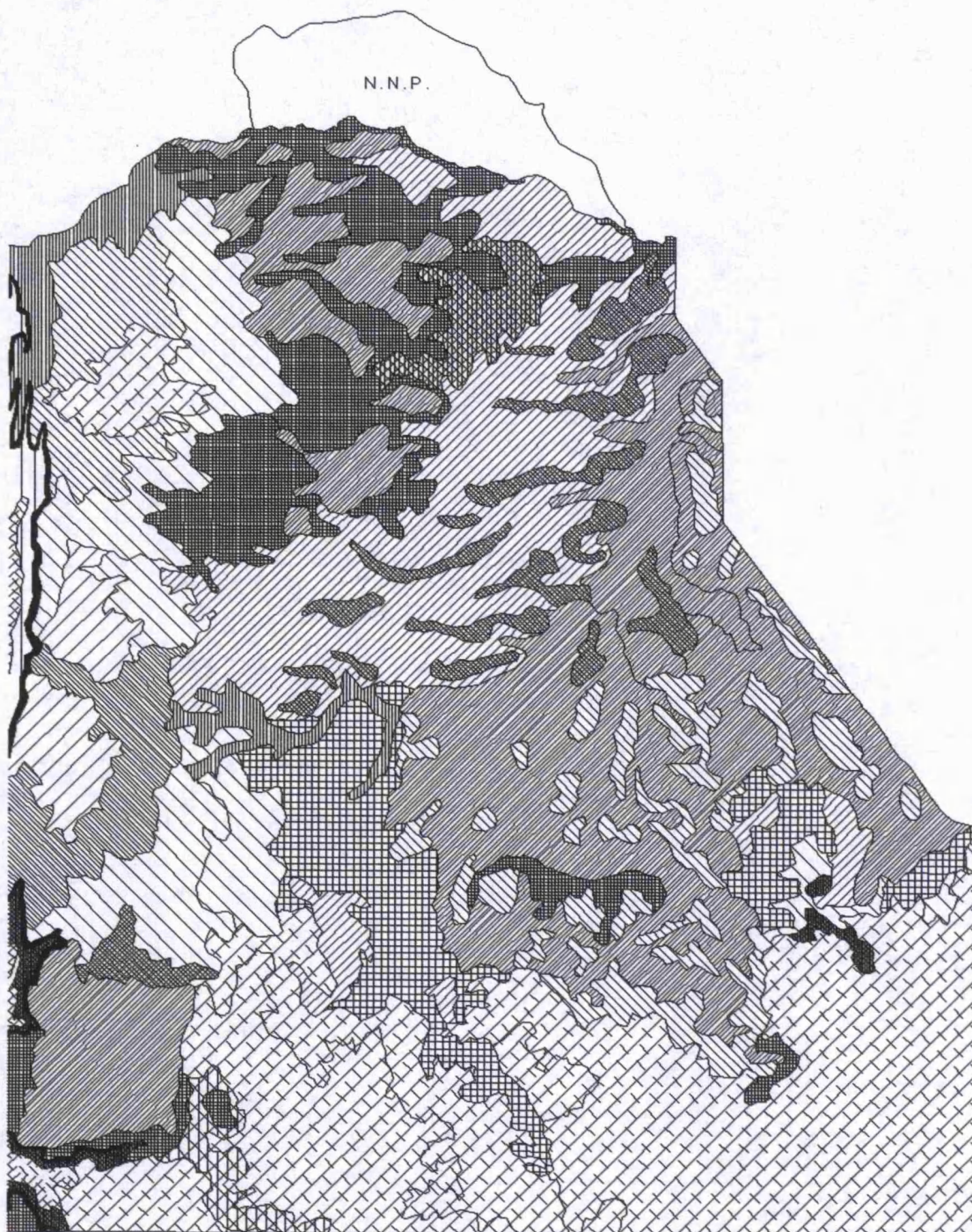


Fig 2.3

Soil map of the Athi-Kapiti plains (Excluding Nairobi National Park)



Scale 1 : 300,000

KEY TO SOIL MAP

- MOUNTAINS AND MAJOR SCARPS** (high relief intensity, slopes in general >16%)
 MU Soils developed on various basement system rocks
 MUP - Well drained, very shallow, brown, rocky and stony soils (LITHOSOLS)
- MV Soils developed on various volcanic rocks**
 MVP - Well drained, very shallow, dark reddish brown, rocky and stony soils (LITHOSOLS)
- HILLS AND MINOR SCARPS** (low relief intensity, slopes in general >16%)
 HP Soils developed on pyroclastic rocks (Ol Doinyo narok agglomerate)
 HPP - Well drained, very shallow, very dark greyish brown, rocky and stony soils (LITHOSOLS)
- FOOTSLOPES** (at the foot of mountains, hills and scarps slopes in general 3-8%)
 FX Soils developed on colluvium derived from various volcanic and basement systems
 FXC - Various greyish brown to brown soils (no field data)
- FV Soils developed on colluvium derived from various volcanic rocks**
 FVC - Various reddish brown soils (no field data)
- PLATEAUS** (Slopes in general 0-50%)
 LP Soils developed on pyroclastic rocks (Ol Doinyo Narok agglomerate)
 LPdp - Imperfectly drained, moderately deep, very dark grey to black, very firm, rocky, stony and gravelly, cracking clay calcareous in the deeper subsoil (pellic VERTISOLS, rocky phase)
- UPLANDS** (Dissected plains, major rivers deeply incised, slopes in general 2-16%)
HIGH LEVEL UPLANDS
 UI - Soils developed on intermediate and basic, volcanic rocks (Ngong and Ol Esayeti Volcanic and Olorgesailie biotite phonolite)
 UIC1 - Complex of :- Well drained shallow to moderately deep, reddish brown, friable, stony and gravelly clay loam (luvic PHAEZOZEMS, partly lithic phase)
 Imperfectly drained, moderately deep, very dark greyish brown to black cracking clay in places gravelly (pellic/chromic VERTISOLS)
 UIC2 - Complex of imperfectly drained, dark greyish brown to black clay soils of depth, consistence, calcareousness, and stoniness (pellic VERTISOLS and vertic VERTISOLS)
 UP Soils developed on pyroclastic rocks (Kerichwa Valley tuff)
 UPP - Well drained, very shallow, dark greyish brown to dark brown, gravelly clay (LITHOSOLS and lithic PHAEZOZEMS)
 UPph - Imperfectly drained, shallow to moderately deep, very dark grey to black firm, gravelly and stony, cracking clay (vertic PHAEZOZEMS, partly lithic phase)
- LOW LEVEL UPLANDS**
 UU Soils developed on various basement system rocks
 UUC - Complex of well drained, deep to shallow, reddish brown to brown, friable to firm, sandy clay loam to clay (chromic to dystric LUVISOLS/CAMBISOLS, partly LITHOSOLS)
- PLAINS** (low relief intensity, slopes in general <5%)
STEPPED, HIGH LEVEL PLAINS
 PR Soils developed on quartz-feldspar gneisses (basement system rocks)
 PRb - Well drained, deep, dark reddish brown to reddish brown, friable, sandy loam to sandy clay loam (orthic FERRALSOLS to ferralic ARENOSOLS)
 PRdp - Imperfectly drained, moderately deep, dark grey to black, very firm gravelly, cracking clay in places saline (pellic VERTISOLS, partly saline)
 PRap - Imperfectly drained, moderately deep, dark greyish brown to black, very firm, gravelly clay, abruptly underlying 10-30cm of gravelly sandy clay loam (eutric PLANOSOLS)
 PRdp-PRap - Association of soils of unit PRdp and soils of unit PRap
- PU Soils developed on undifferentiated Basement System Rocks** (various gneisses and granulites)
 PUC - Association of :- well drained, moderately deep, reddish brown to brown, friable clay loam
 - Imperfectly drained, moderately deep, dark greyish brown, very firm, gravelly clay, abruptly underlying 10-30cm of gravelly sandy loam (eutric PLANOSOLS)
 - Imperfectly drained, deep, dark grey to black, very firm, gravelly, cracking clay (pellic VERTISOLS)
- PI Soils developed on intermediate volcanic rocks** (Kapiti Phonolite, Mbagathi trachyte, Olorgesailie biotite phonolite and phonolitic nephelinite)
 Pla - Imperfectly drained, very deep, dark greyish brown, firm clay loam to

- clay, abruptly underlying 20-40cm of loam clay to clay loam (eutric PLANOS)
- Pld - Imperfectly drained, very deep, dark grey to black, stony and bouldery, cracking clay in places with slightly saline, calcareous, deeper subsoil (pellic VERTISOLS, stony phase and partly saline phase)
 - Plc - Complex of :- Well drained, shallow to moderately deep, dark reddish brown sandy clay loam to sandy clay in many places rocky and st (chromic CAMBISOLS/LUVISOLS)
 - Soils of unit Pla, but shallow to deep
 - Soils of unit Pld, but shallow to deep

PP Soils developed on pyroclastic rocks (Athi tuff and Kerichwa valley tuff)

- PPh - Moderately well drained, very deep, dark greyish brown, firm clay (verti luvi)
- PPd1 - Imperfectly drained, moderately deep to deep, very dark grey to black very firm, calcareous, cracking clay (pellic VERTISOLS)
- PPd2 - Imperfectly drained, moderately deep, very dark grey to black, firm gravelly, cracking clay (pellic VERTISOLS and vertic RENDZINAS)

PX Soils developed on various parent materials

- PXC - Complex of :- well drained, very shallow to shallow, greyish brown to dark grey, calcareous, gravelly clay (orthic RENDZINAS)
 - well drained, shallow, dark brown to very dark brown, friable gravelly clay (orthic LUVISOLS, lithic phase)
 - Imperfectly drained, moderately deep, very dark greyish brown to black, firm, calcareous, gravelly and stony, cracking clay

BOTTOMLANDS

BA Soils developed on alluvial deposits

- BAd - Imperfectly drained, very deep, very dark grey to black cracking clay, with stratified deeper subsoil (pellic VERTISOLS)
- Region or area with major scarps

CHAPTER 3

GENERAL METHODS

3.1 Introduction

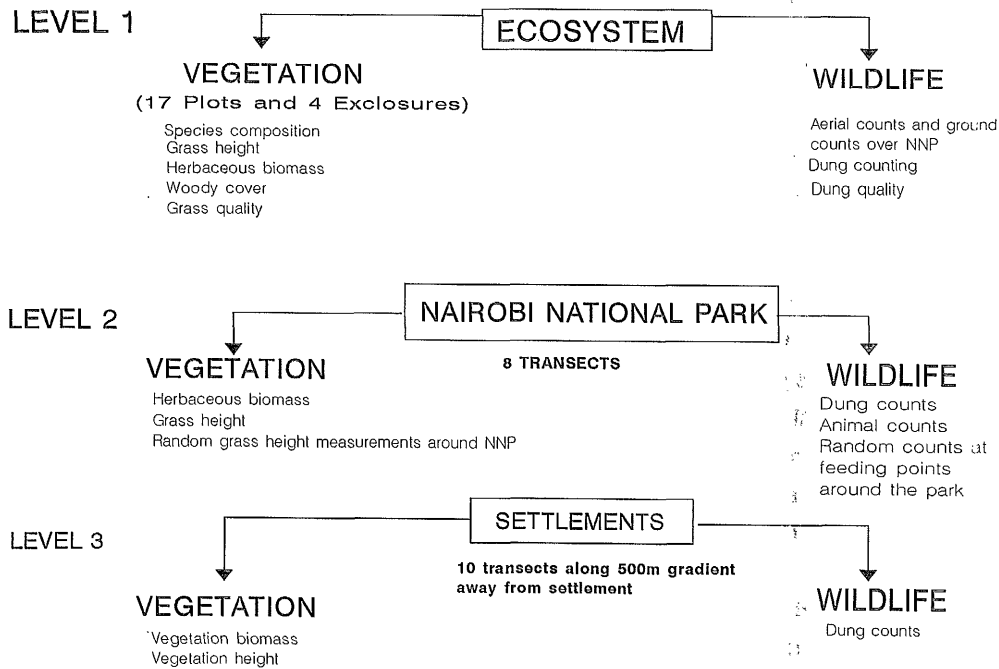
The project was approached from three levels (Fig. 3.1): the whole ecosystem level, the Nairobi National Park and individual settlements. At the ecosystem level data were collected on the patterns and pulses of vegetation biomass and quality, and their subsequent effect on wildlife numbers, movements and distribution over the ecosystem. Aerial censuses were conducted over the park and plains to map out the distribution and estimate the numbers of wildlife and livestock during the wet and dry seasons. Dung was counted on the same scale to show patterns of occupancy over time and space, and to relate these to vegetation conditions.

The next level was the Park where habitat utilization patterns were analysed. NNP is an important concentration area for some of the plains herbivores, acting as a feeding and watering area in the dry season. Information on habitat utilization patterns was obtained by counting the numbers of herbivores by species along 8 transects located in areas of different biomass and habitat types. Vegetation biomass and dung density were also measured to derive a relationship between patterns of occupancy, biomass depletion and to track any shifts in habitat use as grass biomass declined. Game counts were also conducted once every 2 months (with a break in 1993) with the help of the Kenya Wildlife Service personnel and volunteers from the East African Natural History Society.

The third level was that of the settlement, or boma. Outside NNP, humans are an important determinant of distribution of livestock, vegetation biomass and quality (Muchiru, 1994). Each morning, livestock leave the bomas (cattle enclosure), eating, defaecating and trampling the vegetation in the immediate vicinity of the homestead. This is repeated in the evening when the animals return. As a result vegetation around bomas sites is normally of higher quality (Muchiru, 1994) and form due to concentration of nutrients from urine and faeces. This may act as a significant attractant to the wildlife. Transects were run radiating out from the settlements in order to measure the changes in wildlife and livestock distribution and occupancy along this gradient of use. Wildlife and livestock dung counts were used to demonstrate this and to determine the distances wild animals maintain away from settlement.

Fig 3.1

**SAMPLING LEVELS
FOR THE ATHI KAPITI STUDY**



3.2 Site selection and the study duration

Initial reconnaissance surveys of the whole area began in September 1991. The aims were to gain some basic understanding of the area for selection of sampling sites and to introduce the project to the local residents of the area. Over 75% of the ecosystem is on privately owned land and a good rapport with the local land owners was an important prerequisite to the success of the project.

3.2.1 Scientific basis for site selection

Three transects running in a south-easterly direction were selected for sampling the study area. The main criteria was to ensure maximum coverage of the Athi-Kapiti ecosystem taking into account sampling effort and the type of information that was desired. The spread of plots would allow for wide comparison between the distribution of wildlife and livestock, vegetation biomass and the herbivore occupance in different parts of the system. Each transect had 5 plots. The first transect ran along the escarpment into an open plain in the extreme southwestern end of the ecosystem at Eluai. The rim of the escarpment has variable soils (Stanley-Price, 1974) derived from volcanic rocks. Five plots were selected along the escarpment based on the soil and vegetation types. Being so close to the rift valley, the soils are still young and are at variable stages in their development. This transect had the most variation in soil types and was used to set the number of plots that would be sampled in each transect.

A second transect ran from just south of the Kiserian town at Oloontepes ending at the open plains towards the Konza-Kajiado railway line, at Olmirui. There are fences running along the railway line and prevent much wildlife from moving further into the plains along the southern edge of the ecosystem.

The third transect started at the Livestock research station, commonly referred to as the Sheep and Goat ranch. This station borders the Park along the Athi-river boundary, adjacent to the industrial town of Athi-river. The last point of this transect was several kilometres away from the Konza township at Ilpolosat (Fig. 3.2).

A further 2 plots were selected in the Park, covering open grasslands and Acacia woodlands.

Visible vegetation differences on the ground, soil maps and various other factors such as drainage, terrain and accessibility were used to identify suitable sampling sites; 17 sites were selected in all. The next stage involved seeking permission from owners of land on which 15 of these sites were located.

3.2.2 Practical problems

Getting authorization for sampling on private property proved to be the most difficult part of the process. Many of the landowners were suspicious of our motives. To them we simply wanted to buy land or worse, to take it away from them. Research was seen simply a front for our "real" motives. As a result the process of setting up study sites, and resetting new ones where land owners suddenly changed their minds became a time-consuming activity running over 7 months. By March 1992 all the 17 plots had been set in the selected areas, 15 outside the Park and 2 inside. These are shown in (Fig. 3.2).

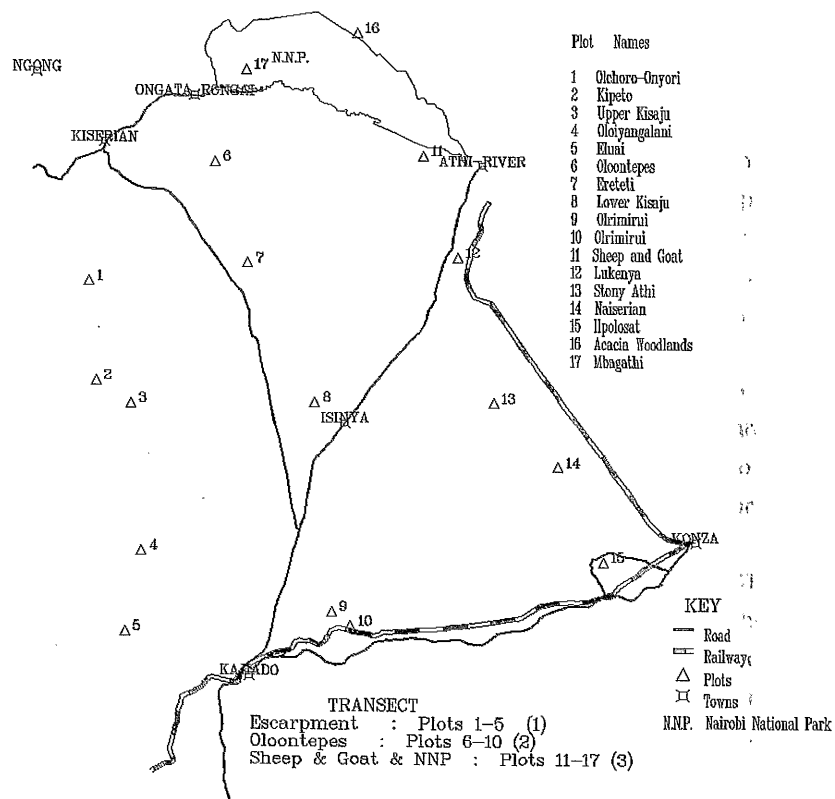
In April 1992, 4 exclosures were constructed outside the Park, one on the first plot along the escarpment, the second on the first plot of the third transect, and further 2 on the last plot of the second transect. The aim of constructing these exclosures was to determine the effects of excluding large herbivore grazing on vegetation biomass, quality and species composition. It would also provide information on the impact of rainfall on the above vegetation characteristics.

Except in NNP, the other exclosures had to be located near settlement for security against loss of the fences. Many other unexpected events prolonged the duration of the project. Most notable was a drought which begun in mid 1993 and lasted till early 1994. The extreme dry conditions forced many Maasai residents to move their livestock in search of pasture once their forage was totally depleted. Sampling near settlement sites was interrupted by the removal of livestock, the key component in this part of the study.

Where negotiations for new study sites were still underway, the movement of male members of the families left an authority vacuum and no further sites could be set. There was also increased hostility against wildlife which had moved into the Park after depleting vegetation outside. Much of the hostility was directed towards the regulations prohibiting livestock grazing in the Park even when conditions were so desperate. As a result wildlife related work was not welcome.

I also decided to continue with the ecosystem sampling during the drought. The impact of drought conditions on vegetation and water resources and resulting impact on wildlife distribution, numbers and use patterns were important to capture. This inevitably prolonged the study period.

Fig 3.2
Location of the 3 transects and 17 plots
sampled for vegetation biomass, species
composition and wildlife occupancy



3.3 Plant biomass, quality and composition

Above-ground plant biomass may be measured directly using a variety of techniques. Some involve harvesting the vegetation and are laborious, time consuming (Brower and Zar, 1977) as well as destructive due to the clipping and sorting involved (Frank and McNaughton, 1990; McNaughton, 1979a). A non-destructive but labour intensive technique the canopy intercept or the pin-frame method was selected for sampling the grasslands in this study and the Point-Centre Quarter method for sampling woody vegetation.

3.3.1 Pin Frame

The pin-frame consists of a wooden frame, usually one metre long with holes angled to the horizontal, drilled through at regular intervals, usually 10 cm apart. It is held above the ground by adjustable stands which allow sampling to be done at various heights depending on the vegetation type. The pins are put through the holes and the number of contacts the pin makes with the vegetation is recorded. Sampling is done by placing the frame at randomly determined points. This allows for sampling to be done on the same plot many times over, with only minor disturbances. The hits-per-pin measurements are calibrated with clipped plots to relate standing crop to the number of contacts a pin makes when passed through vegetation. This method has been recognized as a suitable estimator of herbaceous biomass, species dominance and frequency as well as species composition (McNaughton, 1979a).

There are possible sources of errors inherent in this technique. These include vegetation movements in the wind and the effect of plant growth form. The probability of contact with the different plant parts is a function of pin diameter and size of parts, both of which contribute to sampling error (Frank and McNaughton, 1990). To minimise this error, calibrations for individual species can be made, or a large sample taken.

3.3.2 Herb layer biomass

All the 17 permanent plots were sampled with the pin-frame for herbaceous biomass, species composition, dominance and frequency. Between 1992 and early 1993 biomass was sampled once per season. From February 1993, the sampling frequency was increased to once every two months to coincide with measurements of wildlife occupancy.

Biomass and species composition were sampled in 5 plots along each of the 3 transects, and on 2 plots inside the Park (Fig. 3.3). Each plot was divided into 4 subtransects running parallel to each other 25 metres apart. Each subtransect was further

divided into 5 points, 50 metres apart. Sampling was done at each of these points using 5 pins, set on a pin-frame designed for 10 pins. Altogether, there were 20 sampling points per plot making a total of 100 pins per plot and 1700 pins for the whole ecosystem. The choice of 5 pins rather than 10 was made to allow the spread of the sampling effort.

The number of times each pin came into contact with the herbaceous plants were counted. Each contact was categorized as leaf, stem, flower or sheath. Also recorded was the condition of the part touching the pin, i.e. whether green, brown or litter. During the wet season it was possible to identify each species of plant hit. Similar information was recorded but this time by species. During the dry season when the grass was dry, only the plant parts hit and their condition was recorded.

In certain wet seasons, the grasses did not flower sufficiently due to inadequate rainfall. In others, flowering was sufficient but the flowering culms were removed by herbivore grazers concentrating on certain plots, immediately following the rains. In the absence of flowers sampling became difficult. When this happened, species composition data were collected only on plots where species identification was possible. Vegetation biomass data were sampled for the rest.

Eleven data sets were collected in all, 4 during the wet and 7 during the dry. Of the 4 wet seasons samples, one, the January 1992 sample, was incomplete, as site selection was still underway.

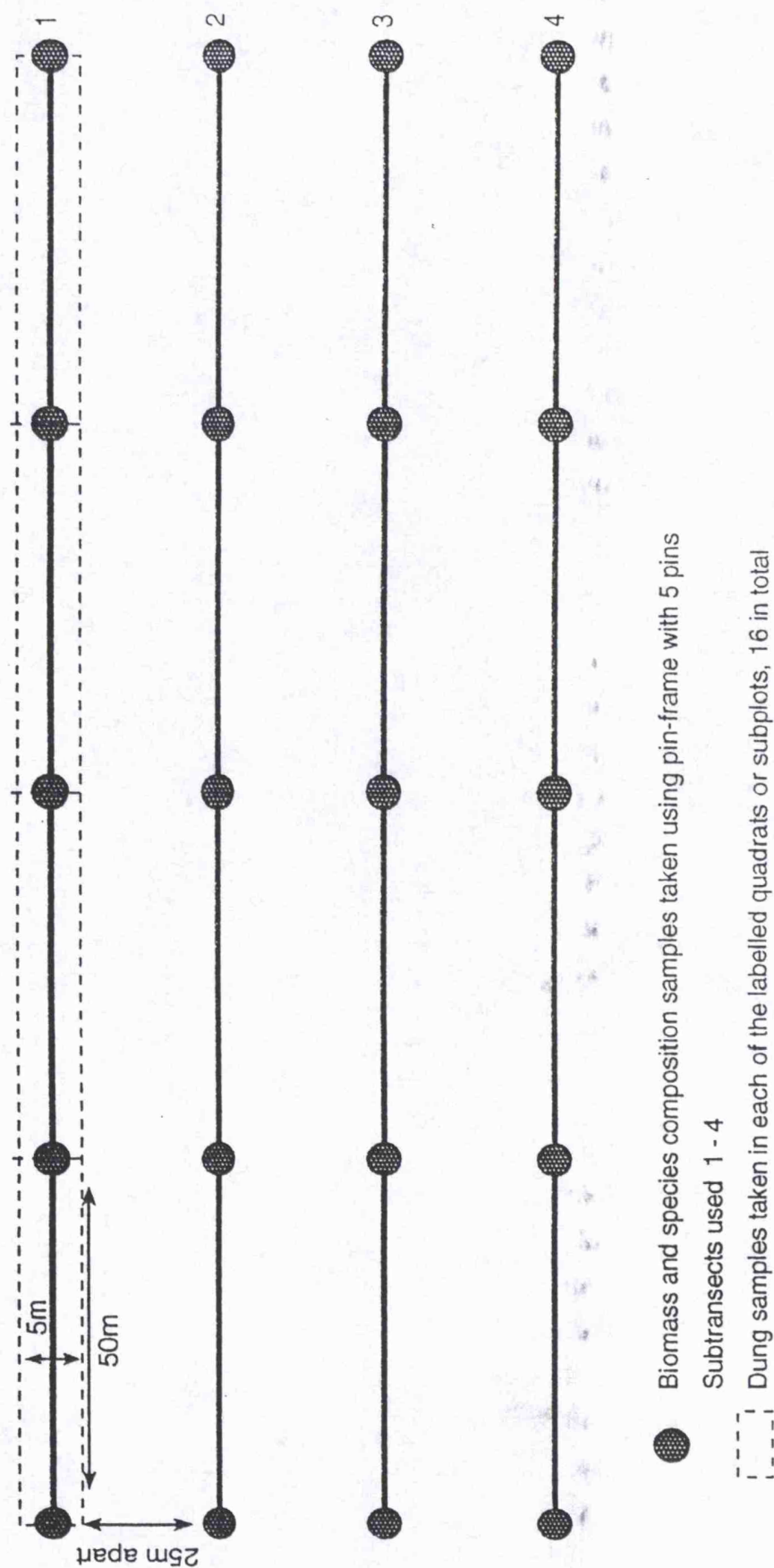
Biomass data were analysed using various statistical methods including analysis of variance, t-test, regression analysis and the Detrended Correspondence Analysis (DCA).

3.3.3 Biomass (Pin-Frame) Calibration

Measurements obtained using the pin frame need to be calibrated against weights of vegetation clipped in plots of a known area in order to obtain biomass (g/m^2). A regression equation was derived by sampling a known area using the pin-frame, clipping the vegetation in this area, drying it, weighing it and regressing the weights (in g/m^2) against the average number of hits (hits-per-pin). Vegetation for the calibration was measured in 0.25 m^2 quadrats, 12 in the wet seasons of 1993 and 30 in 1994. Vegetation in the quadrats was sampled using 5 pins on a pin frame. A total of 30 pins were used to sample each quadrat. The measurements were taken at the end of the growing season. After taking the pin frame measurements all the vegetation in the quadrat was clipped and taken for sorting. In 1993 the vegetation was sorted by species, plant parts and condition, i.e. green, brown or litter. Due to the arduous task of sorting, only 12 plots were clipped before vegetation deterioration set in. These clipped samples were dried in ovens at 80° for several days and then weighed. A regression was established by

Fig 3.3

Representation of the lay out for vegetation and dung sampling
in the 17 plots in the ecosystem



calibrating oven-dried biomass from clipped plots to the average hits-per-pin. Statistical analyses of the 12 samples showed that the sample size was inadequate and in the wet season of 1994, a further 30 samples were taken. This time the vegetation was separated by type (grass or forb), the parts and condition only. The initial procedure of drying and weighing was followed. The two sets of data were combined and a relationship derived using a simple regression analysis. The regression formula derived from this relationship was used for converting hits-per-pin measurements into biomass estimates. A calibration for Nairobi National Park grasslands was already available (Gichohi, 1990).

3.3.4 Grass height

Five measurements of grass height were taken around each of the biomass sampling points. The sampling was done at the same time as the vegetation biomass. Relationships between height, biomass and quality of the grasses was analysed using simple regressions.

3.3.5 Grass quality

Nutritional quality was sampled in two wet and two dry seasons in parallel with biomass and species composition and along the same subtransect. Grass was clipped several metres away from each of the 20 sampling points to avoid clipping-induced changes in areas that would subsequently be resampled for biomass and species composition. A sward of grass comprising both leaves and stems was clipped at the 5 points along each subtransect and mixed in a bag to make up one sample. Four samples were collected per plot and a total of 68 over the whole ecosystem per season. After clipping, the samples were placed in appropriately labelled paper bags and oven or air dried and milled in preparation for chemical analysis (section 3.12).

3.3.6 Species composition of the herb layer

Species composition was recorded on the 17 permanent plots during the wet season when the grasses and forbs were flowering vigorously. These measurements were repeated over the 3 wet seasons of June 1992, February 1993 and May 1994. In May 1994 an incomplete sample was taken because a part of the ecosystem in which plots 14 and 15 are located did not receive sufficient rainfall to induce flowering. As a result, these two plots were sampled for biomass alone.

Ideally, sampling should have been done at the end of the growing season when most growth had taken place and peak biomass could be obtained. However, sampling had to be conducted earlier because grasses in many areas were heavily grazed and

flowers removed during the rainy season. Samples were therefore taken when flowering was complete and as soon as plots were accessible after the rains, giving ample time for substantial growth. The vegetation composition data were used to calculate the percentage contribution of each species and the species diversity for each site.

Species diversity between plots and habitats for grasses and forbs was determined using the Shannon Index of diversity, H' (Magurran, 1988). This diversity index is calculated from the following equation:

$$H' = -\sum p_i \ln p_i$$

where p_i = the proportion of individuals in the i^{th} species.

This proportion was calculated from the total number of hits obtained for species i for each plot over the total number of species hit for all species in the same plot.

The variance of the diversity H' was calculated using the following equation

$$\text{Var } H' = \frac{\sum p_i (\ln p_i)^2 - (\sum p_i \ln p_i)^2}{N} + \frac{S-1}{2N^2}$$

where:

S = no. of species of i^{th} species,

N = total number of species sampled.

The t-test was used to calculate the significance of differences between the diversities of various sites using the following formula:

$$T = \frac{H'_1 - H'_2}{(\text{Var } H'_1 + \text{Var } H'_2)^{1/2}}$$

where H'_1 and H'_2 are the diversities of samples 1 and 2 respectively.

The degrees of freedom were calculated using the following procedure

$$df = \frac{(\text{Var } H_1 + \text{Var } H_2)^2}{(\text{Var } H_1)^2/N_1 + (\text{Var } H_2)^2/N_2}$$

(to compare the diversities of 2 different areas)

Where:

H_1 is diversity of site 1

H_2 is diversity of site 2

P_i is the proportional abundance of the i^{th} species = (n_i / N)

S is number of species

N is total counts of all species

Taylor (1978) points out that if the Shannon index is calculated for a number of samples, the indices themselves will be normally distributed. This property makes it possible to use parametric statistics including the analysis of variance.

A species by sample ordination was done using the Detrended Correspondence Analysis (DCA). This analysis helps to cluster areas of similar or related species composition allowing for patterns to be sought within and between such clusters. A computer program to perform the calculations written in FORTRAN and known as DECORANA (Hill, 1979) was used.

3.4 Measurements of woody vegetation

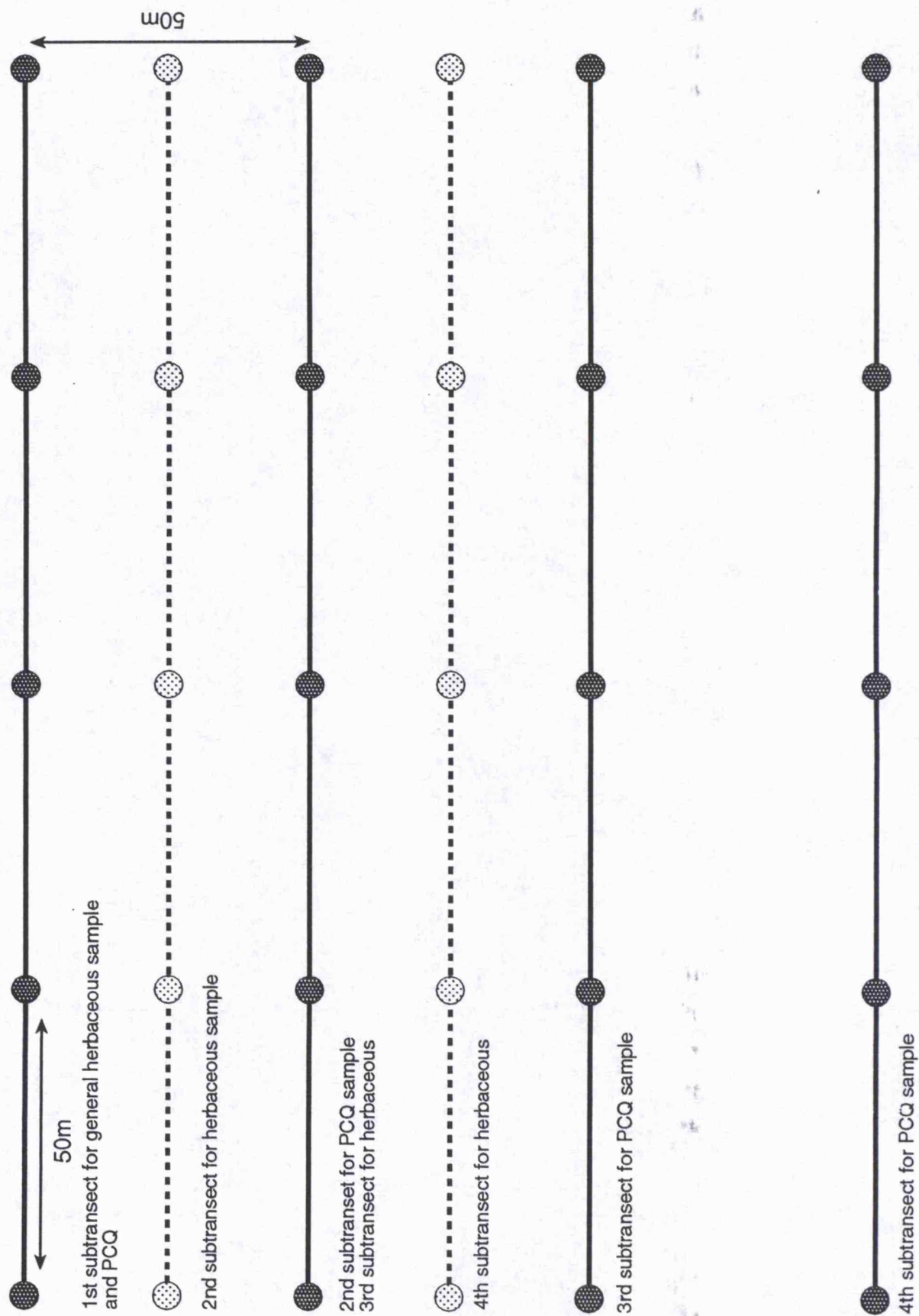
3.4.1 Point-Centre-Quarter method

The PCQ method first devised by Cottam *et al.*, (1953) and Cottam and Curtis (1956) is a plotless sampling technique suitable for sampling vegetation communities in which the dominant growth forms consist of woody plants or shrubs of large size. Points located at fixed or random intervals along a line transect are sampled. A preliminary survey is carried out to determine the minimum sampling interval that reduces the chance of the same individual being measured twice at successive points. The area around each point is divided into four 90° quadrats and the point-to-tree distance measured in each quadrat, thus generating 4 point-to-tree distances at each point. This method theoretically determines the distances between a random point to the first, second, third and fourth nearest neighbours. At each point the diameter of the tree or shrub is measured and the species recorded.

A modified PCQ method was used to sample vegetation in 5 wooded plots. A second measurement in each quadrat, the nearest neighbour from the first tree (tree-to-tree distance) was taken giving a total of 8 measurements per point (Waweru, 1985). The subtransects used for herbaceous samples (see section 3.3.2) were realigned for PCQ to give larger distances between subtransects in order to avoid double sampling trees. The first and third subtransects in the herbaceous biomass sample became the first and second subtransects for PCQ respectively. The third and fourth PCQ subtransects were set 25m and 75m away from subtransect 4 of the herbaceous biomass (Fig. 3.4).

Measurements taken included the point-to-tree or shrub distance, the species of tree, distance to nearest neighbour from the first tree in each quadrat, height and diameter of each tree or shrub sampled. The major tree species growing in the ecosystem is the dwarf *Acacia drepanolobium* which sometimes matures in a stunted form especially where intense browsing or frequent fires occur. Many trees of this species grow to less than one metre in height. Although trees below the one metre mark are not normally sampled, they

Fig 3.4
Layout for PCQ sampling points in each of the plots sampled



were measured in this study as they constituted a sizeable proportion of the population. The PCQ data were used to give descriptive information on the distribution, density, composition, species frequency, dominance and importance value for woody vegetation.

Various weaknesses of this method include its susceptibility to bias if the spatial pattern of tree distribution is not random (Pollard, 1971).

Data were analysed for mean density, relative density and relative frequency using custom made programs in Dbase IV. The mean density per unit area was calculated as:

$$\bar{d} = \Sigma d_i / \Sigma n$$

where

\bar{d} is the mean point to plant distance

Σd_i is sum of all the point-to-plant distances for individual number i

Σn is the total number of individuals measured

The relative density (RD) for each species was calculated as

$$RD_i = n_i / \Sigma n$$

Where

n_i is the number of individuals of species i counted,

Σn is the total number of individuals of all species counted

RD_i is the relative density of species i

Relative frequency of the species i Rf_i was estimated as follows:

$$Rf_i = f_i / \Sigma f$$

Σf is the total of the frequency of all species.

3.5 Establishment of grazing enclosure

The effects of excluding large herbivore grazing on the herbaceous plant layer were observed on 4 permanent exclosures each measuring 9 m x 9 m. All exclosure plots were selected for similar vegetation with adjacent corresponding plots in order to minimise initial differences between plots and exclosures. The exclosures were fenced off using cedar posts and chain link to keep out large herbivores. Two exclosures were constructed in open grasslands and 2 in wooded areas.

3.5.1 Herb layer biomass

Baseline information was collected on vegetation biomass before exclosing the area using the pin-frame. 4 small subtransects were run in each exclosure as on the large

plots. The subtransects were 2.3 m apart, and the interpoint distance within the subtransects was 1.5 metres. A distance of 1.0 metre was left along the inside edge of the fence to avoid possible edge effects. Samples were collected at these points for standing crop biomass and species composition using the pin frame and vegetation height at the same frequency as earlier described. The exclosures were constructed in plots 1, 10, 11 and 16.

3.5.2 Determination of vegetation quality

Food quality was measured in the exclosures during the wet seasons of February 1993 and June 1992. The same procedure of clipping and weighing was followed in exclosures as plots. Vegetation was clipped at about 0.5 metres from the edge and in between the subplots to avoid vegetation changes on the sampling points. After clipping, the grass was oven dried, ground and analysed for crude protein as already described.

3.6 Wildlife distribution, movement patterns and range use

Wildlife of the Athi-Kapiti plains exhibit seasonal migrations at different scales. The wildebeest and zebra migrate long distances in response to various seasonal changes in the ecosystem. The spatial and temporal distribution of wildlife and livestock seem to follow the patterns in vegetation and water availability. In the wet season both water and food are widely available and herbivores and livestock range widely. Wildlife distribution, movement and occupancy patterns were determined using three methods. Of these, two were direct counting methods, - the total ground counts conducted in Nairobi National Park and sample aerial surveys conducted over the whole ecosystem. The third was an indirect method which used dung as a measure of relative occupancy and therefore habitat use.

3.6.1 Total ground counting in Nairobi National Park

In the mid-1960s the warden of Nairobi National Park in collaboration with the East African Natural History Society (EANHS) began monthly counts. Initially, 10 blocks were used for the counts, but some large ones were later subdivided, making 15 counting blocks (Fig. 3.5). Animals had been counted monthly between 1960 and 1976 with a break in 1967, (Foster and Coe, 1968; Hillman, 1979) and when conditions did not allow. In 1976 the counts stopped but in 1989 were reinstated with the help of EANHS, Kenya Wildlife Service (KWS) and Wildlife Conservation International (WCI). Much of these long term data have remained unpublished and are used in this study for certain comparisons.

For this study, KWS, the EANHHS and this project conducted total counts by blocks in the Park, initially once every 2 months. The small size of the Park and the good road network made conditions ideal for total counts and although no error can be attached to these counts, the low cost and use of volunteers' time allowed for frequent counting. Our project made initial attempts at conducting ground counts during the early part of the study but the large movements of wildlife between blocks particularly during the dry season made it unsuccessful. The movements may have resulted in double counting of individual animals and herds particularly wildebeest and zebra which were numerous. Individuals may have been missed altogether. With many observers however, it was possible for all blocks to be counted simultaneously thus reducing the probability of double counting.

Game count participants counted wildlife very early in the morning of the first Sunday of every second month. Counting started at 7.00 am. One vehicle with 2 or more counters was allocated a block. Sometimes due to shortage of counters, one vehicle would be assigned two manageable blocks. The blocks were searched for each animal, and numbers recorded by species and block. The animals counted were assigned two basic categories; young or adult. The major species counted included zebra, wildebeest, Coke's hartebeest, Grant's gazelle, Thomson's gazelle, eland, giraffe, warthog, lion, cheetah, impala, rhino, waterbuck, buffalo and ostrich. Also recorded were vegetation conditions, an estimate of the last rainfall in days, weeks or months, and any other incidental information of interest. KWS was responsible for collection of the data forms at the end of the game counts. In 1993, the counts were halted by the KWS pending evaluation of the data and resumed in 1994.

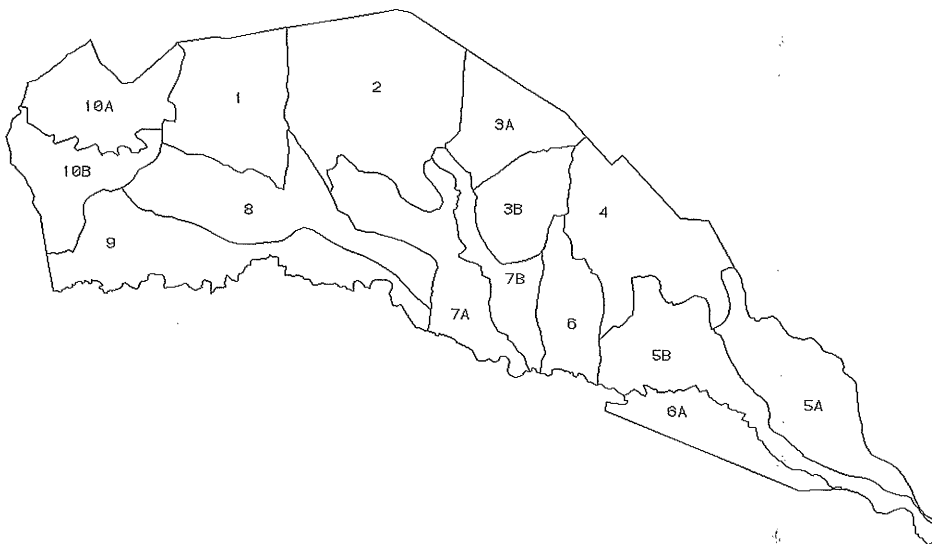
After the counts, data were summarised by block, logged into the computer by this project and analysed by season, species as well as distribution by block. Seasonal numbers and distribution patterns were compared for species groups and individual species.

3.6.1.1 Problems of counting

Several problems were encountered during analysis of ground counts. These included:

- Control of data by another agency. KWS was in charge of collecting data forms from all participants at the end of the counts. However, the collection was not done promptly and data for some blocks was misplaced or lost as a result. Five counts were discarded due to this problem.
- Lack of rigorous control on the quality of data due to use of multiple counters.

Fig 3.5 Nairobi National Park counting blocks



Although many of the volunteers from the EANHs and the KWS were experienced, there were the occasional counters who could not identify certain species, or did not know how to fill out the data sheets. Several sessions were held early in the study to help with species identification and to standardizing block searching and data recording. Despite this eland was sometimes mistaken for oryx. Fortunately these were easier problems to rectify though time was wasted in the process.

From analysis of previous block counts conducted by the volunteers and the experience of the Park managers, the advantages of simultaneous block counting outweighed the shortfalls.

3.6.2 Aerial census over the Athi-Kapiti Plains

3.6.2.1 Introduction

The Athi-Kapiti plains including the park cover an area of approximately 2500km². The area is dominated by poorly drained "black cotton" soils which become sticky during the wet season. It has few all weather roads and as a result much of the rangeland is inaccessible during the wet season. Under these conditions, ground counting of large herbivores and wildlife would have been impractical if not impossible. The aerial survey method which is more efficient over large sometimes inaccessible areas was used to estimate the populations of ungulates on the Athi-Kapiti plains.

The Department of Survey and Remote Sensing (DRSRS) of the Ministry of Planning, formerly KREMU conducted all the aerial counts for this project under a collaborative agreement. The department is involved in monitoring all rangelands in the country, and provides different government ministries, the KWS and other interested agencies with information on distribution and trends in livestock, wildlife and other resources in Kenyan rangelands. Normally, the data are collected at the district level, on a coarse scale of 5 km by 5 km or 10km by 10 km. I commissioned DRSRS to conduct more intensive surveys, selecting a transect size that would provide a compromise between accuracy, time and cost.

In order to understand the principles of aerial counting, I participated in several aerial counting exercises over the Amboseli ecosystem. This provided training on planning and organization of aerial surveys as well as aerial counting techniques. The important aspects of aerial counting learnt included:

- the definition of the strip width in which wildlife and livestock are observed, counted and recorded.
- actual counting techniques - use of photography and tape recorders during a counting exercise and recording of environmental variables.

- techniques of calibrating speed of the aircraft using known distances on the ground.
- recording of altimeter readings during a count.

3.6.2.2 Aerial counting

Aerial counting methods include the quadrat or block method, the total count method and the transect method. The aerial transect method is the most popular sampling method employed over large areas. The principle is that the aircraft flies on a straight line from one side of the census zone to the other at a fixed height above the ground. Streamers are attached to the wing struts of the aircraft so that the observer sees a strip demarcated on the ground. The width of the strip can be decided in advance and the streamers positioned so that the desired width is obtained. The transects are the sample units, and the observer counts all the animals seen between the streamers (Norton-Griffiths, 1978).

The transects can all be of different lengths if necessary, and it is rare to find a census zone that does not dictate transects of variable length. The two main characteristics of aerial transect sampling are therefore:

- (i) the transects are parallel to each other and cross the census zone at random points along a base-line, and
- (ii) the aircraft flies down each transect line once and the observers count all animals seen between the streamers.

Examples of transect counts are given by Bell *et al.* (1973), Norton-Griffiths (1974), Pennycuik and Western (1972) and Sinclair (1973).

In general the transect method is superior to quadrat or block sampling in cost effectiveness, ease of navigation, reduction of boundary effects (as the observer has a physical mark in the form of a streamer), sampling error and fatigue of crew. The main cause of sampling error is related to uneven distribution of animals over an area. Sampling error is aggravated the more bunched or aggregated the animals are. Aggregation or herding leads to a bigger variance between the numbers of animals found in each sampling and may sometimes lead to an "all-or-nothing" effect depending on the method used.

Sampling error can only be reduced by minimising the effect of this clumping. The strategy, therefore, is to create at the outset - i.e. at the census design stage - a population of sample units that has as low a variance as possible (Cochran, 1963; Yates, 1960). The use of transects rather than quadrats allows for the collection of more information about the census zone and leads to smaller sampling error. The transect

method is however ineffective in very broken country, when the vegetation is very thick and/or patchy, and when the country is very mountainous. In these cases some form of block sampling would be preferable to quadrat sampling.

The transect method was selected over other aerial counting techniques for three main reasons:

- (i) It provided coverage of the whole range which is too large and in places inaccessible to vehicles especially during the rains.
- (ii) It provided a sample count of the dominant mammal species including livestock and plains game.
- (iii) It has been recommended for its reduction of sampling error (Norton-Griffiths, 1978).

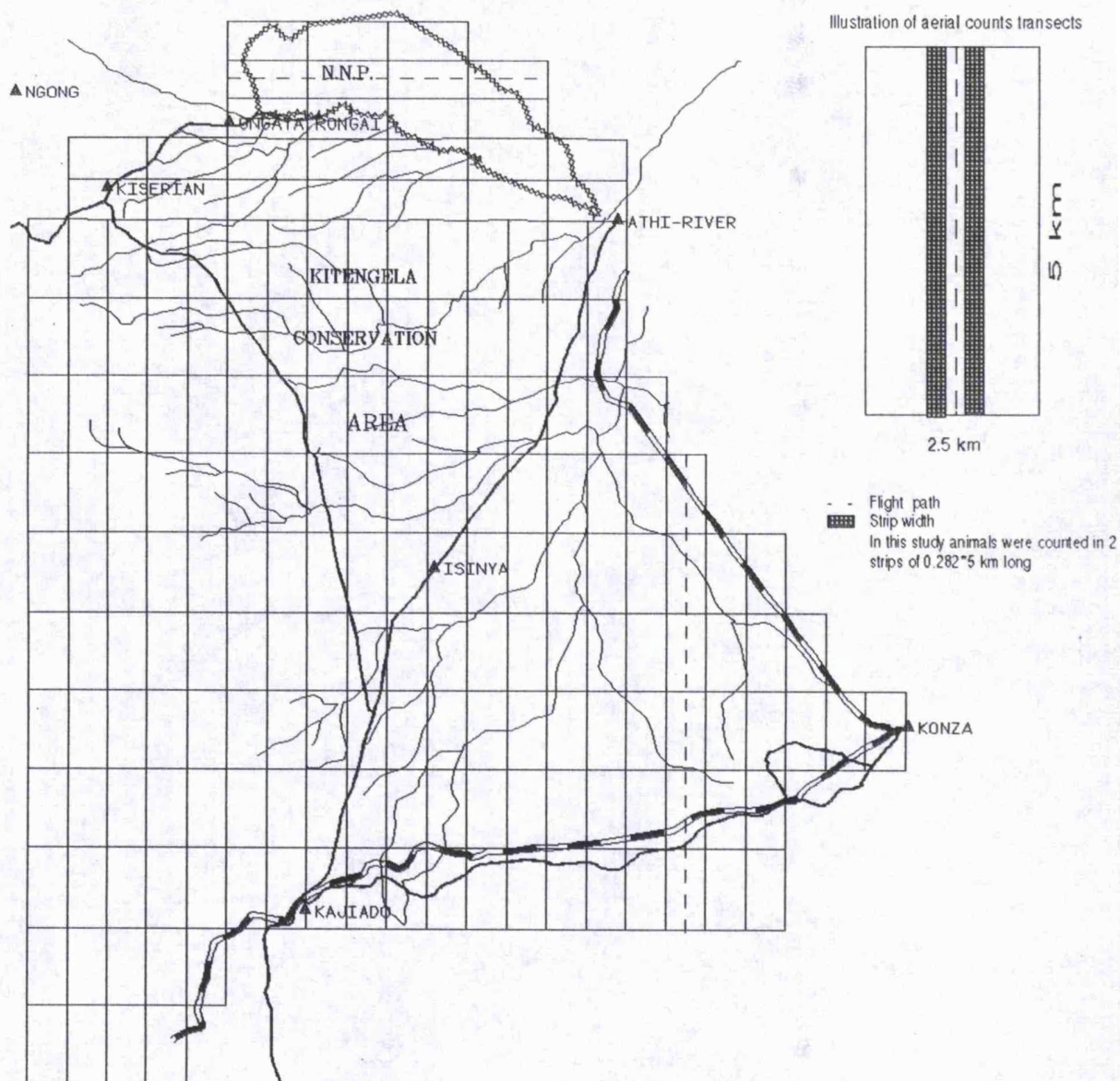
A series of systematically arranged transects measuring 2.5 km by 5 km was traversed during the aerial censuses over an area of approximately 2287 km². Counts were aligned to suit the general flow of traffic as most of the ecosystem lies over busy air space used by both the international and local flights. Transects were aligned in an east/west direction over NNP and areas immediately bordering it to coincide with the general flow of light aircraft using the Wilson airport. Over the rest of the ecosystem the transects were aligned in a north/south direction (Fig. 3.6). Animals were counted on a 282 m strip in each transect. The strip width was determined by rods on the wing struts and a mark on the window for the observer's eye, (Western, 1976; Norton-Griffiths, 1978). Animals were counted in each transect. When large herds were encountered they were photographed and an estimate of their number made in case of camera or film failure. The data were recorded on tape recorders during the count.

The first survey was conducted in March 1992 at the height of the dry season, the second in June 1992 during the wet season and the third in October of 1992. Over the first year (1992) aerial counts were to be conducted seasonally - 4 counts -, and when necessary during the second year. However, only three counts were possible in 1992, due to DRSRS' commitments to other agencies. A total of 6 counts were conducted in all, 3 in 1992, two in 1993 and one in 1994. Of these, three were wet (June 1992, January 1993 and April 1994), and the other three dry season surveys (March 1992, October 1992 and October 1993).

Information collected during the census included:

- Wildlife numbers by species and their location in the transect,
- Livestock numbers,
- Settlement - numbers of traditional maasal huts and permanent houses,
- Location of water resources,

Fig 3.6
Map showing the Athi-Kapiti plains and Nairobi National Park
including the area sampled by aerial surveys



- Agricultural activities e.g crop agriculture plots sighted,
- General vegetation conditions such as vegetation greenness and cover, and other environmental variables.

The aerial survey data were transcribed and logged into the computer at DRSRS after the counts and passed on to the project in this raw form for analysis. The Jolly Method 2 (Jolly, 1969) was used to derive population estimates and standard errors of each species as follows:

Population estimates of the aerial surveys were calculated (Jolly, 1969) for equal sized sampling units as follows:-

$$1. \quad \text{Population mean } \hat{Y} \\ \hat{Y} = N \cdot \bar{y}$$

where

N = number of sample units in population (i.e area/strip width, number of census units needed to fill the census area completely)

\bar{y} = sample mean i.e $\sum y/n$

y = number of animals counted in any one unit

n = number of sample units in sample

$$2. \quad \text{Sample variance } s^2_y = \frac{1}{n-1} \cdot \{ \sum y^2 - \frac{(\sum y)^2}{n} \}$$

This is the variance between animals counted in all units

$$3. \quad \text{Population variance } \text{Var}(\hat{Y}) = \frac{N(N-n)}{n} \cdot s^2_y$$

$$4. \quad \text{Population standard errors } SE(\hat{Y}) = \sqrt{\text{Var}(\hat{Y})}$$

95% confidence limits of $\hat{Y} = t \cdot SE(\hat{Y})$

t for $n-1$ degrees of freedom.

The data were manipulated in DBase IV. Density distribution maps by species for each count were initially drawn to show the trends, but later combined for season and by species groups. Overlays of other important features over the ecosystem such as rivers, roads and soils were made. GIS Arc info. (3.4) proved to be a very important tool in this exercise.

3.6.2.3 Problems

Few problems arose as a result of using another agency to collect the aerial data. Most significant was the inability to have the counts undertaken at the most appropriate time for the project. Although every effort was made to count at the time requested, other commitments to government sometimes took precedence. In 1992 for example only three counts were possible, though the request had been made for four seasonal samples, two wet and two dry. Other problems were:

- The opportunity to gather incidental but sometimes very critical information by this researcher during the counting exercises was not available. A better understanding of the ecology of the area could have been gained from the flights, but the experience of DRSRS ultimately offered certain advantages. These were:
- No time was lost training counters and going through the problems of hiring aircraft and pilots.
- There was a better chance of using the same aircraft and counters.
- Data could be collected in a standardized format adding to the existing database for the ecosystem.

3.6.3 Dung counting to estimate relative occupancy patterns

3.6.3.1 Introduction

The dung of large herbivores has been used to obtain both spatial and temporal data often difficult or impossible to obtain from the mammals themselves (Coe and Carr, 1983). These difficulties range from problems of visibility in scrub or wooded habitats to logistical problems raised by the necessity to cull large samples in order to obtain statistically useful data on food selection and diet quality.

The greatest benefit of faecal material to a researcher is that it is moderately persistent. The accumulation of dung over time provides information on occupancy for an extended period of time. The time frame over which dung can be left to accumulate can range from minutes to years. Use of an area during the night can also be determined from the same information. The droppings can be used as a relative measure of habitat occupancy by different species of herbivores in an ecosystem.

Several complex techniques have thus been developed to derive the maximum possible ecological information from the dung. The size, shape and odour of bovid dung are quite characteristic of each species and make it easy to identify pellet groups. Various methods, which have primarily been used in the study of deer have been the subject of a detailed critical review by Neff (1968). In practice the most reliable information obtained from pellet counts concerns the measure of habitat occupancy by

different species. In addition to the study of deer, faecal group counts have also been employed in the study of lagomorphs (Cochran and Staines, 1961); rodents (Emlen *et al.*, 1957) and game birds (McClure, 1945). The most widely used technique has been that of pellet groups counts, first developed by Bennett *et al.*, (1940) and used in this study.

There may be temporal variations in defaecation rate, which, together with temporal patterns of habitat use, may lead to non-random defaecation. Louden (1979) successfully used the technique of 'standing crop' faecal accumulation assessment in the study of habitat use by roe deer (*Capreolus capreolus*). His results showed remarkably little variation in the number of dung groups recorded per sample plot within a particular vegetation type, yet consistent differences between vegetation types. Similar results have been reported for red (*Cervus elaphus*), and sika (*Cervus nippon*) deer showing a clear correlation between relative use of habitat-types estimated by faecal accumulation and measured by other independent methods (direct count, browse damage etc.). Differential distribution of dung between habitats enabled patterns of habitat use by particular species of animals to be established.

Pellet counts may be made in quadrats of known size or transects, once or repeated seasonally or over a specific period, e.g. weekly, monthly, etc. Detailed study of the decay patterns of the dung must however be undertaken before the technique can be used to estimate wildlife population numbers with any confidence (as, for example, Mitchell *et al.*, 1985). The reasons for selecting this method was to estimate relative use of vegetation over space and time by the various ungulate species. Therefore no attempt was made to estimate wildlife population numbers.

Results of the dung counting method can be affected markedly by non-random patterns, temporal or spatial. Nonetheless, it has remained the most regularly used technique.

3.6.3.2 Methods

Habitat occupancy by various species in the ecosystem was estimated using dung. To help in identification of dung, sample collections were taken from known species. These were air dried and used as reference material.

Once every two months dung was counted on all the vegetation plots. The piles were counted and scored by animal species along the subtransect lines as follows: A sweeping method (Whitesides *et al.*, 1988) was used in the dung counting exercise. A recorder walked along a marked centre line on the subtransect with two observers on either side. The recorder held the tape at the 2.5 m mark to ensure that the two observers did not count outside the subtransects. Each subtransect was divided into 5

m wide by 50 m long subplots within which all undisturbed dung piles were counted. The sections were named subtransects 1 to 4. Once a pile was counted it was disturbed or destroyed to avoid double counting. 16 subplots were altogether sampled in each plot. 2 types of dung droppings were encountered, definite piles which were most common and dung 'trails' commonly dropped by sheep and goats (sampled together as 'shoats') while walking. Defining a pile on trail dung was difficult and the possibility of over or underestimating real. Nevertheless, an attempt to estimate a pile was made following observations of 'shoat' during defaecation. The majority of large herbivores on the other hand stop to defaecate and their dung is normally dropped in definite piles. The remaining 16 plots in the ecosystem were all sampled in a similar way.

Quantity of dung, was analysed for "occupance" by species for plots, season and habitat. Dung measurements were used only for relative comparisons of occupance by plot, species and through time.

3.7 Use of dung to determine diet selectivity in herbivores

3.7.1 Introduction

Estimating the nutritional quality of the diet of free-ranging herbivores is one of the most difficult tasks facing the ecologist or wildlife manager. Conventional techniques available include chemical analysis of diet subsamples obtained through fistulation e.g (Engels *et al.*, 1971; Githaiga, 1991), chemical analysis of gut contents from culled animals e.g (Staines and Crisp, 1978; Staines *et al.*, 1982) or analysis of vegetational samples taken by hand from the various forage species seen to be eaten. Forage collected by investigators may often be of a different chemical composition than those chosen by the animal because animals tend to be selective in both individual plants and plant parts that they ingest (Weir and Torrel, 1959). Thus stomach contents or faeces are frequently analyzed because they presumably are a more accurate representation of the diet selected by the animal.

Erasmus *et al.*, (1978) suggested that amongst herbivores, an estimate of dietary quality of the ingesta could simply be determined from analysis of the nutrient status of faeces. They demonstrated a linear relationship between chemical content of dung and ingesta for both lignin and protein nitrogen: perhaps the most important determinants of dietary quality. A linear relationship between lignin content of diet and dung was perhaps not surprising since lignin represents the one component of the diet that is virtually indigestible; 100% of the lignin ingested remains in the dung.

Other methods to estimate diet quality in herbivores are based on correlations between digestibility and the chemical composition of the diet or faeces. Such techniques

have been used in studies on both wild and domestic ruminants e.g. (Short and Remmenga, 1965; Erasmus *et al.*, 1978; Holloway *et al.*, 1981; Holechek *et al.*, 1982a; Leslie and Starkey, 1985; Wofford *et al.*, 1985; Mubanga *et al.*, 1985). The faecal index most commonly used is faecal nitrogen (N), used in this study as a measure of diet selectivity among herbivores. Faecal cellulose, neutral detergent fibre (NDF), acid detergent fiber (ADF) and lignin have also been used. Sinclair *et al.*, (1982) suggested the use of faecal N as an index of food quality for snowshoe hares, (*Lepus americanus*).

Stomach content N has been shown to be higher than dietary N in all animals, suggesting that the stomach contents were contaminated by endogenous N, most likely amylolytic and proteolytic enzymes. In contrast to poor prediction of dietary N by stomach content N, both colon and faecal N were very good predictors of dietary N. The regression equations of dry matter digestibility (DMD) and colon content and faecal N were also highly significant. Similar results were found by (Holechek *et al.*, 1982a; Wofford *et al.*, 1985). However, in both of these studies, faecal N was a better predictor of dietary N than of DMD. Most faecal N is of metabolic origin and is excreted in proportion to intake or digestibility. However, when dietary N is high, a greater proportion of faecal N comes from the food (Greenhalgh and Corbett, 1960).

Strong correlations between faecal N and dietary N have been found in deer, (*Odocoileus hemionus*) (Leslie and Starkey, 1985; Mubanga *et al.*, 1985), elk, (*Cervus elaphus*) (Mould and Robbins, 1981), snowshoe hares, (Sinclair *et al.*, 1982), several domestic and wild African ruminants (Erasmus *et al.*, 1978), and cattle (Holechek *et al.*, 1982a; 1982b; Wofford *et al.*, 1985).

Several investigators (Marten *et al.*, 1963; Erasmus *et al.*, 1978; Holechek *et al.*, 1982a; 1982b; Wofford *et al.*, 1985) have suggested that indices of diet quality are more useful in detecting trends in diet quality, e.g., seasonal changes in food quality, than for determining absolute values.

The use of faecal N indices to predict diet quality has, however, received some criticism (Hobbs, 1987; Robbins *et al.*, 1987). When forages contain high concentrations of protein-binding phenolics, faecal N values are elevated, resulting in overestimates of dietary N (Mould and Robbins, 1981). In addition, faecal N reflects N-digestibility, dry matter intake, and metabolic nitrogen, thus making it an unreliable indicator in some instances. Hobbs (1987) particularly cautions against using this index for within-season comparisons of two populations from different habitats because within-season regressions may not be significant although data pooled across seasons may be. However, Leslie and Starkey (1987) suggested that many of the criticisms of the faecal N index are unwarranted and that the faecal N index is valid in other situations. These situations

include examining seasonal changes in diet quality within a population, single-season comparisons between years for a single population, and comparisons between two populations occupying similar habitats and consuming similar diets. Thus, in these situations, and when animals are not feeding on diet high in phenolics, faecal N indices can be used with good reliability.

3.7.2 Data collection for faecal quality

Data were collected along the subtransects described in section 3.6.3.2 by species. The intention was to collect 2 samples per subtransect for each species, but it became clear that most species were not represented in all the plots. Where possible, a minimum of 10 samples was collected for each species per sample for wet and dry season over the ecosystem. Samples for some of the less numerous species such as buffalo and eland were more difficult to find. For these any dung found within the subtransects was collected. During the chemical analysis the sample size for common species such as zebra was reduced due to financial constraints. Once collected the samples were dried, ground and analysed using the same techniques as the vegetation.

3.8 Wildlife utilization patterns in Nairobi National Park

Grass biomass and height was measured over a period of several months in the dry season of 1993 when animals concentrated in the Park and part of the wet season in 1994. Initially 7 transects were selected on the basis of vegetation height in the following areas: the Acacia woodlands, a burnt site on the Sosian area, Ormanyi valley grasslands, Songora ridge grasslands, the swamp edge below the observation point and the other between the Hyena Dam and the fence next to the army barracks and the open grasslands of aerodrome plains (Fig. 3.7). The transects covered a range of grass heights and biomasses from high to low. The aim of choosing a cross-section of transects across a grass height gradient was to determine whether herbivore use was based on this gradient. An additional plot was sampled in the Hyena dam swamps to illustrate the changes in vegetation and herbivore use patterns as the swamp receded during the dry months. Due to the very wet conditions of the swamp area, only 3 points were sampled in this transect. This small transect was numbered 6.2, and the main plot in these swamps 6.1.

In January 1994 an additional transect was sampled at the forest-edge after it became clear that this area was in a different height category.

3.8.1 Vegetation

Vegetation samples were collected from June 1993 to June 1994. A total of 14 samples were collected during this time. The samples were usually collected 3 weeks after the last day of the previous sampling in 550m long transects in plots 1, 2, 3, 4, 7 and 8. Due to the small size of the swamp-edge habitats, transects 5 and 6.1 were shorter, 300m. Biomass was sampled on points, 50 m apart using a 10-pin pin-frame as described in section 3.3.2; 12 points in plots 1,2,3,4, and 7; 7 in plots 5 and 6.1 and 3 in plot 6.2. 10 measures of grass height were taken randomly around the point.

3.8.2 Wildlife

Wildlife dung (occupance) was sampled in the same transects. Dung was counted and recorded by species in subtransects measuring 50m long and 5m wide using the methods described in section 3.6.3.2.

3.8.3 Wildlife counts

Wildlife was also counted along the transects by species. One counter recorded the numbers of wildlife on the left side of the transect, the other on the right. An estimate of the distance the animal was away from the transect line was also estimated. A range finder was used as a means of confirming distance estimates during the training sessions. Once a good level of accuracy was attained without the range finder the counts began. Animals were recorded at 50m, 100m, 200m, 300m up to 500m. In most cases by the 200m -300m distance, there were vegetation changes in some of the areas. Therefore, for analysis animals counted between 0 to 200m on either side of the transect line were used.

A different method of determining the vegetation selectivity patterns in Nairobi Park was attempted and adopted from Sinclair (1985). In this method animals were counted by species at a point or area where they were found grazing and 10 grass height measurements were also taken at random. Grass height was averaged for each feeding area and analysis for height-based feeding preference done.

3.9 Large herbivore use patterns around settlements

3.9.1 Introduction

Localized vegetation factors affect herbivore distribution and use patterns (Georgiadis *et al.*, 1989). Human impacts of the savanna ecosystems through pastoralism, fire and woodcutting have been implicated in the maintenance of diversity (Western, 1982). Recent evidence indicates that pastoralism has been a factor in East Africa since

6000 B.C. (Mgomezulu, 1981), 4000 years earlier than previously thought. Bell (1971) suggested that the highest concentration of wild ungulates are found in areas of past and present pastoral activities.

In general settlement has the effect of taking up areas that would otherwise be used by wild herbivores. During the life of a settlement, cattle, sheep and goats forage on a large area, leaving in the morning in search of pasture and water, and returning every night except during the droughts when animals are moved elsewhere for better pasture. The animals continually deposit large quantities of nitrogen-loaded faeces and urine over a limited area with resultant impact on plant growth and productivity due to enhanced levels of usually limiting nutrients. Other conditions such as soil-water relations are affected. Apart from this, other activities such as livestock grazing and trampling further change the immediate surrounding of the settlements in a way that may subsequently influence herbivore use patterns. In studies on nutrient levels around settlement, Stelfox (1986) found higher levels of nitrogen, phosphorus, sulphite, calcium salts and organic material in and around settlement sites compared to controls 250 m away.

Abandoned Maasai bomas have also been implicated in diversifying savanna ecosystems. Muchiru (1994) found that the grazing conditions were better at such sites and herbivores used them preferentially. He also found that these impacts perhaps lasted for several hundred years.

Factors that dominate vegetation sometimes vary in a continuous and systematic way. For example, livestock use intensity decreases steadily along a transect radiating from a watering point (Georgiadis *et al.*, 1989). Activities such as woodcutting also result in drastically altered landscape. Jensen (1983) showed that trees and shrubs around Maasai settlement were cut for building, perimeter fencing and fuelwood. As a result a ring denuded of woody vegetation developed around the settlement. Shrubs were further browsed by goats or trampled by livestock. Settlements are therefore of critical importance at the local scale and perhaps at the ecosystem scale and as a result may effect a structure of herbivore communities.

Initially, 3 areas were selected for this study based on the wildlife distribution patterns from the aerial surveys. These included the western end of the ecosystem bordering the escarpment, the Kitengela, used during the migration and sometimes through the dry season and the Olmirui and Enkiggirri areas in the south eastern part of the ecosystem, used in the wet season. The western end was later omitted due to difficulties in convincing landowners about the value of the study and the perpetual absence of families who often moved their cattle in search of better pasture and water

during the dry season. Too many other factors would also interfere with the quality of data including abrupt changes in vegetation, topography, presence of many watering points, an all weather road and the location of most settlements on slopes.

Settlements were therefore sampled in two localities, the southeastern part of the ecosystem and the Kitengela. Transects were selected to minimise variance in herbivore use and to provide sufficient area to accommodate a 500 m long transect starting at the settlement. Settlements with watering points very close by were avoided as these attracted herbivores during the dry season and created feeding gradients (Georgiadis *et al.*, 1989) that would distort the settlement gradient analysis. The transects also avoided the entrance to the homesteads and the bomas, areas that are excessively trampled as livestock and people go in and out each day. They also avoided human altered sites such as agricultural plots. Once these were excluded and the site was still suitable, it was bisected into north/south or east/west halves, and a transect run from the settlements. Random numbers were then used to select the precise location of the transect. An assumption was made that the impact of settlement on both vegetation and herbivore use was evenly distributed around the settlement, except at the entrance. If the conditions along a particular transect were unsuitable (as outlined above) then that transect was eliminated. In the end most settlements areas were only able to accommodate one or two transects.

A total of 10, ½ km long transects were set radiating from settlements. The transects were laid in areas of uniform vegetation to avoid variation due to habitat differences. Two were located at Olrimirui radiating from one homestead, 4 in Enkigirri, radiating from 3 homesteads and 4 in Kitengela radiating from 3 homesteads. Initially the samples were taken once a month but after October 1993, the sampling was stopped. Since the aim was to look at large herbivore use around active settlement and to see the interaction between livestock and wild herbivores, the exodus of cattle from the ecosystem and the concentration of wildlife in the park during the 1993 drought made many areas unsuitable for the study. Sampling was resumed after the rains of April 1994, and the return of the Maasai with their cattle.

Two samples were collected in July 1994 in order to capture the use patterns during the rapid transition between the wet and dry seasons in the south eastern part of the ecosystem.

3.9.2 Measurements of vegetation gradient away from settlement

The transects were divided into 50 m portions for biomass sampling. 10 pins set on a pin frame were used at each of the 50 m points and the numbers of plants hitting the pin, the plant part and its condition were all recorded as described in section 3.3.2.

3.9.3 Wildlife use of areas around settlements

Herbivore use of areas around settlement was estimated using fresh dung as an index. Dung piles were counted and scored for by species as described in section 3.6.3.2 along the transect gradient in an area of 25 m by 5 m through the 500 m length. The counted piles were disturbed or destroyed to prevent repeat counts. The frequency coincided with that of the biomass sampling.

Comparisons were made between transects, sites, seasons and species use of sites using analysis of variance, t-tests (Zar 1984). Simple regression analysis was used to tease out any relationships between dung distribution and distance away from settlement.

3.9.4 Human settlement and land use in the northern Kitengela

Aerial photographs were taken over the northern Kitengela in order to illustrate human landuse activities. The photographs were taken in October 1994 by Photomap International, a photography and mapping agency. The scale of the photography was 1:20,000 stereographic cover, 60% overlap on an area of approximately 300km². Maps were produced from the photos to show houses, industrial sites, cultivated and fenced areas, rivers, roads and major tracks. For purposes of illustrating human landuse and discussing possible impacts on the wildlife migrations, only part of this information was used.

3.10 Rainfall data

Rainfall is an important factor in any terrestrial ecosystem. Its amounts and variability drive the primary production pulses and provide drinking water for herbivores. Its measurement can sometimes be critical in understanding the ecological dynamics of an ecosystem.

There were five active rainfall stations in the ecosystem. Three were operated by the meteorological department at Ngong, Wilson Airport and Kajlalo town. The other one was located at the Cheetah Gate (one of the gates to Nairobi National Park next to the Athi-river town) where data was already being collected by personnel of Kenya Wildlife

Service. The final station was at the Isinya Community Centre in Isinya where data was being collected by the agricultural department (Fig 3.8).

In addition three more were installed. The initial intention was to collect rainfall data as described by Stanley-Price (1974) but it soon became apparent that with the large human population in the area, the rain gauges would be tampered with. Whilst it was possible to pay someone to guard the enclosures, it was impractical to do so with the rain gauges. Two rain gauges were installed at local schools at Ereteti and Enkigirri where a teacher agreed to undertake the task of recording the daily rainfall. The teachers were interested as the exercise would provide them an opportunity to get more weather recording instruments from the meteorological department once evidence of carefully recorded data was provided. This could also be used by their schools as part of their science program.

Loiyangalani had an existing station and personnel but needed a new rain gauge. This was provided. Initially the rain gauges were checked on a weekly basis to ensure that data were being recorded correctly. Once quality was assured the frequency of visits was altered to once every two weeks or monthly. Data were used to show the distribution of rainfall over the ecosystem.

3.11 Statistical analysis

3.11.1 Biomass calibration

The average number of grasses or herbs hitting a pin were regressed against corresponding weights by quadrats. A regression analysis was done in order to derive a formula giving the relationship between hits-per-pin and weight (mass). Initially, two separate regressions were derived, one for forbs and the other for grasses. A non-linear regression with the intercept forced to zero was used, based on the assumption that when no vegetation was hit biomass was zero.

3.11.2 Interactions between vegetation and large herbivores

3.11.2.1 Grass height as a factor in structuring large herbivore communities

Grass height was analysed against relative occupancy to determine its effects on large herbivore distribution. Plots were grouped by grass height using wet season data selected due to the wide range of heights in this season. Five classes ranging from the shortest to tallest grass in approximately 10 cm classes were obtained. The grouping was done using the Least Significant Differences (LSD) and the Tukey test following an analysis of variance.

Once the data were grouped into these height classes, an analysis of variance was done to confirm these groupings. Browsers were left out of the analysis since their presence in various plots depended on the presence of browse vegetation and not grasses.

A further analysis of variance was conducted to determine the variation in occupancy along the height gradient. A regression analysis was also conducted on dung data cumulated along the increasing height gradient was to determine the strength of the relationships.

3.11.2.2 Vegetation quality as a factor influencing large herbivore distribution patterns.

Dung data were averaged by plot, season and species groups and regressed against average seasonal crude protein to test their relationships.

3.11.2.3 Biomass and wildlife occupancy relationships

An attempt to order biomass along increasing quantity using analysis of variance and LSD was made using the wet season data.

3.11.2.4 Wildlife selectivity patterns

Although it was already evident from the height occupancy analysis that the small wild grazers were selecting higher quality areas than the medium and large grazers further analysis to support this was derived from the amounts of faecal protein in the dung of various species.

Dung was analysed for levels of faecal protein to gauge vegetation selectivity patterns of large herbivores. An assumption was made that the presence of high levels of protein in the dung was a measure of vegetation selectivity.

Relationship between body size and the quality of dung was determined using a regression analysis. Body weights of the various species of ungulates from (Foster and Coe, 1968; Western, 1973 and Appendix 1) were regressed against the crude protein in dung for both wet and dry season.

3.12 Analytical methods

3.12.1 Protein analysis

Grass quality was determined by a micro-Kjeldahl technique (Havilah *et al.*, 1977). This technique converts organic nitrogen to ammonia by selenium-catalysed acid digestion and the ammonia is subsequently determined by colourimetry using the sodium salicylate/sodium dichloroisocyanurate technique with absorbance measured on a manual

spectrophotometer at 667nm. The nitrogen content (mg/g) was multiplied by 6.25 to give protein content, converted to a percentage of dry weight.

Faecal quality or crude protein in the dung of large ungulates was analysed in a similar way.

Fig 3.7

Areas sampled for habitat utilization in Nairobi National Park

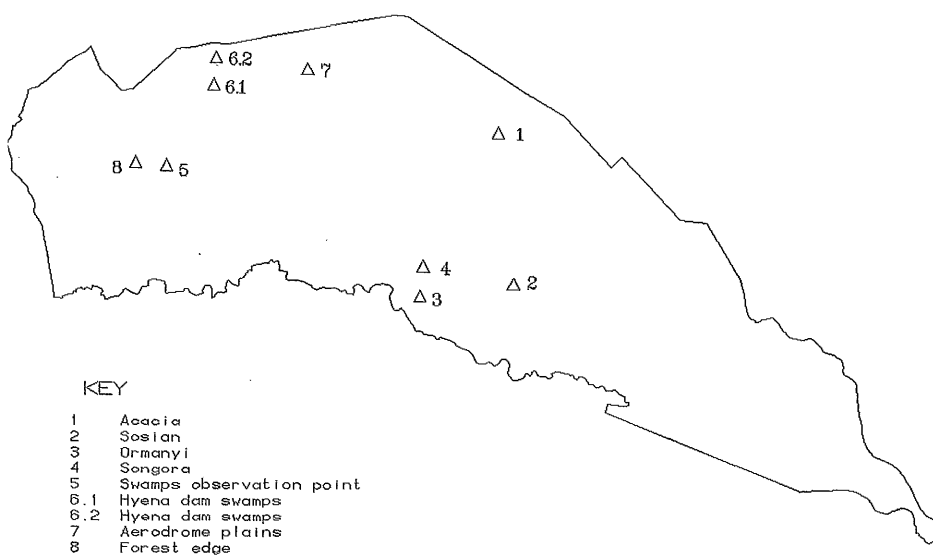
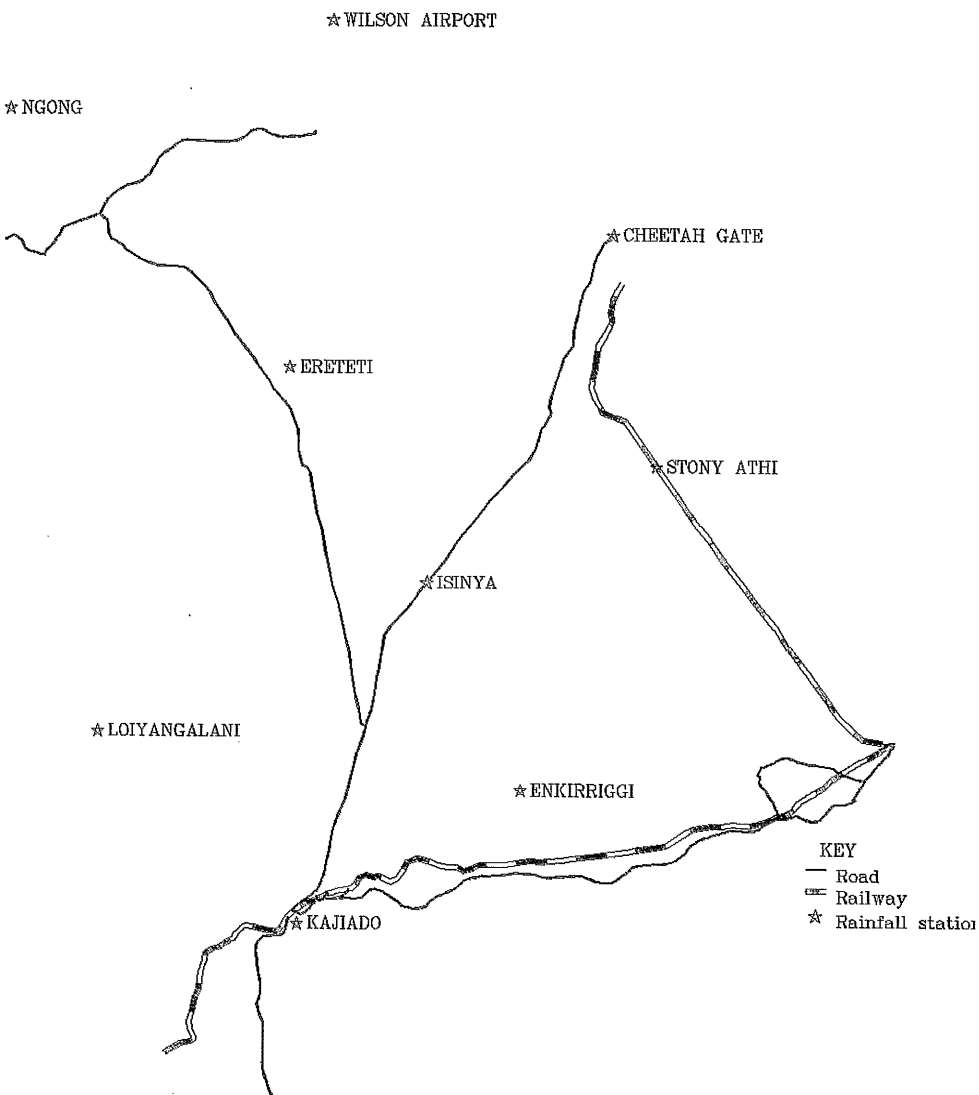


Fig 3.8
Location of rainfall stations in the Athi-Kapiti plains



CHAPTER 4

VEGETATION OF THE PARK AND THE PLAINS

4.1 Biomass Calibration

The regression equation for forbs was $Y=44.68x$, ($r^2=0.76$, $F=126.28$, $df(1,39)$, $p \leq 0.05$). A similar regression for grasses alone gave an equation $Y=41.07x$, ($r^2=0.97$, $F=1168.25$, $df(1,34)$, $p < 0.01$). The curves from these equations were tested for coincidence and parallelism to determine whether they were significantly different to warrant their separate use. Both tests showed that the differences between the curves were not significant ($F=0.18$, $df(1,71)$, $p \geq 0.05$ and $F=1.19$, ($df(2,71)$, $p > 0.05$) for parallelism and coincidence respectively. The data for forbs and grasses were combined and a new regression derived where $Y=43.31x$ ($r^2=0.98$, $F=1496.34$, $df(1,34)$, $p \leq 0.05$), (Fig. 4.1).

This new equation was used to convert hits-per-pin measurements from the 15 plots outside the park into biomass (g/m^2). Differences between NNP vegetation and those of the plains were very large however, both in quantity and height (see section 4.2. Fig. 4.5 & 4.6) and so a regression derived in an earlier study by Gichohi (1990), $Y=64.638x$ (Gichohi, 1990) was used for conversion of data for Nairobi National Park.

4.2 Seasonal patterns in herbaceous biomass

Biomass over the ecosystem increased during the rainy season and decreased during the dry conditions. The peaks in February 1993 and May/June 1992 (referred to as June 1992) followed periods of heavy rain (wet season) while the troughs in March 1992, September 1992 and June 1993 to January 1994 coincided with the dry season (Fig. 4.2 a-d & appendix 2). October 1993 showed the lowest biomass measured at the end of a dry spell. The general trend in biomass was the same over the whole ecosystem, but the extent of the changes were highly variable over time (Fig. 4.3, 4.4, 4.5, 4.6). Peak biomass in plots such as 16 and 17 of Nairobi National Park were large compared to those of plots 10, 12 and 13. Although there was significant growth during the wet seasons, the peaks within the plains differed between plots but were not as marked as those in the Park (Fig. 4.7). Plots 1, 10, 12 and 13 had a lower mean vegetation biomass than the Park and other less grazed sites on the plains such as plot 5. Dry season patterns varied in a similar way (Fig. 4.8).

Sharp drops in biomass were recorded over the whole ecosystem during the prolonged dry spell between April 1993 and March 1994. Mean ecosystem biomass

Fig. 4.1
REGRESSION OF MEAN HERBACEOUS BIOMASS AGAINST AVERAGE HITS PER PIN
EQUATION $Y=43.31X$

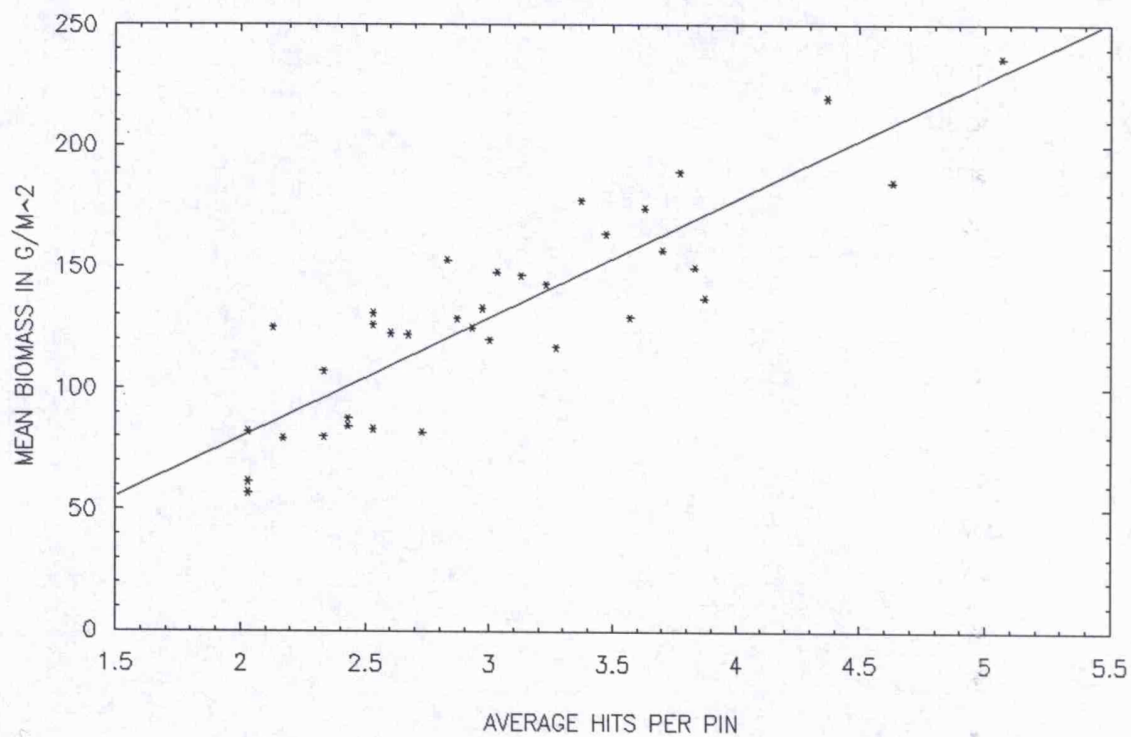
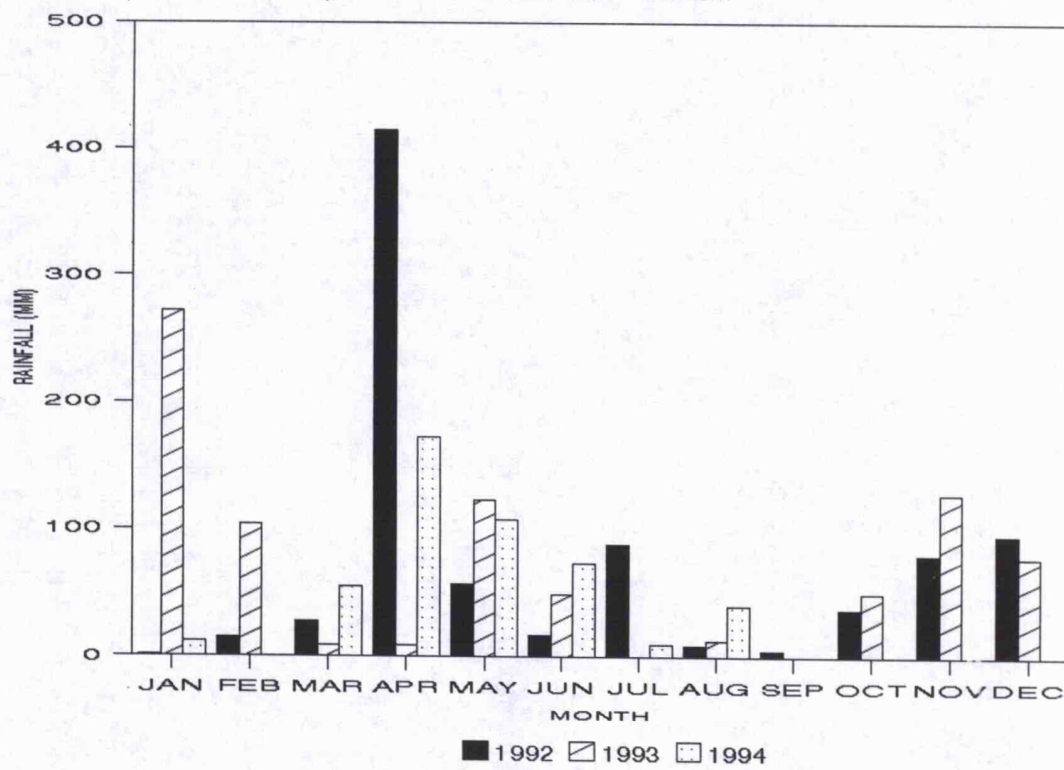
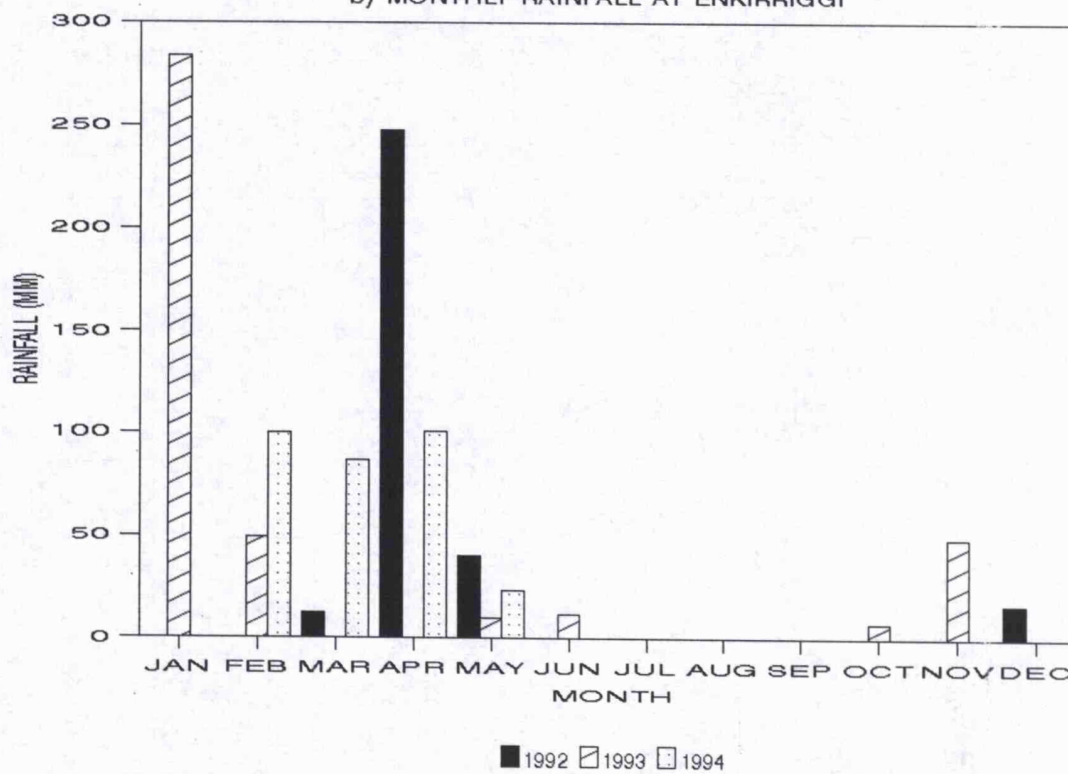


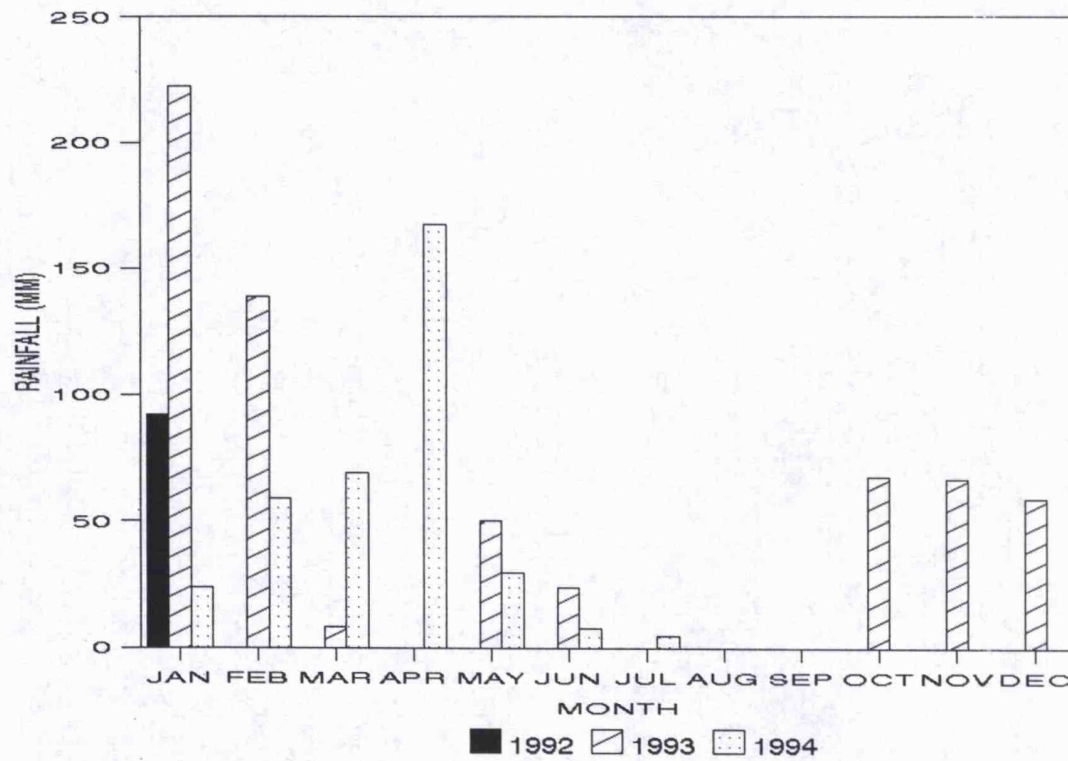
FIG 4.2
a) MONTHLY RAINFALL AT WILSON AIRPORT



b) MONTHLY RAINFALL AT ENKIRRIGGI



c) MONTHLY RAINFALL AT ISENYA



d) MONTHLY RAINFALL AT KAJIADO

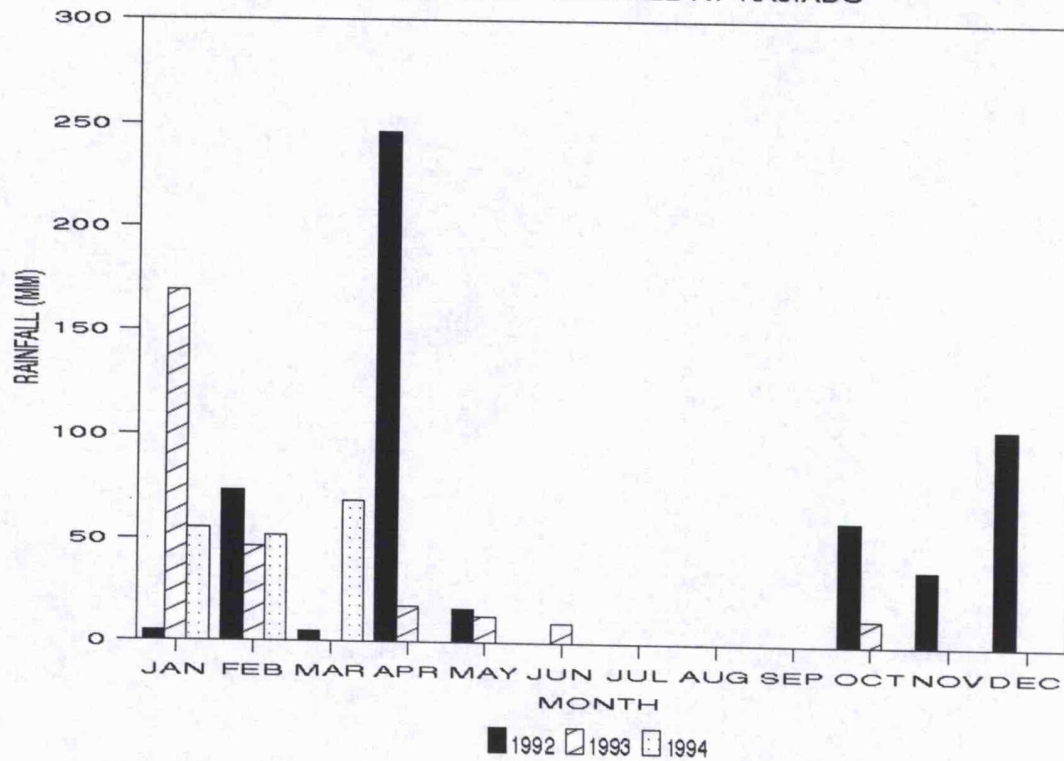


Fig 4.3
CHANGES IN HERBACEOUS BIOMASS
BETWEEN 1992 AND 1994
(PLOTS 1-5)

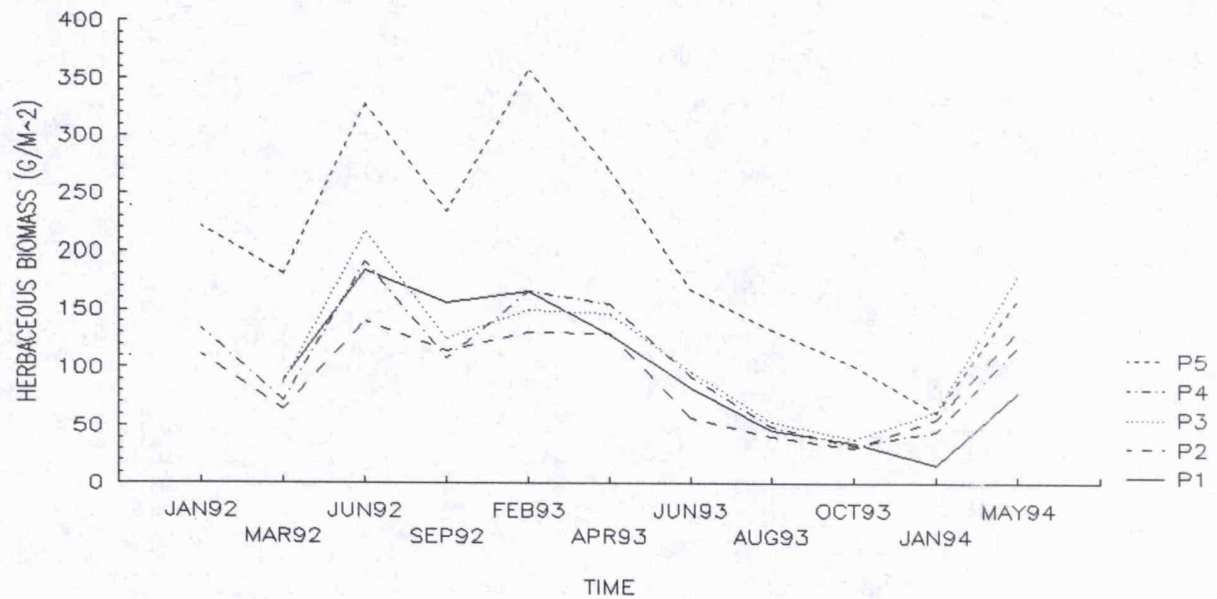


Fig 4.4
CHANGES IN HERBACEOUS BIOMASS
BETWEEN 1992 AND 1994
(PLOTS 6-10)

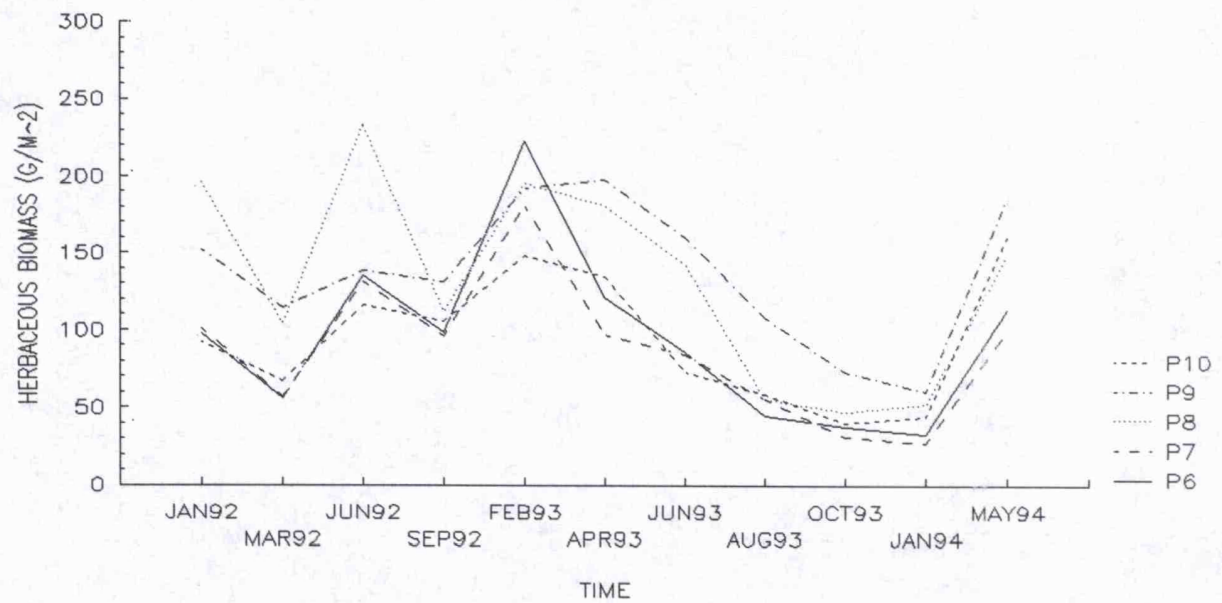


Fig 4.5
CHANGES IN HERBACEOUS BIOMASS
BETWEEN 1992 AND 1994
(PLOTS 11-15)

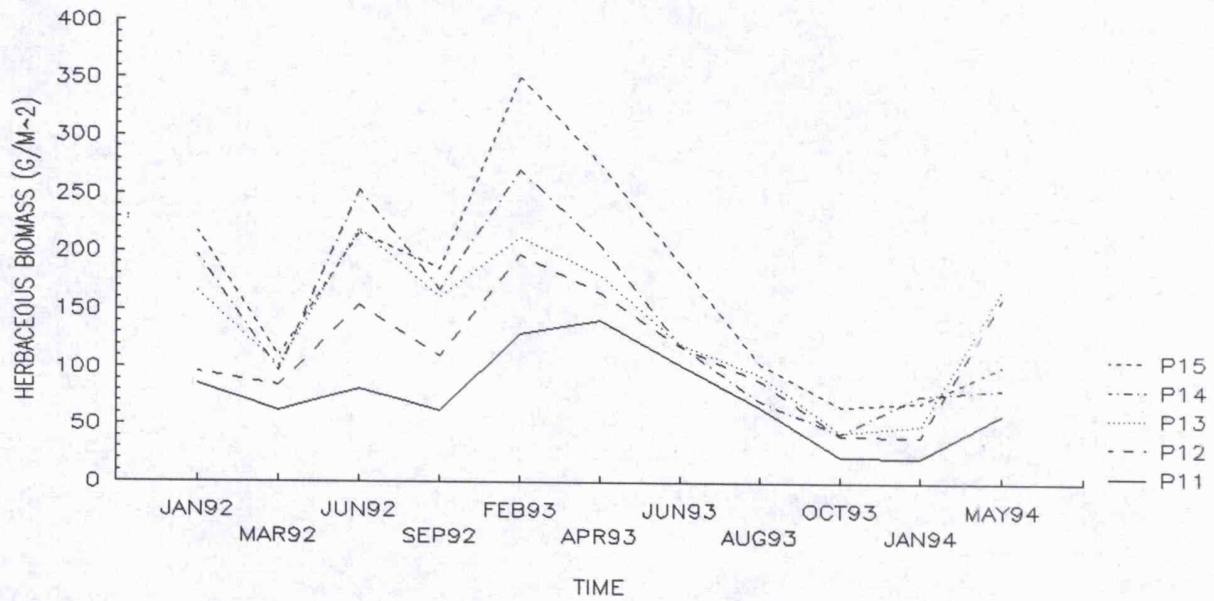


Fig 4.6
CHANGES IN HERBACEOUS BIOMASS
BETWEEN 1992 AND 1994
(PLOTS 16-17)

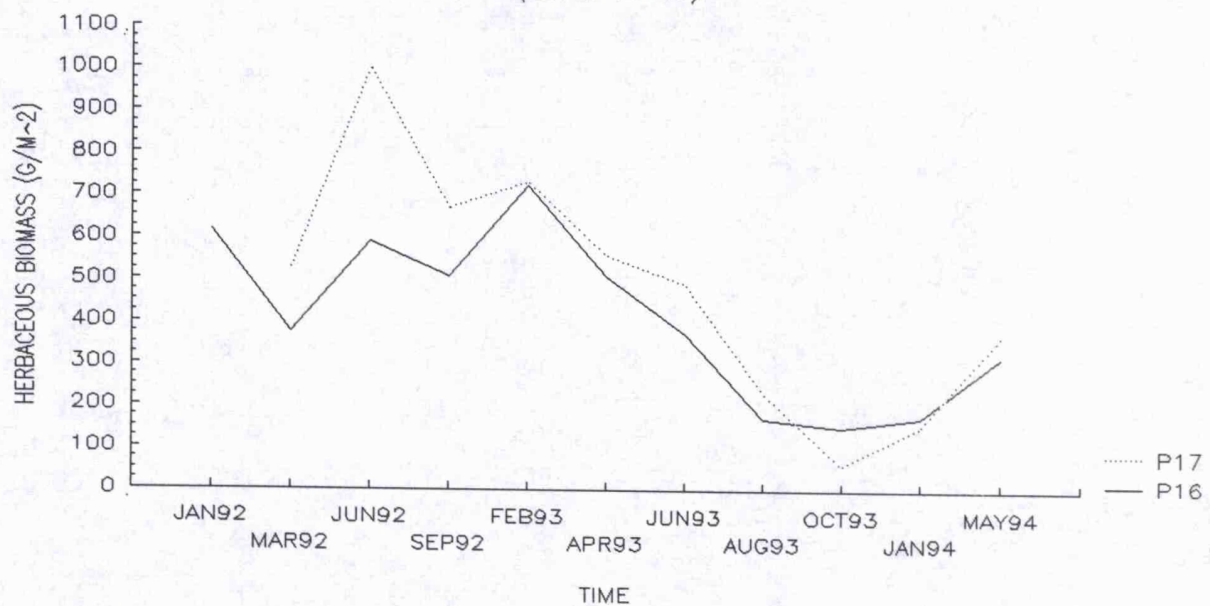


FIG. 4.7
GRASS AND FORB BIOMASS ACROSS PLOTS FOR WET SEASON

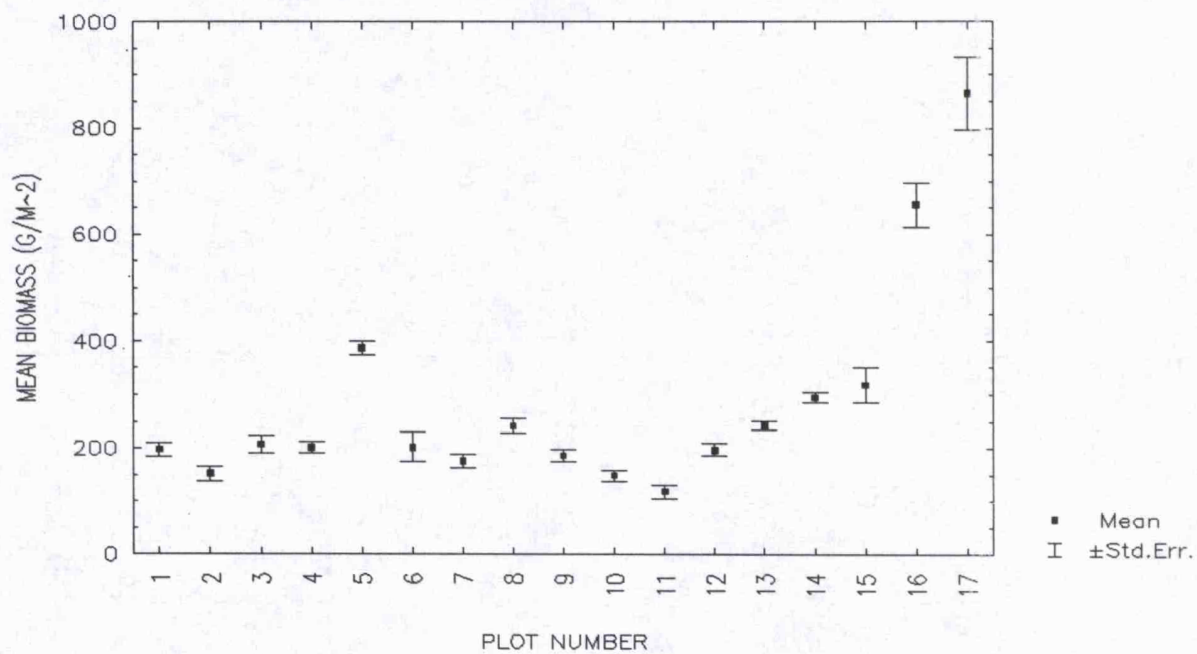
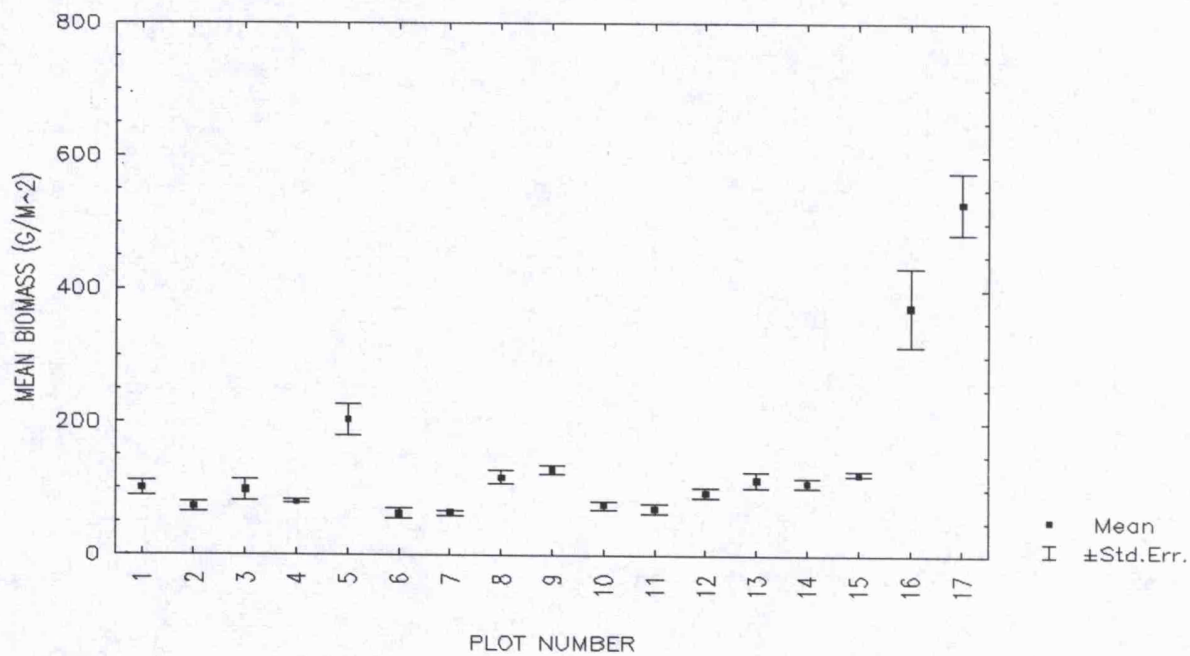


FIG. 4.8
GRASS AND FORB BIOMASS ACROSS PLOTS FOR DRY SEASON



fell from $237.82 \pm 18.28 \text{ g/m}^2$ in February 1993 to $45.21 \pm 3.77 \text{ g/m}^2$ in January 1994. The areas most affected by the drought were plots 1, 7, 11, 16 and 17. The largest declines occurred in the Park where herbaceous biomass fell by 507.76 g/m^2 and 475.09 g/m^2 in plots 16 and 17 respectively. These drops in biomass were more severe than expected in any given dry season. Rain normally falls between March and May of each year, and again between September and November of the same year. During the study however, the heaviest rains occurred in February 1993 and did not fall again until the following year. The short rains were essentially missed and the results were the sharp drops in vegetation quantity described above.

Rapid recovery followed after the rains. These started as scattered showers in the early part of 1994 and became heavier in April 1994, the point at which the prolonged dry spell is said to have been broken. Mean herbaceous biomass for the ecosystem increased to $138.76 \pm 7.53 \text{ g/m}^2$ in May 1994. The largest increases in biomass were in plots 16, 17, 3, 13 and 9 (Fig. 4.9).

4.3 Variation in herbaceous biomass between the Park and plains

Comparisons of vegetation biomass between the park and the rest of the plains for the wet season months revealed that the mean biomass over the plains was $165.25 \pm 4.53 \text{ g/m}^2$ and that of the Park was $620.06 \pm 45.26 \text{ g/m}^2$, a three fold difference within the same ecosystem. During this period biomass was significantly higher in the Park (Anova test: $F=503.98$, $df(1,258)$ $p \leq 0.05$). The multiple range test showed that the biomass was not homogeneous in these 2 areas. Plot 17 in the Park had $1000.59 \text{ g/m}^2 \pm 87.502$ in June 1992, the highest standing crop biomass in any of the areas sampled.

Grasses were also taller in the park than the plains particularly in the wet season. Their mean height in the Park was $50.80 \pm 2.33 \text{ cm}$ compared to $19.74 \pm 0.68 \text{ cm}$ on the plains (Fig. 4.10). An analysis of variance showed the differences between the Park and plains to be significant (Anova test: $F=158.69$ $df(1,134)$ $p < 0.05$). The plains were dominated by prostrate and shorter growing species and the Park by more taller forms.

By the time the dry season set in and growth ceased, much of the grass outside the park where most animals were had been depleted. As vegetation on the plains was depleted, some species of wildlife began their trek back to the Park. Although many wildebeest and zebra moved back into the Park in the dry season, livestock and many wild herbivores still remained on the plains. The plains were exposed to intense grazing during the wet season and moderate grazing during the rest of the year while the Park experienced intense grazing during the dry seasons. These are normally longer than the wet season. The average plains biomass during the dry season was $94.99 \pm 2.73 \text{ g/m}^2$

FIG 4.9

PRE-DROUGHT(FEBRUARY 1993), END OF DROUGHT
(JANUARY 1994) AND POST DROUGHT(MAY 1994)
MEAN HERBACEOUS BIOMASS

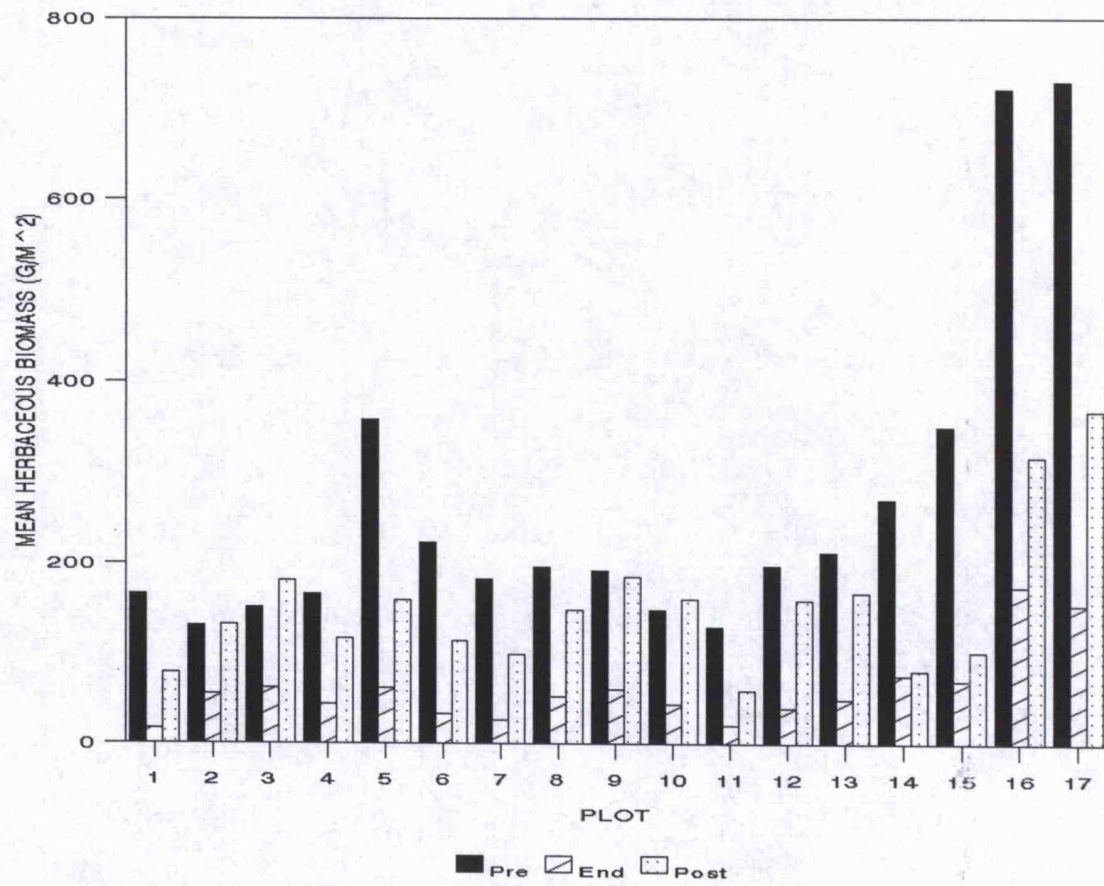
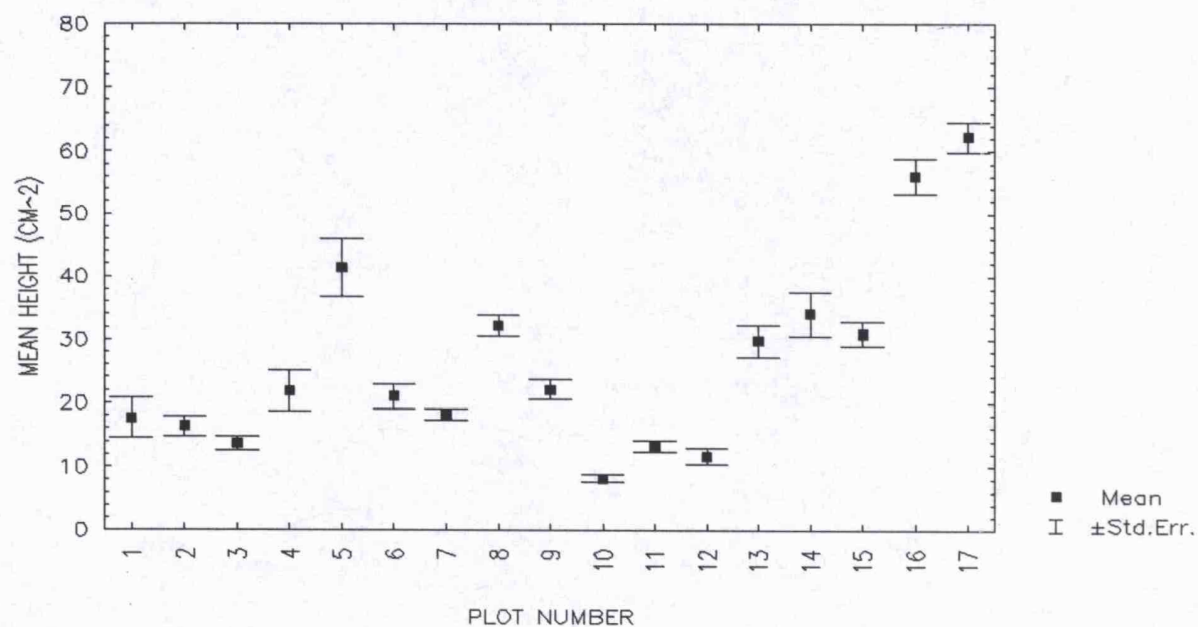
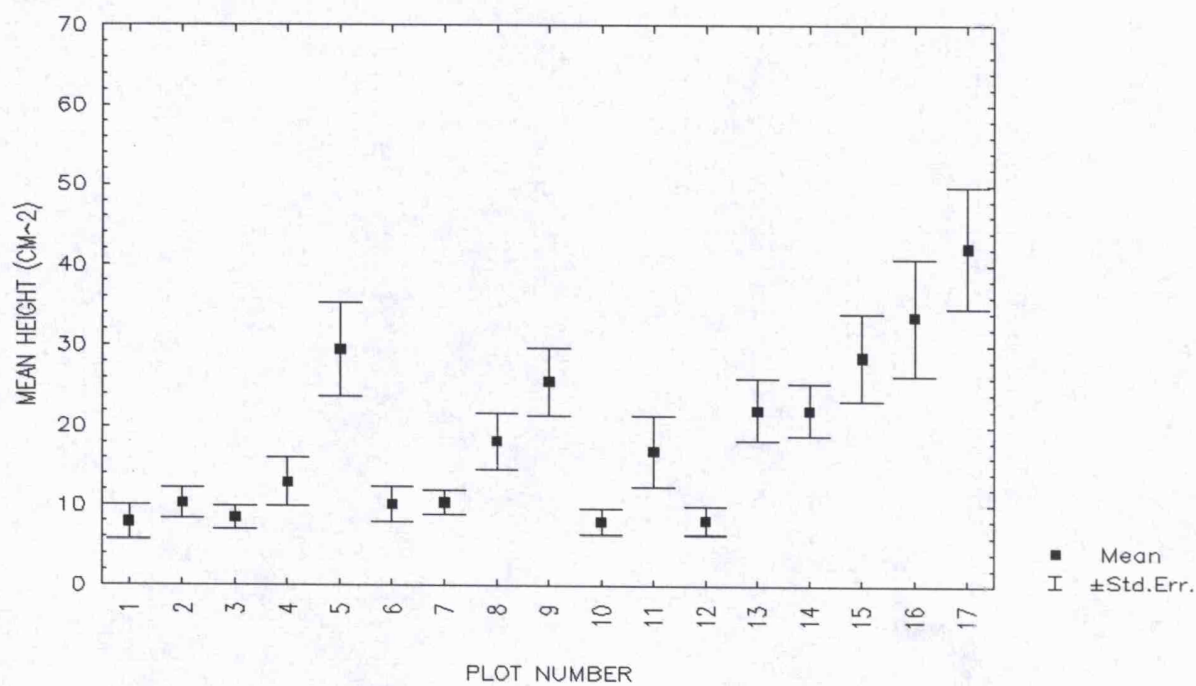


FIG 4.10
VARIATION IN MEAN GRASS HEIGHT ACROSS PLOTS
a) WET SEASON



b) DRY SEASON



while that in the Park was $352.69 \text{ g/m}^2 \pm 27.24$. There was a decline of 42.5% and 43.2% on the plains and park respectively. The magnitude and pattern of decline in biomass is clearly visible in for example Fig. 4.6, from the wet season of February 1993 to the dry month of October 1993.

Grasses were also much shorter. The mean height in the Park was 37.89 ± 2.74 cm while the plains were down to $15.92 \text{ cm} \pm 0.59$. The differences between the Park and plains was still highly significant (Anova test: $F=135.44$, $df(1,474)$, $p<0.05$) though less so than the wet season.

4.4 Trends in grass quality

The wet season quality was on the whole higher than the dry season quality throughout the ecosystem (Fig. 4.11, 4.12). The overall ecosystem average quality during the dry season was $3.62\% \text{ crude protein} \pm 0.07$, ($n=135$) and wet season was $8.40 \pm 0.17\% \text{ crude protein}$, ($n=104$). Within and between season variation was tested using data from March 1992 and September 1992 (Dry), June 1992 and February 1993 (Wet). Results of a multifactor analysis of variance showed that season accounted for most of the variation in quality ($F=1000.00$, $df(1,238)$, $p \leq 0.05$). Within season plot variation was also significant but accounted for less variation ($F=5.964$, $df(16,238)$, $p \leq 0.05$).

Wet season variation in quality between plots over the whole ecosystem was significant ($F=3.77$, $df 16,87$, $p \leq 0.05$). Mean quality varied from $6.34\% \pm 0.34\% \text{ crude protein}$ in plot 16 to $10.48\% \text{ crude protein} \pm 0.82$ in plot 10 in the wet season. Plots 1, 10, 12 and 7 had the highest quality vegetation while plots 16, 17, 5 and 14 had the least. The distinct high quality areas were 1, 10 and 12 and low quality areas, plots 16 and 17. The Kruskal Wallis ranks made this distinction very clear. Plots 16 and 17 were ranked 13.79 and 16.58 respectively, and plots 1, 10 and 12 ranked 71.86, 83.00 and 75.92 respectively. The high and low quality plots fell in the extremes of the rank.

The dry season variation within plots was also significant ($F=3.39$, $df 16,118$, $p \leq 0.05$). With the exception of plots 9 and 10, 12 and 1 all the others had crude protein values below 4%. Plots 16, 15, 6 and 3 had the least.

4.5 Variation in grass quality between Park and plains.

The overall average quality on the plains was $8.67\% \text{ crude protein} \pm 0.17$; ($n=91$) and $6.48\% \text{ crude protein} \pm 0.19$ ($n=13$) in the Park. The highest crude protein was recorded in grasses of plot 10 and 12 with $10.48\% \text{ crude protein} \pm 0.82$ and $10.05\% \text{ crude protein} \pm 0.88$ respectively, both located on the plains. A one-way analysis of variance of wet season quality between the Park and plains showed significantly higher

Fig 4.11
MEAN VEGETATION QUALITY FOR WET SEASONS IN THE ATHI-KAPITI PLAINS
(n=8)

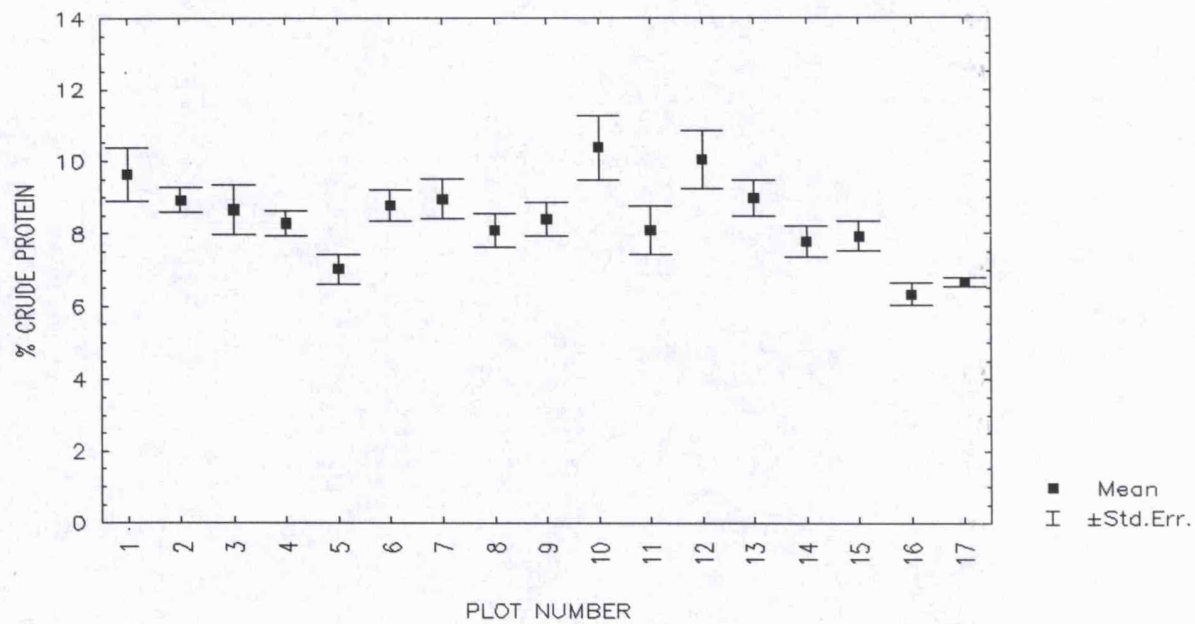
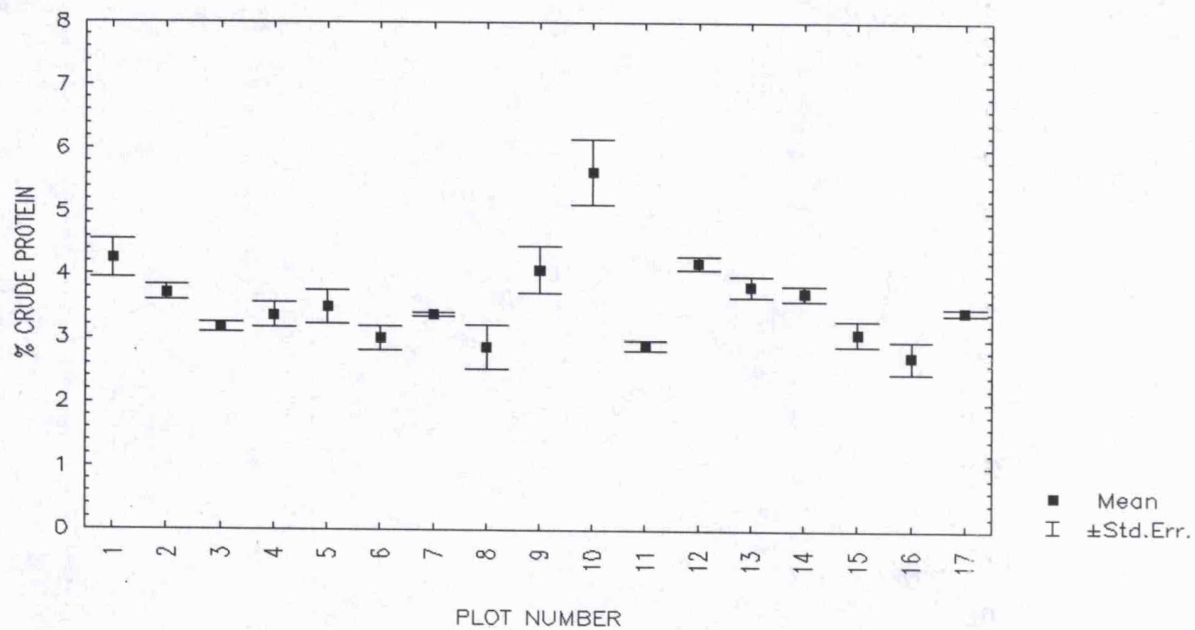


Fig. 4.12
MEAN VEGETATION QUALITY FOR DRY SEASONS IN THE ATHI-KAPITI PLAINS
(n=8)



values on the plains ($F=22.57$, $df(1,102)$, $p \leq 0.05$).

In the dry season average % crude protein on the plains was 3.68 ± 0.79 and 3.15 ± 0.19 inside the Park. The dry season differences were also significant though not as large ($F=5.10$, $df(1,133)$ $p=0.05$). Although the variation was significant, the multiple range test did not detect any differences between the range of protein values and treated them as homogeneous groups. Similar low quality values were reported in the Park in the dry season in an earlier study by (Gichohi, 1990).

4.6 Differences in grass quality between habitats

The mean quality of grasses in the woodlands was 8.28 ± 0.17 ; ($n=32$), and 8.44 ± 0.202 ; ($n=71$) in the open grasslands in the wet season. In the dry season, the mean quality was 3.62 ± 0.194 ; ($n=17$) in the woodlands and 3.59 ± 0.139 ; ($n=42$) in the open grasslands. An analysis of variance on habitat and season showed that no significant variation could be attributed to habitat alone ($F=0.140$ $df(1,158)$ $p>0.05$). Season was however highly significant ($F=399.38$ $df(1,38)$, $p<0.05$).

4.7 Relationship between quantity, height and quality of the herb layer

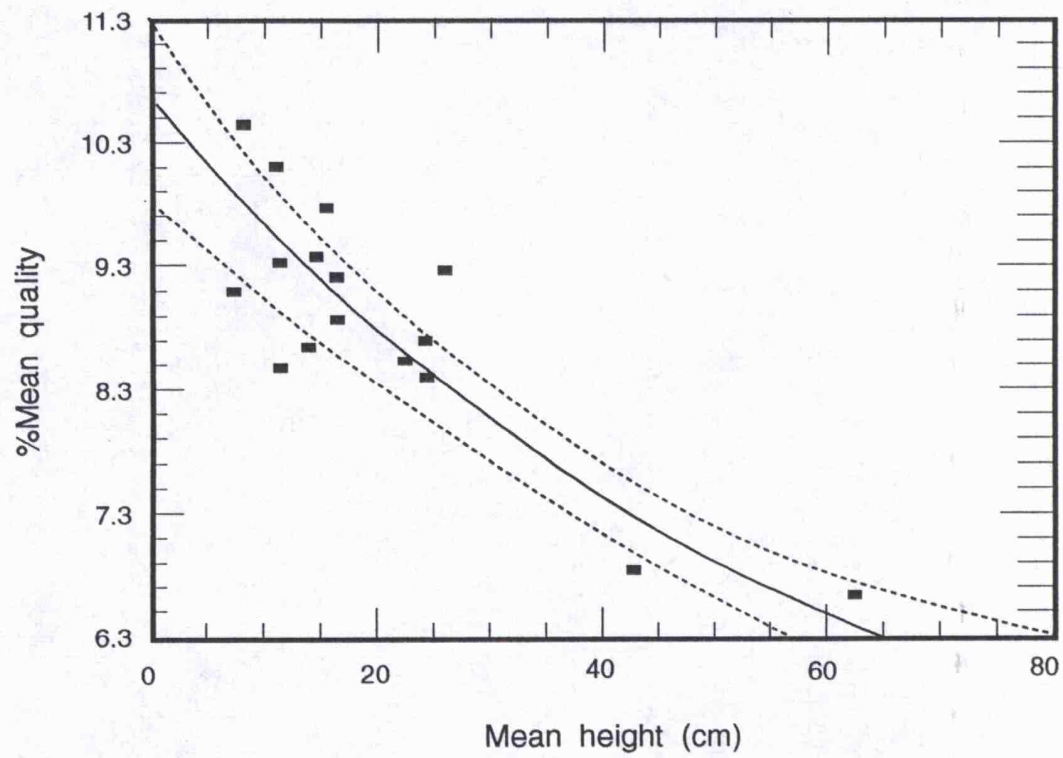
There was a distinct relationship between quantity, growth form and quality. The general changes in seasonal quantity and height of the herbaceous vegetation were accompanied by inverse changes in quality. Plots with the highest quantities of grass had the poorest vegetation nutritionally, and the tallest grasses. Plots 16 and 17 were again very distinct. Wet season biomass was extremely high, the grasses were tall and of low quality. Plots 10, 12 and 13 had the lowest herbaceous biomass, the shortest grasses but of high nutritional value. Results of a multiple regression of mean biomass and mean height against average crude protein showed that the change in quality could be explained by trends in mean height; $t_{(16)}=-4.34$ $p \leq 0.05$. Mean height was a better predictor of quality trends. The relationship between mean biomass and mean crude protein was however not significant ($t_{(16)}=-1.60$ $p \geq 0.05$). A partial regression showed that the variation in quality was best explained by changes in mean height. The addition of mean biomass into the regression did not improve the fit; (multiple $r^2=0.76$, $F=48.18$, $p \leq 0.05$). A linear regression of quality against height gave a reciprocal model where $Y=1/(0.095 + 0.000988x)$; $F=80.794$, $r^2=84.34$ $p \leq 0.05$, (Fig. 4.13).

A multivariate analysis on quality, height and biomass using decorana gave a cluster based on height and biomass as the first axis. This clustered the high biomass plots of the park and plot 5 on the plains close together (Fig. 4.14a). Axis 1 was plotted against mean % crude protein (Fig. 4.14b) and mean height (Fig. 4.14c). The tall

Fig. 4.13

Regression of mean herbaceous % crude protein
against grass height

$$Y = 1 / (0.095 + 0.000988X)$$



.....95% confidence limit

FIG 4.14a

ORDINATION OF THE TWO AXES OF A DECORANA ANALYSIS DESCRIBING THE VARIATION
IN PLOTS IN RELATION TO HERBACEOUS BIOMASS AND HEIGHT FOR THE WET SEASON
(POINTS 4 AND 6 HAVE THE SAME EIGENVALUE)

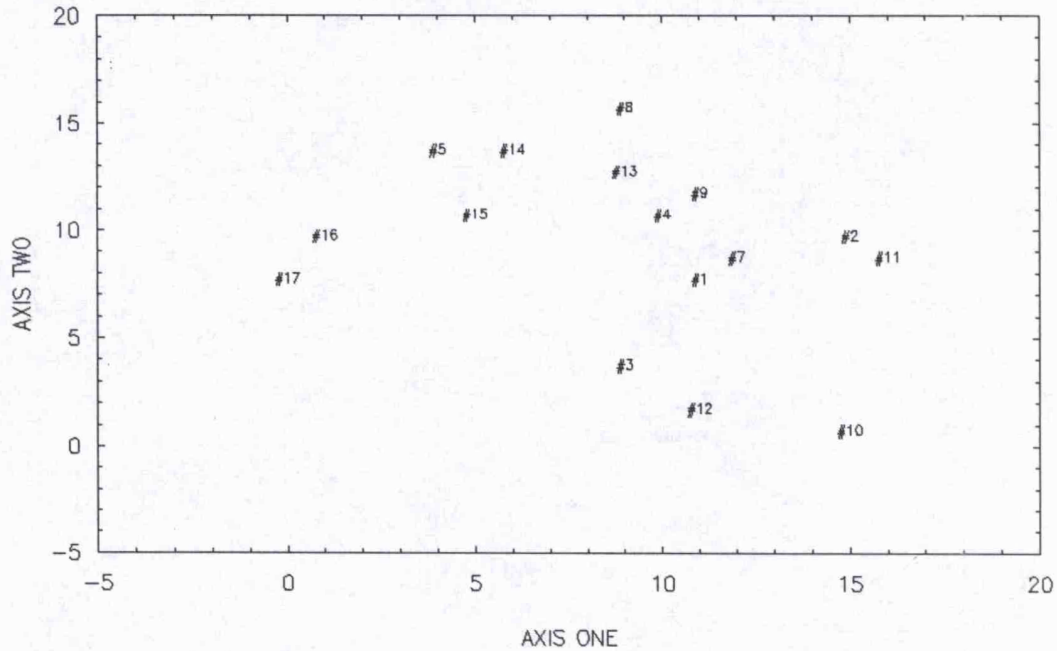


FIG 4.14b

ORDINATION OF THE MAIN AXIS OF A DECORANA ANALYSIS DESCRIBING THE VARIATION
IN PLOTS IN RELATION TO MEAN GRASS QUALITY (% CRUDE PROTEIN)

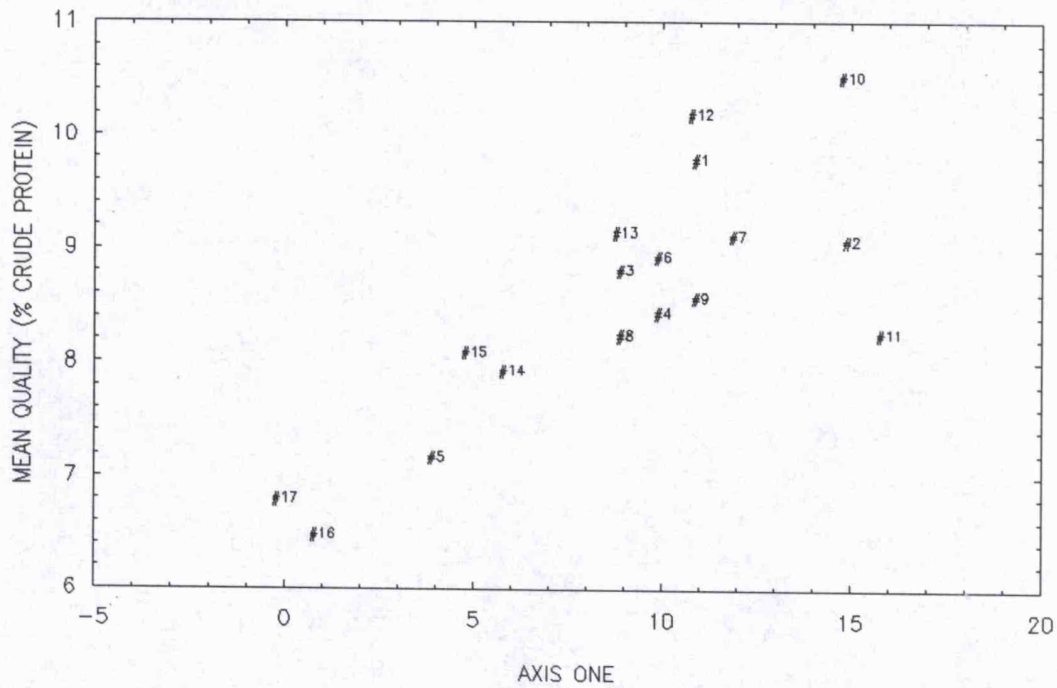
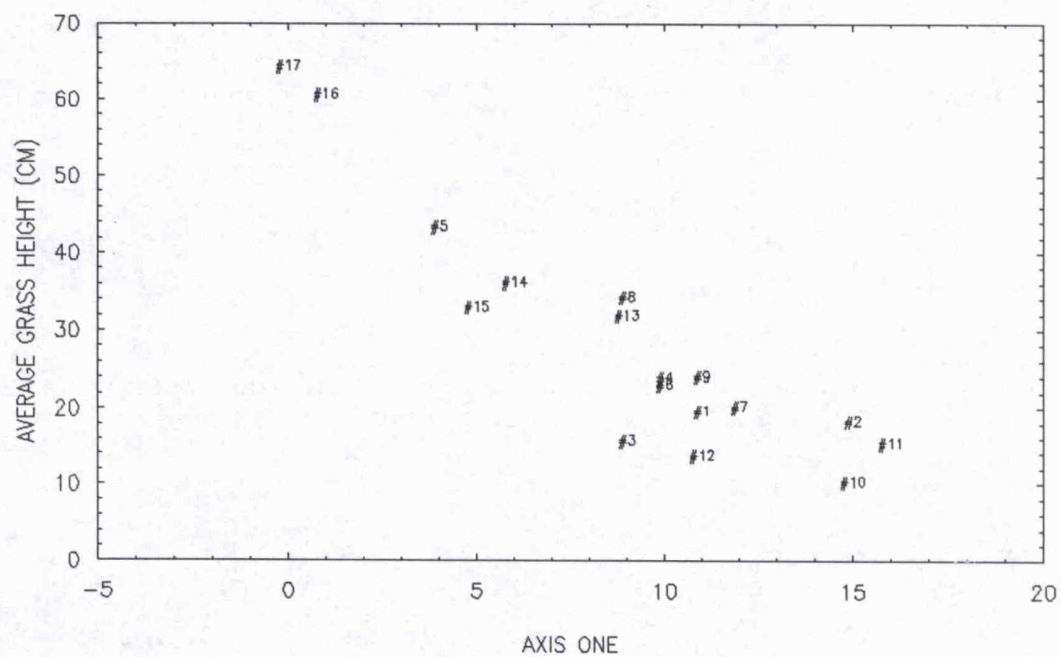


FIG 4.14c
ORDINATION OF TWO AXES OF A DECORANA ANALYSIS DESCRIBING THE
VARIATION IN PLOTS IN RELATION TO AVERAGE GRASS HEIGHT
(PLOTS 4 AND 6 VERY SIMILAR IN GRASS HEIGHT)



vegetation plots, 16 and 17 were clustered together, high on the Y axis, followed by 5, 15 and 14, and the short vegetation plots 2, 11 and 10 were the lowest on the Y axis. This trend was reversed when axis 1 was plotted against average crude protein. This relationship did not hold in the dry season when quality was low in the whole ecosystem.

4.8 Species composition of the herb layer

The major grass species occurring on the Athi-Kapiti plains and in the park is *Themeda triandra*. Though widespread, its relative proportion in specific plots over time was highly variable. In general the species occurred and even dominated in most plots. *Setaria phleoides* dominated in black cotton soil areas, particularly in the *Acacia drepanolobium* woodlands of Nairobi National Park and plot 6 at Oloontepes. *Microchloa kunthii*, *Digitaria macroblephara* and *Sporobolus pellucides* were more common in short grass areas, on slightly raised ground.

Other species seemed to occur only in specific plots, for example, *Microchloa kunthii* was common in the intensely grazed, short grass areas. In some of these plots it constituted over 10% of the total contribution e.g 10, 12, 13. In plot 10, it was the most sampled species in May 1994 with a relative contribution of 18.9%. Plot 10 was the only site where a forb species contributed more than 10% of the total biomass.

The highest diversity was recorded in plots 10, 13 and 17. These three areas had diversity of over 2 throughout the study period. Plot 10 had even contribution by the more common species, for example, in May 1994 no one species contributed more than 20% to total biomass. This was in total contrast to plot 16 in the Park where *Themeda triandra* and *Setaria phleoides* together made up 66% of total herbaceous biomass. Decorana analysis using species by plot matrices showed the distribution of plots that converged in their species composition (Fig. 4.15a, 4.15b, 4.15c), for the 3 major wet seasons sampled. Plots 10 and 13 were low on axis 1, but plot 10 was very high on axis 2. In May 1994 these were even closer, perhaps indicating further convergence in their species composition. Plot 16, 7 and 6 were also located close together, on one extreme of axis 1, and plots 10, 12 and 13 on the other extreme. A close examination of the species combinations in these plots showed the following:

Setaria phleoides was the dominant grass in plots 6, 7 and 16, all plots located in areas of deep cracking black cotton soils.

Microchloa kunthii, *Sporobolus pellucides*, *Digitaria macroblephara* were common species in plots 10, 12 and 13, areas of heavy grazing and more sandy soils.

In between the two extremes were plots 5 and 11. These had *Pennisetum mezianum* as a common species, and *Digitaria macroblephara* also an important species. Plot 15 and 3

were also associated with these plots. Plots 5 and 11 were also located on black cotton soil areas.

In June 1992, plot 10 and 17 were highest on axis 2 and plot 13 was lowest on axis 1. Several major shifts in the location of these plots was noted between June 1992 and May 1994. Plot 9 moved from a distance of 50 on axis 2 in June 1992 to over 200 in May 1994. Plot 17 moved from over 220 on axis 2 to almost zero. Plot 11 moved upwards along axis 2 but remained at approximately the same distance on axis 1.

The dominant species in plot 13 in June 1992 was *Pennisetum stramineum* with a contribution of 21.3%, followed by *Sporobolus pellucides* at 13.7% . By May 1994 the contribution of *Pennisetum stramineum* had declined to 10.6% and that of *Sporobolus pellucides* was up at 18.8% to become the dominant species. *Microchloa kunthii* had contributed 14.8% to total biomass in this sample. The upward shift of plot 9 in May 1994 may have been caused by the increase in *Bracharia eruciformis* which occurred in an insignificant quantity in June 1992 (table 4.1). The shift in plot 17 may have been the result of a large decline in the contribution by *Digitaria abyssinica* and the appearance of *Setaria phleoides* which had been absent in previous samples (table 4.2).

Comparison of major herb species occurring in plots 16 and 10, the 2 plots furthest apart on the axis, showed that very few species of any significance were shared (table 4.3). With the exception of *Themeda triandra* most species occurring in plot 16 were absent in plot 10.

Table 4.1. Changes in species composition of the herb layer between June 1992 and May 1994 in plot 9 at Orlimirui - 8 most abundant

SPECIES NAME	% CONTRIBUTION		% CHANGE
	JUNE 1992	MAY 1994	
<i>Themeda triandra</i>	39.4	32.6	- 6.0
<i>Digitaria macroblephara</i>	23.2	12.0	- 11.2
<i>Pennisetum mezianum</i>	20.5	16.8	- 3.7
<i>Lintonia mutans</i>	5.4	3.8	- 1.6
<i>Sporobolus pellucides</i>	2.7	1.9	- 0.8
<i>Panicum poaeides</i>	2.0	-	- 2.0
<i>Phyllanthus maderaspatensis</i>	1.3	-	- 1.3
<i>Orthosiphon parvifolius</i>	1.0	-	- 0.3
<i>Bracharia eruciformis</i>	0.3	24.2	+ 23.0
<i>Chloris virgata</i>	-	1.9	+ 1.9
<i>Gutenbergia flscheri</i>	-	1.4	+ 1.4

Table 4.2. Changes in species composition of the herb layer between June 1992 and May 1994 in plot 17 in Nairobi National Park.

SPECIES NAME	% CONTRIBUTION		% change
	JUNE 1992	MAY 1994	
<i>Themeda triandra</i>	28.3	29.1	+ 0.8
<i>Digitaria abyssinica</i>	23.1	12.7	- 10.4
<i>Pennisetum mezianum</i>	12.8	9.1	- 3.7
<i>Bothriocloa insculpta</i>	10.7	12.5	+ 1.8
<i>Andropogon schimperi</i>	7.1	10.6	+ 3.5
<i>Kyllinga triceps</i>	3.0	-	3.0
<i>Panicum poaeides</i>	3.0	1.5	- 1.5
<i>Cynodon dactylon</i>	2.7	2.2	- 0.5
<i>Aristida adoensis</i>	2.6	5.8	+ 3.2
<i>Setaria phleoides</i>	0.8	5.8	+ 5.8

Table 4.3. Comparison of the percentage contribution of major grass and forb species sampled in plots 10 and 16 in May 1994.

SPECIES NAME	% CONTRIBUTION	
	PLOT 10	PLOT 16
<i>Bothriocloa insculpta</i>	10.9	0.3
<i>Cynodon dactylon</i>	14.9	0
<i>Digitaria macroblephara</i>	6.3	0.3
<i>Felcia muricata</i>	8.6	0
<i>Harpache schimperii</i>	10.9	0
<i>Microchloa kunthii</i>	18.9	0
<i>Sporobolus pellucides</i>	3.4	0
<i>Themeda triandra</i>	6.3	23.9
<i>Digitaria milanjana</i>	0	10.1
<i>Ischaemum afrum</i>	0	9.5
<i>Setaria phleoides</i>	0	42.9

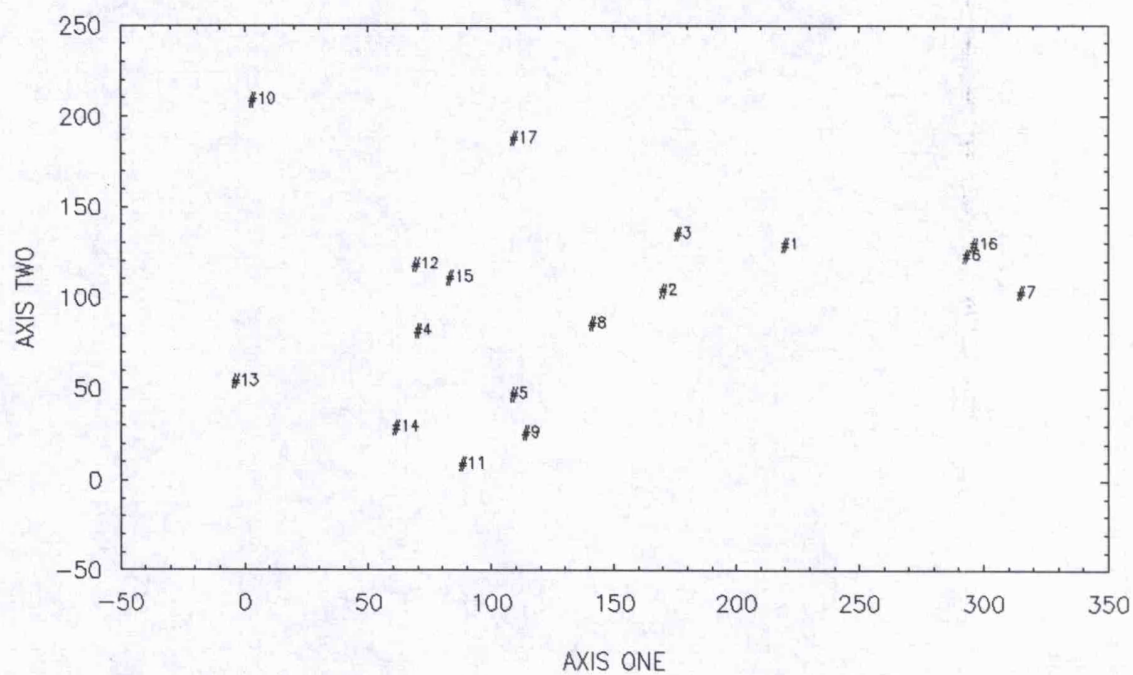
4.9 Woody vegetation

All woodlands sampled in the Athi-Kapiti plains were dominated by the whistling thorn or *Acacia drepanolobium* (table 4.4). The mean tree height was variable and significantly different between plots ($F=24.607$, $df(4,595)$ $p \leq 0.05$). Trees in plots 6, 1 and 14 had a lower mean height than those in plots 16 and 2. The tallest *Acacia drepanolobium* were in plot 2 with a mean height of 134.82 ± 7.72 cm.

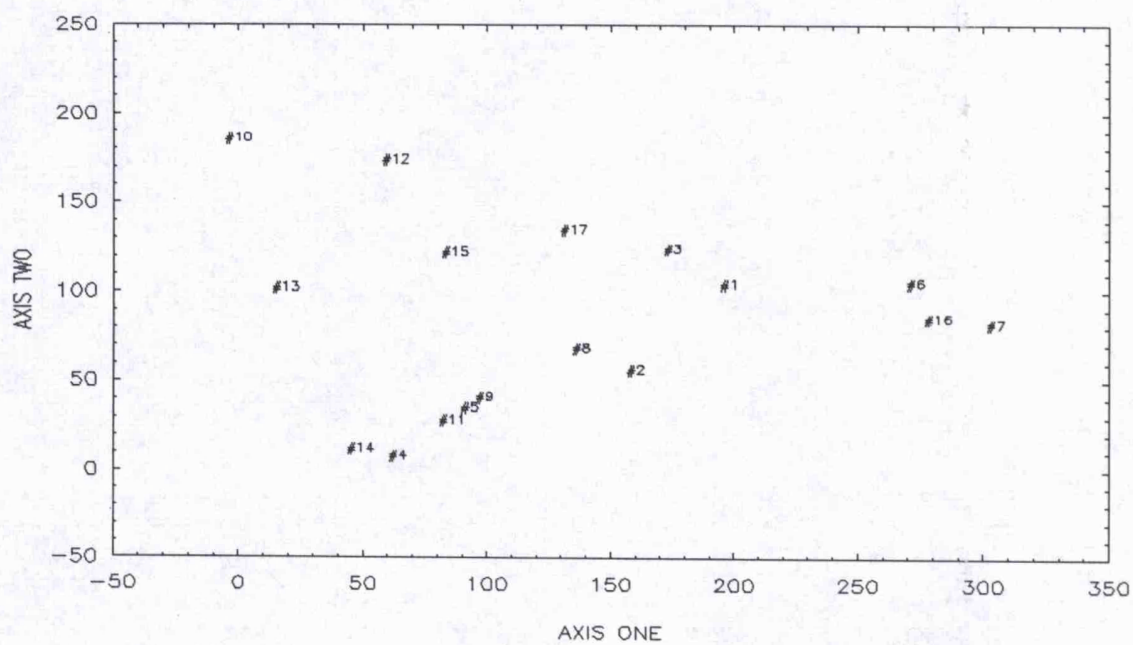
Table 4.4 Distribution and density of woody vegetation in 5 plots sampled in the Athi-Kapiti Plains.

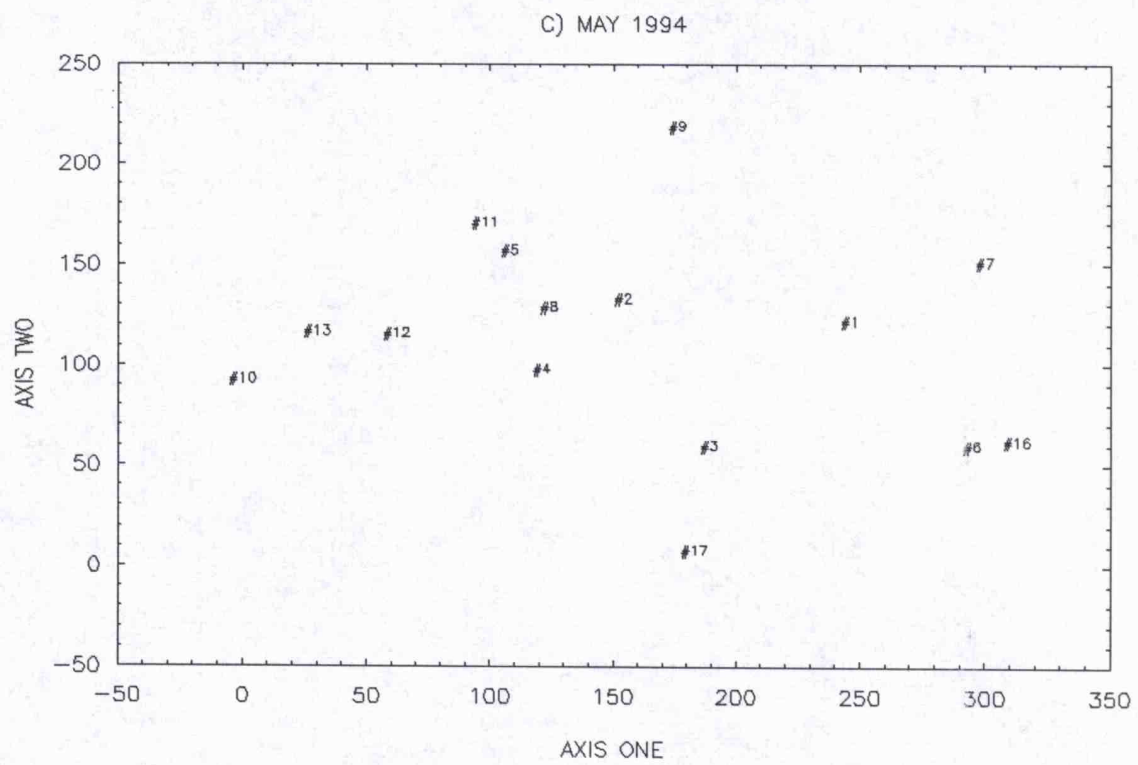
PLOT NO	SPECIES	DENSITY BY SPECIES	TOTAL	
			TREE DENSITY PER HECTARE	MEAN INTERTREE DISTANCES (M)
1	<i>Acacia drepanolobium</i>	129.88	129.88	8.8
2	<i>Acacia drepanolobium</i> <i>Acacia xanthophlea</i> <i>Acacia</i> spp <i>Balanites</i> spp	312.360 8.149 2.716 2.716	325.94	5.5
6	<i>Acacia drepanolobium</i>	1571.07	1571.070	2.5
14	<i>Acacia drepanolobium</i> <i>Acacia</i> spp <i>Balanites</i> spp	212.95 1.90 13.31	228.16	6.6
16	<i>Acacia drepanolobium</i> <i>Acacia mellifera</i> <i>Balanites aegyptica</i>	175.5 3.0 1.5	180.0	7.5

FIG 4.15
ORDINATION OF THE TWO AXES OF A DECORANA ANALYSIS DESCRIBING
THE VARIATION OF PLOTS IN RELATION TO SPECIES COMPOSITION
OF THE HERB LAYER
A) JUNE 1992



B) FEBRUARY 1993





4.10 Impact of grazing on vegetation

4.10.1 Herbaceous biomass

4.10.1.1 Changes within exclosures

Grass biomass began to accumulate once the exclosures were constructed. By February 1993, nine months after construction of the fences, all exclosures recorded higher biomass (tables 4.5 a-d). Exclosures 1 & 16 had reached the peak biomass recorded during the sampling season. The changes within the exclosures were large. In exclosure 1 the biomass recorded in June 1992 was $321.79 \pm 17.01 \text{ g/m}^2$ and the highest $595.08 \pm 30.11 \text{ g/m}^2$. This constituted an increase of 84.9%. Biomass in exclosure 10 increased by 67.3%, from $261.16 \pm 5.07 \text{ g/m}^2$ to $437.00 \pm 52.79 \text{ g/m}^2$ and in exclosure 11 by 123.6%, from $100.91 \pm 4.66 \text{ g/m}^2$ to $225.65 \pm 6.18 \text{ g/m}^2$. Exclosure 16 had the least increase; from $575.92 \pm 4.40 \text{ g/m}^2$ in June 1992 to 801.51 ± 56.00 in February 1993. This was 37.17 % change.

4.10.1.2 Comparisons between exclosures and plots

Vegetation quickly accumulated once the exclosures were constructed resulting in large differences in biomass inside and outside of the exclosure table (4.5). A t-test comparison of biomass in the exclosures and plots showed that biomass in exclosures 1 and 10 was significantly higher than the respective plots throughout (table 4.5 a & b; Fig. 4.16, 4.17). The differences between plots 11, 16 and their exclosures were less consistent (table 4.5 c & d; Fig. 4.18, 4.19). Exclosure 11 had higher biomass than its plot except in September 1992 and February 1993 (table 4.5c). In plot and exclosure 16 biomass differences were not significant during the normal seasonal cycles. However with increased offtake levels in the Park during the drought, differences between the two areas became larger (table 4.5d). The differences between the exclosures and plots in October 1993 were so large that growth on the plots during the rains in the following year was not substantial enough to reduce this difference.

The largest variation in exclosure and plots occurred in plot 1, (Fig. 4.16) followed by plot 10 (Fig. 4.17), both located in high use intensity areas. Plot and exclosure 16 (Fig. 4.19) also varied in similar ways but with less amplitude.

Table 4.5 Comparisons of grass biomass between exclosures and plots. (NS = Not significant)

a) Plot & exclosure 1

Month	Mean Biomass (g/m ²)		t-value	p-value
	Exclosure 1	Plot 1		
June 92	321.79 ± 17.01	164.07 ± 15.79	5.935	0.001
Sep. 92	343.02 ± 32.92	155.45 ± 8.69	5.510	0.002
Feb. 93	595.08 ± 30.11	165.85 ± 19.19	12.022	0.00002
Apr. 93	441.76 ± 32.22	128.15 ± 14.39	8.89	0.0001
June 93	385.03 ± 34.00	82.72 ± 4.97	8.800	0.0001
Aug. 93	356.88 ± 25.65	46.34 ± 5.40	8.991	0.0001
Oct. 93	284.55 ± 12.36	35.08 ± 4.32	19.05	0.00001
May 94	420.97 ± 22.07	77.53 ± 12.40	11.535	0.00001

b) Plot & exclosure 10

Month	Mean biomass (g/m ²)		t-value	p-value
	Exclosure 10	Plot 10		
June 92	261.16 ± 5.07	115.64 ± 13.90	9.834	0.00006
Sep. 92	225.21 ± 19.33	105.22 ± 5.31	5.986	0.0010
Feb. 93	310.97 ± 36.24	147.65 ± 10.64	4.324	0.0005
Apr. 93	372.90 ± 34.05	134.22 ± 21.66	5.915	0.001
June 93	258.13 ± 21.42	72.33 ± 7.26	8.216	0.0002
Aug. 93	231.71 ± 14.36	58.04 ± 8.20	10.50	0.00004
Oct. 93	210.05 ± 15.52	39.85 ± 7.84	9.784	0.0007
May 94	437.00 ± 52.79	159.81 ± 5.81	5.219	0.002

c) Plot and enclosure 11

Month	Mean Biomass (g/m ²)		t-value	p-value
	Exclosure 11	Plot 11		
June 1992	100.91 ± 4.66	80.90 ± 5.63	2.726	0.034
Sept. 1992	70.60 ± 4.27	62.36 ± 6.56	1.05	0.333 NS
Feb. 1993	135.56 ± 13.67	129.03 ± 17.36	0.296	0.778 NS
April 1993	225.65 ± 6.18	140.73 ± 13.38	5.761	0.0012
June 1993	145.52 ± 1.23	102.63 ± 5.63	7.445	0.0003
Aug. 1993	141.19 ± 9.55	65.4 ± 9.50	5.63	0.001
Oct. 1993	126.90 ± 12.58	22.09 ± 3.83	7.970	0.0002
May 1994	168.04 ± 12.19	58.47 ± 9.73	11.173	0.00003

d) Plots and enclosure 16

MONTH	Mean biomass (g/m ²)		t-value	p-value
	Exclosure 16	Plot 16		
June 1992	575.92 ± 4.40	589.50 ± 52.96	-0.255	0.807 NS
Sep. 1992	490.60 ± 25.95	506.70 ± 70.16	-0.215	0.837 NS
Feb. 1993	801.51 ± 56.00	721.95 ± 59.36	0.975	0.367 NS
Apr. 1993	541.02 ± 33.08	508.00 ± 68.92	0.432	0.681 NS
June 1993	619.88 ± 24.74	372.93 ± 16.61	8.287	0.0002
Aug. 1993	379.43 ± 23.46	168.00 ± 13.06	7.88	0.0002
Oct. 1993	435.01 ± 33.35	147.33 ± 1.81	8.61	0.0001
May 1994	642.50 ± 23.94	316.73 ± 16.64	11.173	0.00003

It was also clear that in the absence of grazing different areas accumulated grasses to different levels and rates. Exclosures 1 and 16 occurred within the higher rainfall zone (Fig. 4.20), both had higher standing crop and attained maximum biomass much faster than the other two exclosures, 10 and 11 (table 4.6). Exclosures 10 and 11 both fell within a lower rainfall belt and had lower biomass. The rainfall averages (Fig. 4.20) suggests that exclosure 11 lies in an area of slightly more rainfall than plot 10 and should have accumulated larger quantities of grass, but the results revealed the contrary. Other factors may have acted in concert to produce slower growth rates than expected. These two areas fall under different soil regimes for example. Plot 11 is located on black cotton soils and 10 on more sandy raised ground.

Accumulation of the litter component was greater in the exclosures (Table 4.7).

Table 4.6 Peak grass biomass in various enclosure in the Athi-Kapiti Plains.

Plot №	Maximum Biomass (g/m ²)	Month
Plot 1	571.12 ± 16.230	February 1993
Plot 10	372.90 ± 29.480	April 1993
Plot 11	225.65 ± 5.350	April 1993
Plot 16	801.51 ± 48.5	February 1993

Table 4.7 Comparisons of litter in exclosures and grazed plots

№	Quantity of litter (g/m ²)			p-value
	Exclosure	Plot	t-value	
1	98.31 ± 12.95	0.87 ± 0.50	7.51	0.0003
10	101.35 ± 25.15	8.23 ± 1.64	3.70	0.01
11	28.15 ± 7.05	0.43 ± 0.43	3.92	0.008
16	153.19 ± 20.88	78.86 ± 6.55	3.40	0.01

4.10.2 Grass quality

Vegetation quality in the exclosures ranged from 6.24 ± 0.22 % crude protein in exclosure 10 to 4.88 % crude protein ± 0.21 in exclosure 16 in the wet season. The pattern in exclosure quality followed plot quality, with the highest values in plot 10. High quality was correlated to low biomass in much the same way as described in section 4.3.7. Quality was however substantially higher in the grazed plots (table 4.8). The differences in plots and exclosures 1, 10 and 11 were significant but not for exclosure 16 at $p \leq 0.01$. An analysis of variance for quality between the 4 exclosures showed the differences to be significant ($F=5.60$, $df\ 3,12$ $p=0.0097$). Results for the least significant differences test showed that the quality in exclosure 16 was lower than the other three exclosures.

Table 4.8 Quality comparison between plots and exclosures- February 1993.

№	Mean Quality % CP		T-value	Two tailed P	One tailed P
	Plot	Exclosure			
1	8.85 ± 0.1826 n=4	5.71 ± 0.3929 n=4	7.2349	0.00035	0.00018
10	10.97 ± 0.653 n=4	6.24 ± 0.2220 n=4	6.05	0.0005	0.0002
11	8.87 ± 0.5622 n=4	6.23 ± 0.1619 n=4	4.5041	0.0041	0.00020
16	5.97 ± 0.4359 n=4	4.88 ± 0.2123 n=4	2.25	0.065 ns	0.033

Fig 4.16
Comparison of mean grass biomass between
Plots and Exclosures (1)

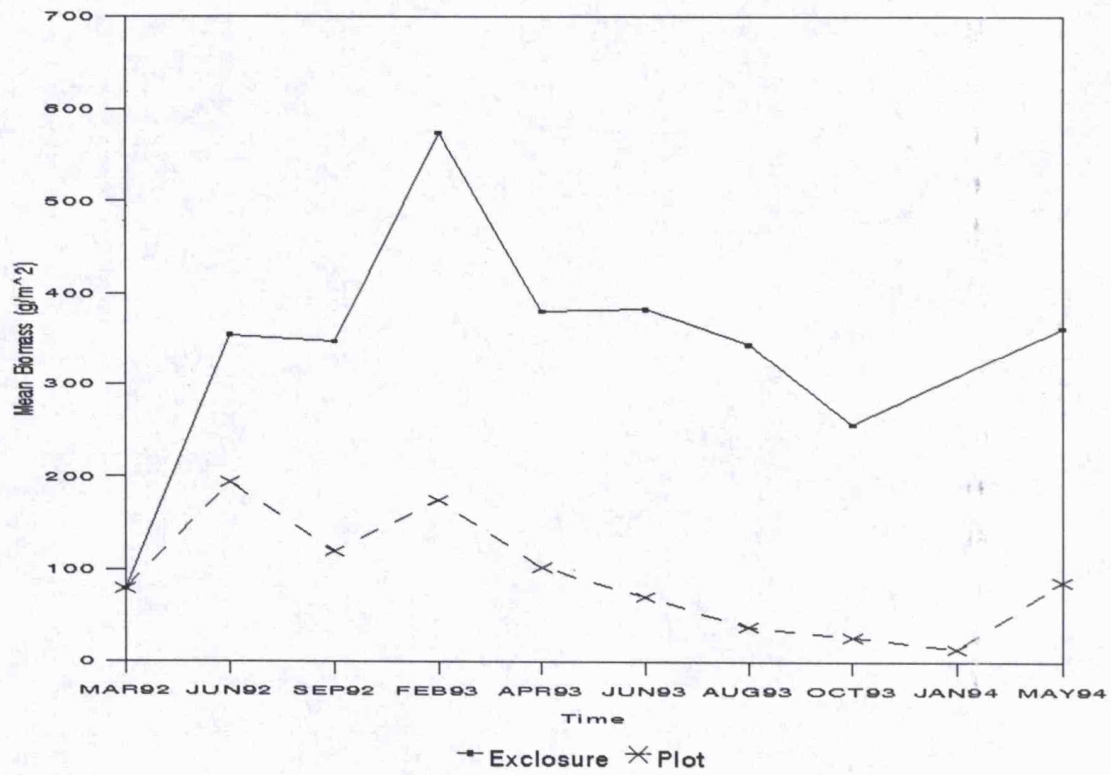


Fig 4.17
Comparison of mean grass biomass between
Plots and Exclosures (10)

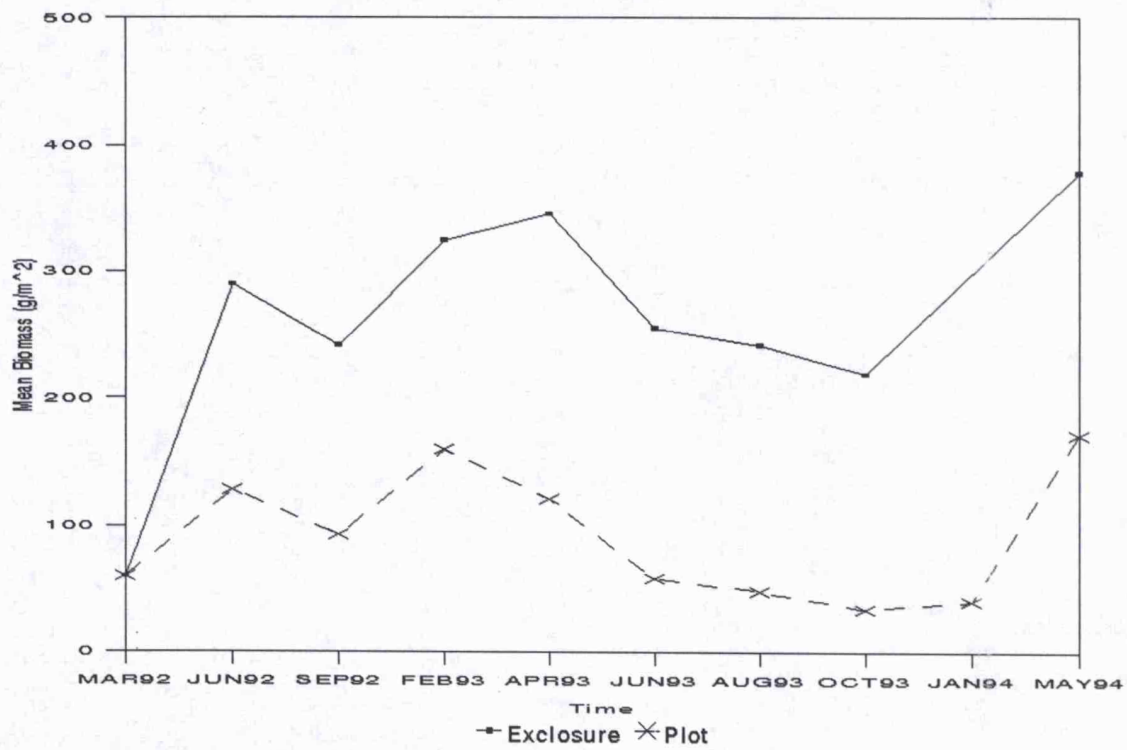


Fig 4.18
Comparison of mean grass biomass between
Plots and Exclosures (11)

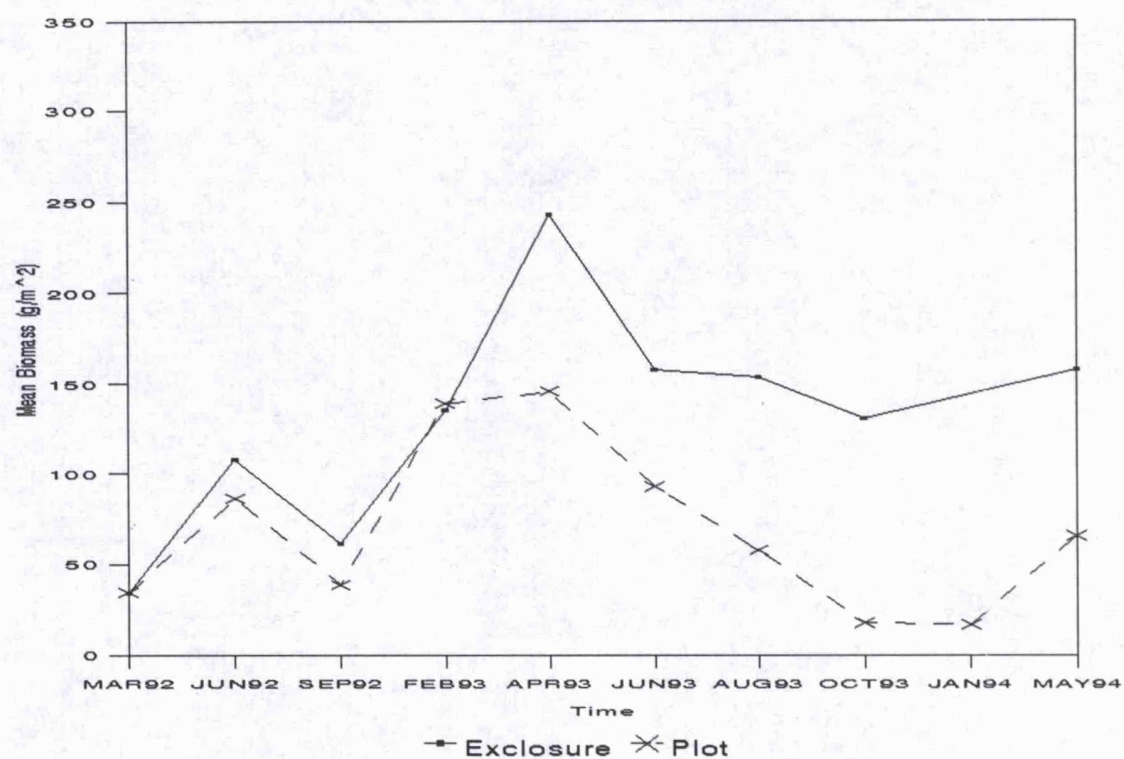
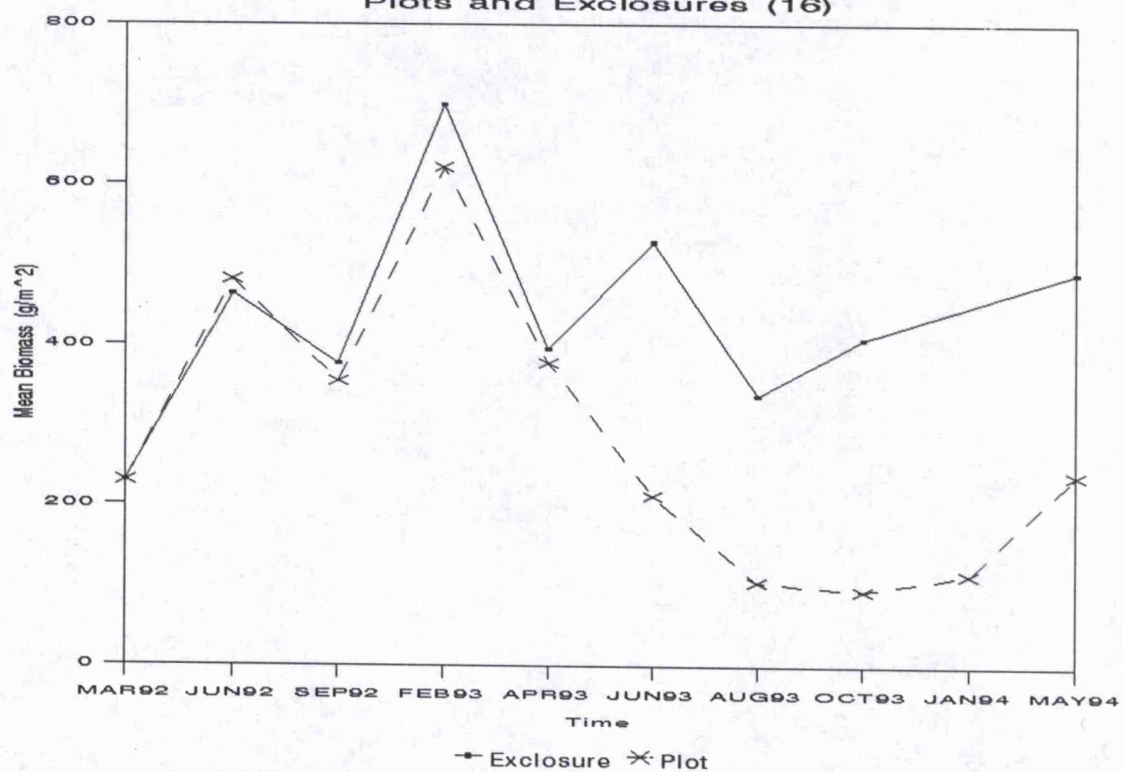


Fig 4.19
Comparison of mean grass biomass between
Plots and Exclosures (16)



4.10.3 Species composition

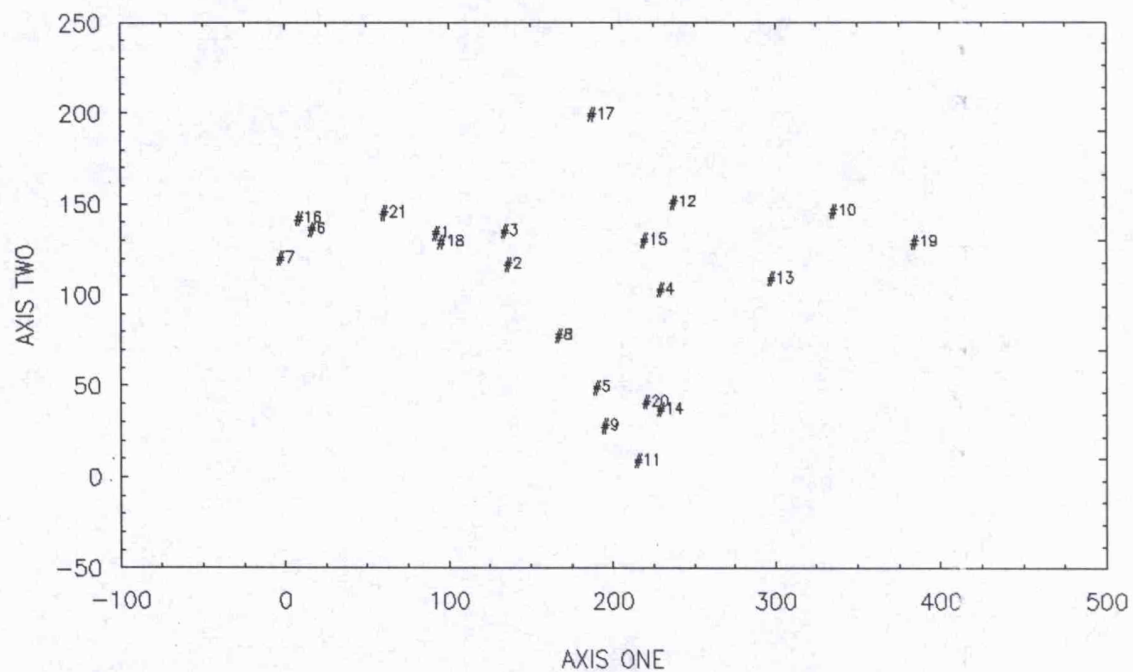
Diversity was generally lower in exclosures (table 4.9). The highest diversity was recorded in exclosure 10 at 1.99 in June 1992. By May 1994, this had declined to 1.27. This decline was caused by a reduction in the number of species, from 16 in June 1992 sample to 9 in May 1994. The contribution of the major species in the exclosure also changed significantly. A t-test comparison of diversity between exclosure and plot for corresponding samples showed significant differences in 1, 10 and 16 in June 1992, all plots and exclosures in February 1993 and between 1, 10 and 11 in May 1994. The t-values increased for plots 1, 10 and 11 over time signifying increasing differences between plots and exclosures.

A species by plot analysis using DCA showed that although there were differences in diversity, the species composition of the exclosures remained markedly similar with the grazed plots around them. All exclosures were closely associated with their respective plots throughout the study period e.g (Fig. 4.21a, 4.21b), the February 1993 scatter (Fig 4.21c), but in May 1994, there was a switch in the scatter of plots along axis 1. The plots that had been on the extreme right moved to the extreme left and vice versa. Plots 3 and 17, 4 and 8, 5, 11, 2 and exclosure 2 were now more closely associated. Contribution of the major species may have changed, some of the more rare species disappeared, but the general species composition remained relatively unchanged.

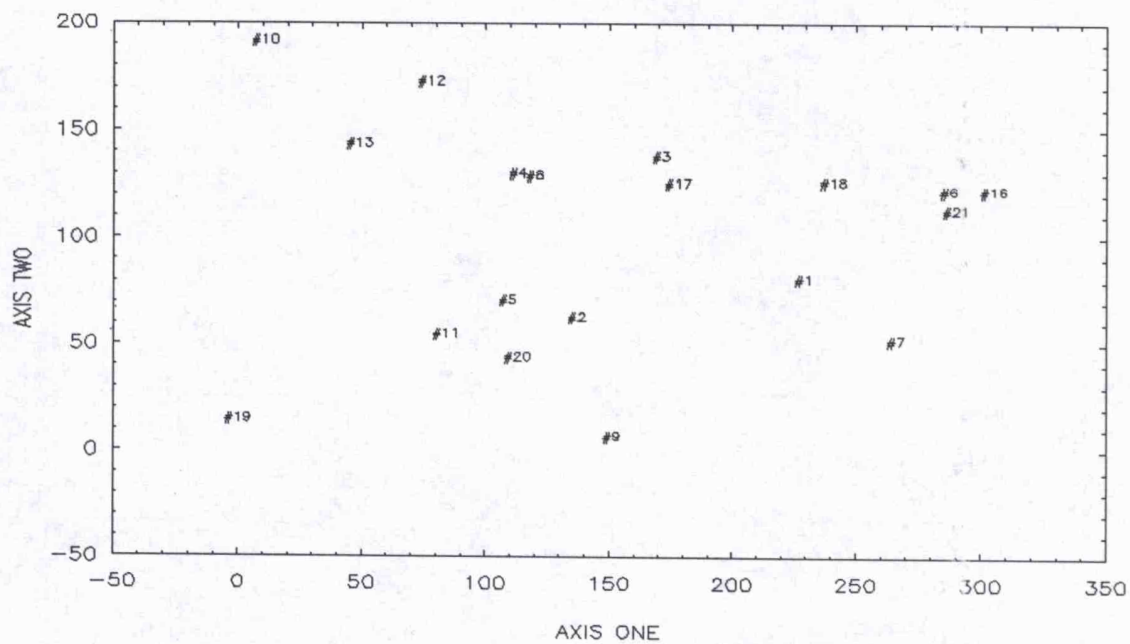
Table 4.9 Comparisons of plant species diversity between the plots and exclosures in the wet season months.

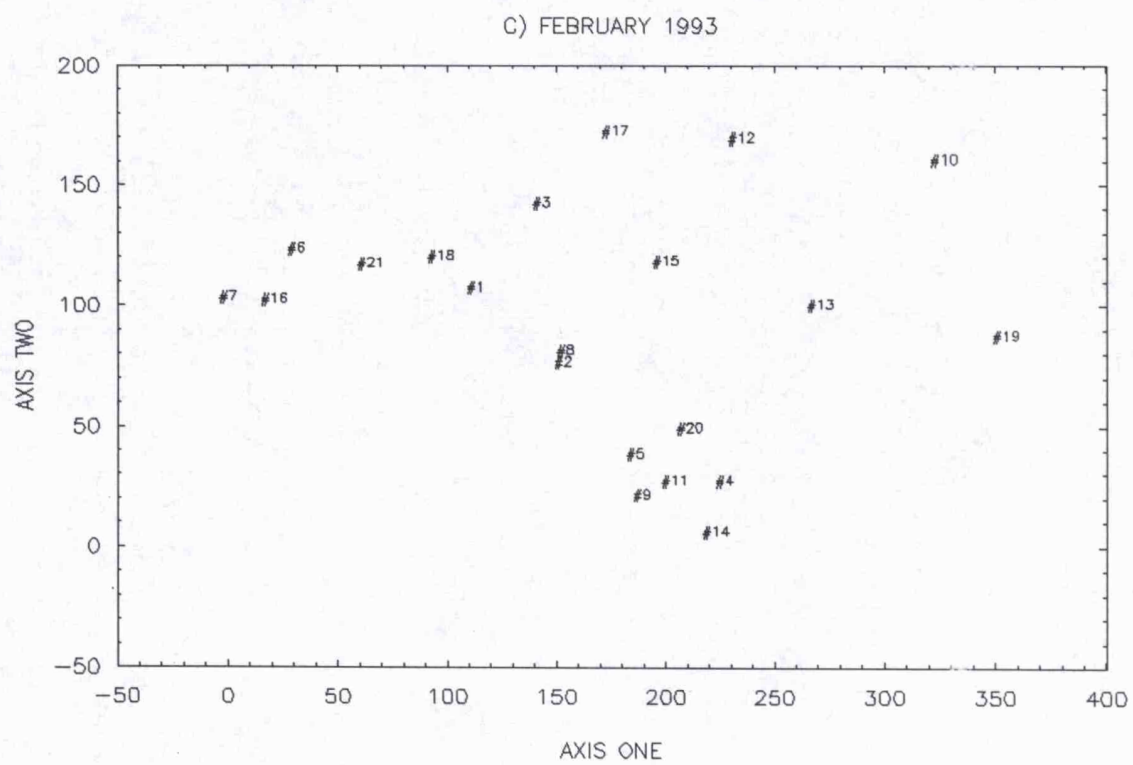
	No	Diversity H'		t-Value	df	P
		Plot	Exclosure			
June 1992	1	1.42	1.14	3.24	824.00	< 0.01
	10	2.50	1.99	7.67	592.23	< 0.001
	11	1.61	1.59	0.14	359.59	> 0.05
	16	1.80	1.60	3.65	1450.52	< 0.05
February 1993	1	1.35	0.82	6.06	503.10	< 0.001
	10	2.60	1.80	13.38	859.40	< 0.01
	11	2.00	1.50	5.97	511.50	< 0.01
	16	1.81	1.65	3.53	1912.01	< 0.01
May 1994	1	2.33	1.29	11.13	306.57	< 0.001
	10	2.53	1.27	23.00	757.86	< 0.001
	11	1.68	1.33	4.29	253.28	< 0.001
	16	1.67	1.63	0.73	570.71	> 0.05

FIG 4.21
ORDINATION OF THE TWO AXES OF A DECORANA ANALYSIS DESCRIBING
THE VARIATION OF PLOTS AND EXCLOSURES IN RELATION TO
SPECIES COMPOSITION OF THE HERB LAYER
A) JUNE 1992



B) MAY 1994





4.11 Interpretation

The biomass patterns in the Athi-Kapiti ecosystem were driven primarily by rainfall, its amount, variability and seasonality, but were highly and significantly modified by grazing. The rains heralded a period of vegetative growth, of food abundance and widespread water availability, a period of recovery following the lean dry season. Nairobi National Park falls in the higher rainfall regime (Fig. 4.20) and had higher total standing crop in the exclosures, followed by areas bordering the escarpment and close to the Ngong hills. The vegetation here was also taller and poorer nutritionally. Areas in the lower rainfall regime represented by the open plains of Olrimirui accumulated lower standing crop of higher nutritional quality. The vegetation was also very short. There was a positive relationship between the rainfall and two vegetation variables namely height and biomass while quality was negatively correlated (Fig. 4.13). The two areas falling in the rainfall extremes had herbaceous biomass, grass height and quality that reflected these relationships.

Biomass trends during the first year when the weather patterns in the country were "normal" were those of growth during the rainy season and decline in the dry, i.e two peaks and two troughs during the year. However the period between April 1993 and January 1994 was characterised by unusually dry weather conditions, with failure of rains country-wide and as expected, intense grazing pressure on the vegetation both inside and outside the park (Fig. 4.3-4.6). Biomass declined steadily on the plains and steeply in the park due to the combination of dry conditions and heavy grazing pressure from large concentrations of wildlife migrants.

The combined effects of grazing and rainfall were ecologically important. Together, they had significant control on vegetation biomass accumulation rates, total food quantity and quality available as well as the distribution of vegetation in both time and space. Vegetation composition, diversity and physiognomy could also be broadly related to these variables. Nairobi National Park and a few areas on the plains e.g the area around Ilopoosat, were not as heavily grazed as the rest of the plains. The Park's grasses were heavily grazed only during the dry season. In the wet months they had sufficient time to recover before they were then grazed down again in the next dry season. The extent and intensity of grazing depended on the length of the dry season, the numbers of wildlife returning to the Park from the plains and the amount of rainfall and therefore growth in the previous wet season.

The general changes in seasonal quantity and height of the herb layer outside the Park were broadly similar but followed a different sequence. With the exception of a few areas such as around Ilopoosat and on plot 5 beyond Oloyangalani much of the grass on

the plains was heavily grazed. The plains were exposed to grazing by both wild herbivores and livestock throughout the year, though grazing was heavier during the wet than dry season. Plots 10, 12 and 13 experienced the most use during the wet season so that by the beginning of the dry season they had little grass left. These plots had the least standing crop of rich, short vegetation that was highly sought after. In the drought, severe food shortages were experienced by wildlife and livestock and the local pastoral Maasai had to move their livestock to other areas in search of pasture. Wildebeest and zebra moved from the short to taller grass areas once the vegetation was exhausted. Several differences in vegetation properties between the Park and plains associated with the use patterns were noted:

- The herb layer in the heavily grazed areas such as Lukenya, Olrimirui and Stony Athi had very short vegetation of low biomass but high quality. Species of small growth form such as *Microchloa kunthii* and *Sporobolus pellucides* dominated. Intense grazing in the wet season seemed to encourage tillering and prostrate growth in grasses (personal observation). Herbivores selected these sites very early in the wet season when vegetation was nutritionally at its best. The grasses would then be freshly sprouting, and comprise mostly young leaf and flowers with very little stem.
- In the Park, low grazing intensity in the wet season coupled with high rainfall produced grasslands that were dominated by tall grasses and forbs. These were of higher mass and low quality. The dominant species in the open grasslands were *Themeda triandra* with *Setaria phleoides* in woody habitats.

Grazing therefore had significant impact on vegetation community structure, physiognomy as well as competitive interactions between plants. In the absence of grazing the general trends were of rapid vegetation accumulation (Fig.4.16-4.19). Even in areas where grasses were short such as plots 1 and 10, once exclosed, the grasses grew tall and upright and lost their tillering form. There was however variation in the maximum vegetation biomass accumulated in the four exclosures. This demonstrated the impacts of uneven distribution of rainfall over the ecosystem. Grass quality also declined.

Comparisons between the exclosures and the grazed plots suggest the conclusion drawn earlier by (Western and Gichohi, 1993), that the Park is itself a large exclosure except after severe dry conditions during which intensive grazing in the Park creates short-term grazing lawns, or after fire has been used. On the plains, differences between exclosures and surrounding grazed plots quickly became obvious. This demonstrated that biomass, height and quality were regulated by grazing to a large extent. Soil

differences may also have been responsible for some of the variation in plot and enclosure 11.

Although no measurements of soils were taken there was spatial variation that could have accounted for vegetation differences particularly in species composition. Areas of deep cracking, black cotton clays like *Acacia drepanolobium* woodlands of the Park, plot 6 at Oloontepes and 7 at Ereteti had grasses that were dominated by *Setaria phleoides* in contrast to other areas. No other differences could be attributed to either soil factors or other habitat differences.

CHAPTER 5

WILDLIFE OF THE ATHI-KAPITI PLAINS

5.1 Seasonal comparisons of ungulate numbers

The mean number of animals using the ecosystem were 55215.7 ± 10680 in the wet season and 42132.7 ± 3956.98 in the dry season. A one-way analysis by ranks showed that these two means did not differ significantly ($H=1.1905$, $p > 0.05$). However this did not reflect the level of seasonal variation for specific species (table 5.1). Cattle, Thomson's gazelle and Impala showed significant declines in the dry season. Cattle were moved out of the plains in search of pasture during the extreme dry conditions. Impala and Thomson's gazelle may have moved out of the plains during the same periods. Since no mass mortality was reported on the plains, one assumption is that impala and Thomson's gazelle moved out of the plains to avoid the harsh food and water conditions. An alternative explanation for the decline in Thomson's gazelle numbers could have resulted from counting errors. Due to their small size and cryptic colour, they are sometimes underestimated during dry season counts.

Whilst the seasonal variation for some species was significant, (table 5.1), the cumulative differences were not large enough to cause an overall change in seasonal means. Within season variance was however much larger for the wet season.

5.2 Seasonal distribution of the main ungulate groups

The aerial survey data indicated that the total numbers of wildlife remained relatively constant although there were movements and shifts in the distribution and concentration centres at the ecosystem level. An analysis of wildlife groups classified as large (buffalo), medium (wildebeest, Coke's hartebeest and zebra), small grazers (Thomson's gazelle, Grants' gazelle and warthog) and browsers showed definite differences in the distribution patterns. Among most species, the distribution changed seasonally in the course of the year. Zebra and wildebeest displayed seasonal, large scale movements. Many other species had smaller, more localized movements. In general, results showed an influx of wildebeest and zebra into the park in the dry season, and an exodus of the same species in the wet season. Numbers of wildebeest in the park were much larger than those of zebra.

Table 5.1 Seasonal differences in wildlife and livestock numbers in the Athi-Kapiti ecosystem.

Species	Dry season average	Wet season average	Test statistic	Sign. Level
Sheep & Goats	107128 ± 2066	114443 ± 16835	0.0476	0.83
Cattle	64556 ± 2342	80338 ± 5148	3.8571	0.05 *
Buffalo	290 ± 182	68 ± 32	1.1905	0.28
Wildebeest	10699 ± 3165	9373 ± 1934	0.0476	0.83
Zebra	13937 ± 922	16173 ± 3877	0.4286	0.51
Thomson's gazelle	1786 ± 610	5125 ± 1163	3.8571	0.05 *
Coke's Hartbeest	4519 ± 722	6441 ± 424	2.3333	0.13
Impala	2712 ± 280	5746 ± 1021	3.8571	0.05 *
Grant's Gazelle	4752 ± 1493	7922 ± 2212	1.1905	0.28
Giraffe	544 ± 77	649 ± 138	0.4286	0.51
Eland	524 ± 152	967 ± 322	1.1905	0.28
Warthog	115 ± 37	83 ± 29	0.4286	0.51
Ostrich	2330 ± 960	2208 ± 289	0.0476	0.83

* Significant seasonal differences at $p \geq 0.05$.

5.2.1 Small ungulates

Small ungulates were widely distributed in the ecosystem. Densities ranged between 0-15 animals/km² except in one area. These were the plains between the Athi river and Kitengela townships and the Athi river-Konza railway line, where a density of 25.3 animals/km² occurred (Fig. 5.1a). These plains have short grasslands on slightly higher ground and until recently were relatively free of human settlement.

In the dry season there was little discernible change in distribution, although these ungulates were more widespread in the park (Fig. 5.1b).

5.2.2 Medium sized ungulates

The medium sized ungulates had specific areas of high concentration during the wet and dry seasons. In the wet season the highest densities occurred around Enkiggirri, Olirirui and other short grass areas within the Kapiti Plains. This area had a density of over 60 animals/km². To the east of this, densities were still high and ranged between 45-60 animals/km². Around the Kitengela and to the north west of the ecosystem, there were areas of high and moderate densities. The Stony Athi along the eastern railway line had moderate densities that fell within the 15-30 animals/km². The rest of the ecosystem including Nairobi National Park had low densities in the wet season (Fig. 5.2a).

In the dry season, concentrations shifted from the south-east to Nairobi National Park reaching a peak density within and around the aerodrome plains. Water may have been the key attractant, since forage was still available in certain parts of the plains when

many of the migrants left (Fig. 5.2b).

5.2.3 Large grazers

The only species in this size class was the buffalo which used the park year round (Fig. 5.3 a & b). Occasionally, incursions into the Kitengela were reported, but these were short-lived and the beasts normally returned to the park. The distribution patterns indicated a slightly more extensive use of the park in the wet than dry season.

5.2.4 Browsers

This category comprised eland, giraffe and impala. Impala were the most numerous browsers in this group with an average wet season estimate of 5745.67 ± 1020.74 . Their distribution was primarily governed by the woody vegetation in the ecosystem and as a result were more confined. The major woody plant is the *Acacia drepanolobium* occurring along the Rift Valley escarpment, around Oloontepes, parts of Olirimirui, on the south eastern part of the ecosystem between Naiserian and Ilpolosot and generally in low lying areas of impeded drainage. Along river courses, *Acacia xanthophloea* is common. Browsers predominated in many areas where grazers were absent or occurred in low numbers, for example, along the escarpment and in the forest of Nairobi Park (Fig. 5.4 a & b).

In the dry season their distribution was more restricted. A careful look on the ground and the distribution maps showed convergence around watered areas close to woodlands.

5.2.5 Livestock

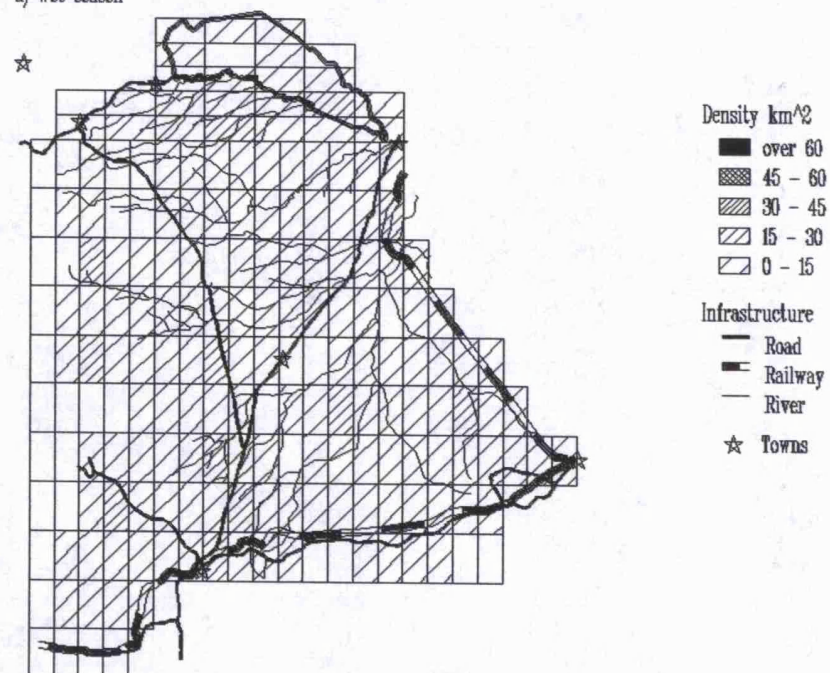
Sheep, goats, cattle and donkey are the major livestock species in the Athi-Kapiti plains. Donkeys exist in very low numbers and camels though counted during the surveys were outside the area of study on a transect that extended just outside NNP, near the Athi-River. Livestock densities were extremely high at over 50 animals/km² in much of the ecosystem (Fig. 5.5 a & b). The eastern part had lower densities which generally corresponded with areas of moderate wildlife density. The big ranches in Machakos district had low livestock numbers compared to the neighbouring Maasai rangelands.

A comparison of mean numbers of all wildlife and all livestock in the ecosystem showed there were 4 times more livestock than wildlife. The mean numbers during the study period were 1.84×10^5 livestock and 4.9×10^4 wildlife.

Fig 5.1

Mean density distribution of small sized wild grazers
(Warthog, Thomson's and Grant's Gazelle) in the Athi-Kapiti Plains

a) Wet season



b) Dry season

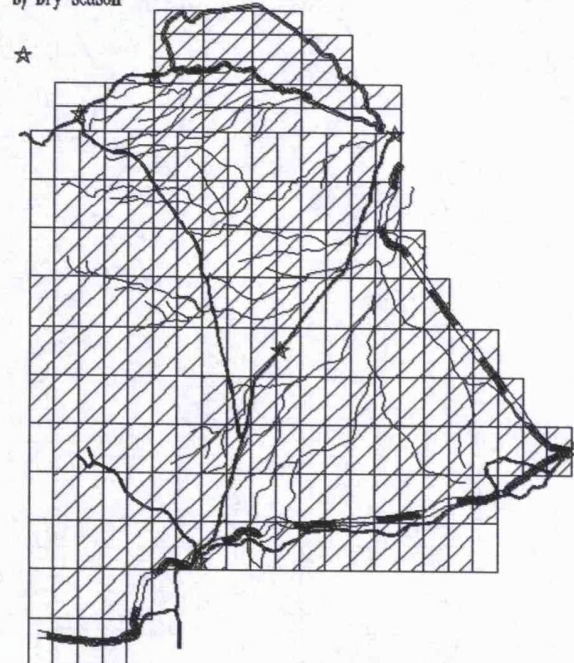
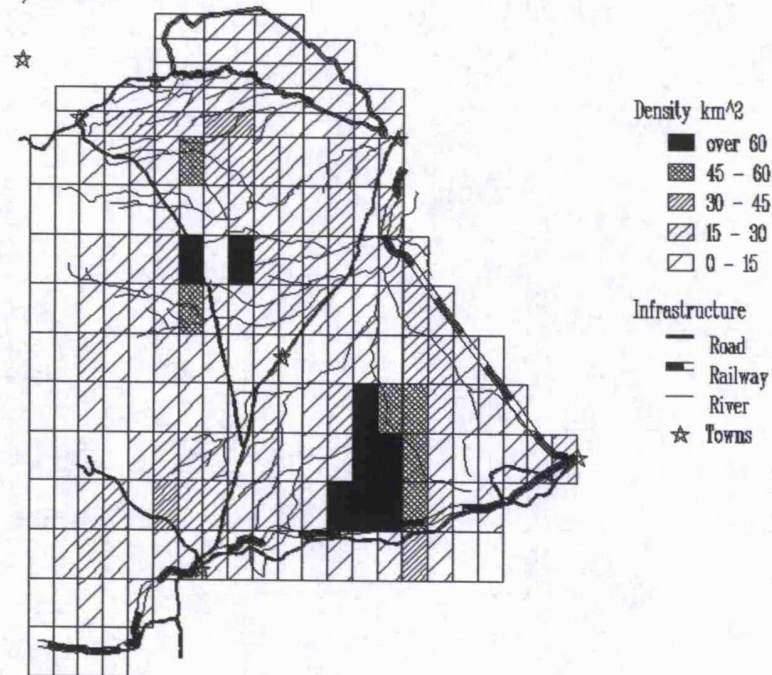


Fig 5.2

Mean density distribution of medium sized wild grazers
(Coke's Hartebeest, Wildebeest, Zebra) in the Athi-Kapiti Plains

a) Wet season



b) Dry season

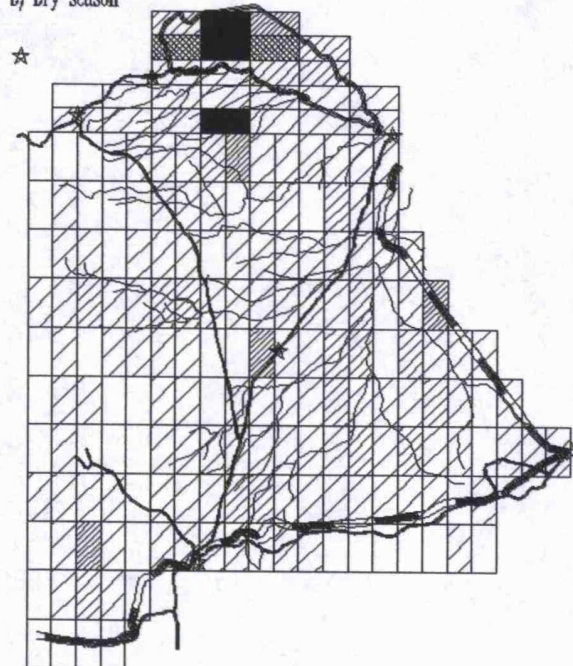
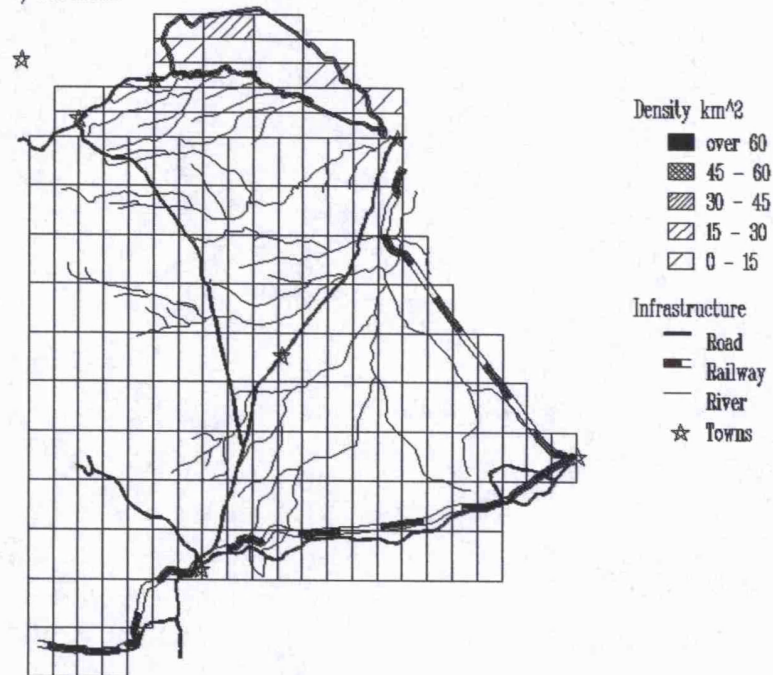


Fig 5.3

Mean density distribution of large sized wild grazers
(Buffalo) in the Athi-Kapiti Plains

a) Wet season



b) Dry season

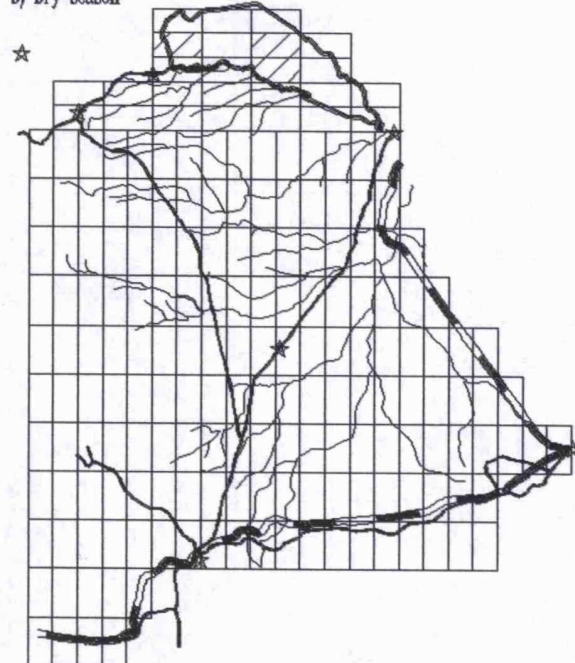


Fig 5.4
Mean density distribution of Browsers
(Eland, Giraffe, Impala) in the Athi-Kapiti Plains

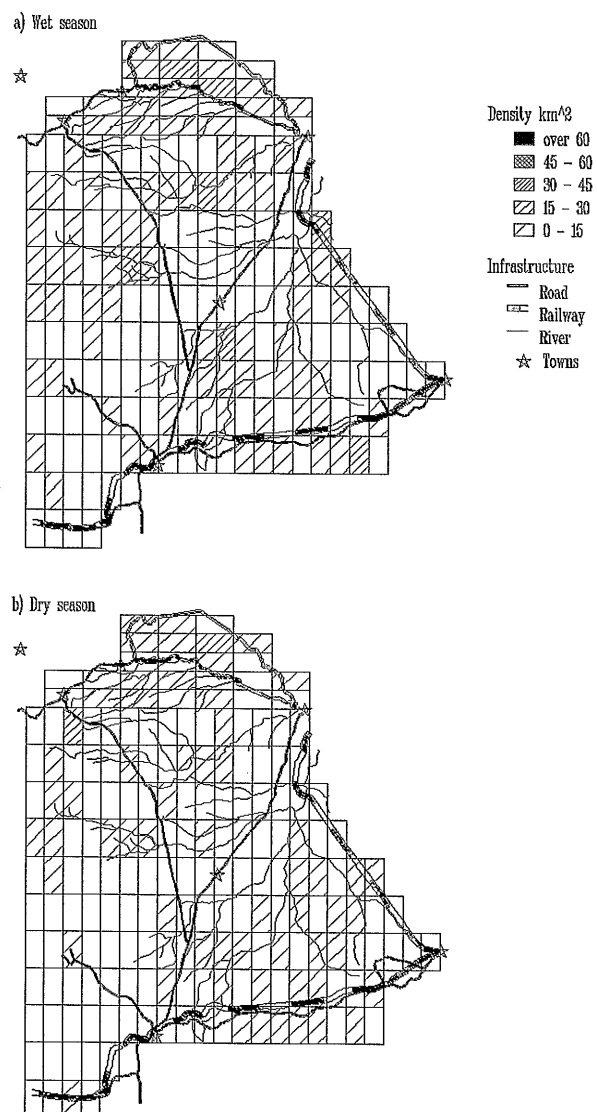
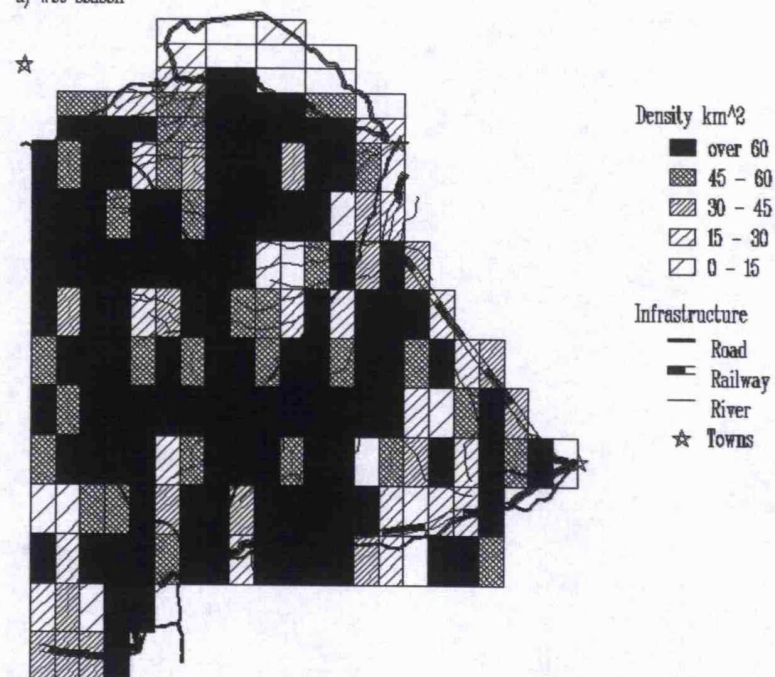
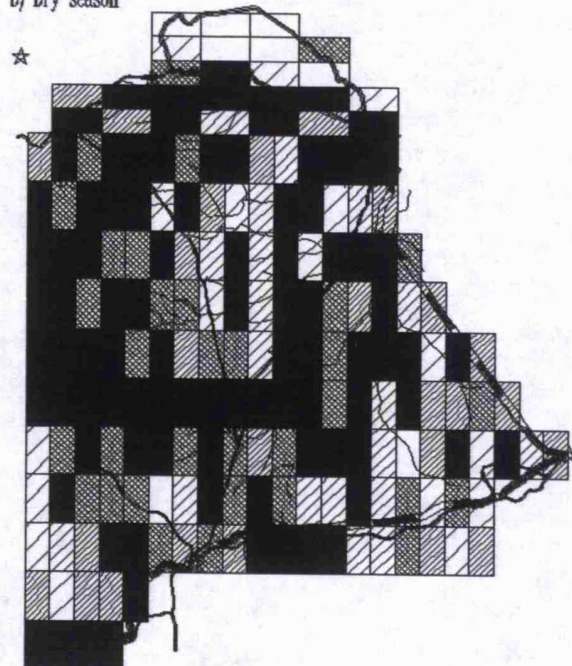


Fig 5.5
Mean density distribution of Livestock
(Cattle, Shoats, Donkey) in the Athi-Kapiti Plains

a) Wet season



b) Dry season



5.3 Species distribution patterns

5.3.1 Wildebeest

This species had the most distinct but shifting seasonal patterns. A large proportion of the wildebeest population in the Maasai part of the plains is migratory. The migrating groups moved into the park during the dry season while a few others remained on the plains.

During the wet season the species concentrated on the south eastern part of the plains where short grasslands occur. These plains lie between Enkiggirri, Olrimirui and neighbouring short grass plains, represented by vegetation plot number 10. High densities of over 82.7 wildebeest/km² were found on these open plains (Fig. 5.6a). Apart from feeding, these areas of high concentration were used by females for calving, an occurrence observed many times. In response, many Maasai moved their cattle to avoid the calving grounds. The neighbouring Machakos ranches had moderate density of wildebeest.

In stark contrast, the park had no wildebeest during most wet seasons. They left with the onset of the rains and did not return until the following dry season. This pattern clearly emerged on the density distribution maps. Occasionally few groups of wildebeest were counted in the park after the main exodus. This happened if counts were conducted shortly after the first rains before all the animals had left, or when there were delays in the outward migration due to the presence of freshly sprouting grasses on previously burnt plots. In the dry season, the distribution patterns shifted visibly as animals moved northwards and westward to the park (Fig. 5.6b). The availability of water in the dams is thought to be a primary cause of the return. The Kitengela, immediately south of the park was also an important dry season area. Some wildebeest stayed outside the park, but close to the Mbagathi river for watering even when forage conditions were very poor. According to the local landowners, these groups were often kept out by predators which waited at the river crossing. A sizeable proportion of the population sometimes remained around the Stony Athi, one of the few rivers with permanent pools of water. In general the density distribution was high in the park, low on the plains but more widespread.

In the early part of the study, wildebeest were common along the escarpment and at Eluai. For example in the early part of 1992, large numbers of animals were observed during ground reconnaissance in the *Acacia drepanolobium* woodlands of plot 1 and just beyond plot 2 in a low lying area with plenty of water pools and similar grasslands. With time, the species became increasingly confined to the eastern part of the plains and large herds commonly seen at Eluai disappeared (see dung occupancy section).

5.3.2 Zebra

The density of zebra was not as high as that of wildebeest, but the species was more widely distributed in the whole ecosystem. Like wildebeest, zebra were absent from the park in the wet season and used a wide range of habitats on the Athi-Kapiti Plains (Fig. 5.7 a & b). In the dry season migrant zebra normally returned to the park earlier than the wildebeest, but left later in the wet season, thus using the park for longer periods. Wet season concentrations occurred around Ololoitikoshi (means place of the zebra) where there was a density of over 60 zebra/km². These concentrations were lost in the dry season. The only obvious shifts in distribution in this season was their concentration in the park during the dry season with a density of 45-65 zebra/km² where they had previously been low. Elsewhere on the plains density distribution was low except at Eluai where 30-45 zebra/km² were recorded. A large proportion of the total population therefore remained outside the Park (see section 5.4.2), generally close to watered areas e.g along the Kisaju river, the Stony Athi, and sometimes where water in private dams and cattle troughs was available. Compared to wildebeest the seasonal distribution shifts for this species were not as obvious.

5.3.3 Coke's hartebeest

The wet season distribution of this species was more widespread than wildebeest, but it occurred in much smaller numbers. The highest densities were located on the eastern part of the ecosystem in the Machakos district ranches. Large scale livestock ranching took up much of this part of the plains in the early part of the century but despite this many of the ranches have maintained wildlife. There is however, little mixing between the populations in the ranches and those on the maasai plains except where fences are absent. The dry and wet season patterns were similar (Fig. 5.8 a & b). A total of 5479.83 ± 570.06 was estimated for the whole ecosystem.

5.3.4 Thomson's gazelle

The species occurred at low densities but was widely distributed. The wet season distribution map showed very low numbers in the park in both the wet and dry seasons (Fig. 5.9 a & b).

5.3.5 Grant's gazelle

The population of the Grant's gazelle was also widespread on the plains with higher densities on the eastern part of the ecosystem. Its distribution was similar to that of Thomson's gazelle.

5.3.6 Livestock

Livestock were the dominant herbivores on the plains, and were widespread over the ecosystem. They did not occur in the park, although the distribution maps give that impression. Some transects straddled the park and its neighbouring areas outside and no boundaries were distinguished during the counts.

5.3.6.1 Sheep and Goats

These two species normally occur in groups and were counted together as 'shoats'. Their co-existence in the flock is probably due to differences in their feeding behaviour. Goats are predominantly browsers while sheep are grazers. Although they behave as two species, from the point of view of spatial distribution, they are effectively one species.

'Shoats' were the most numerous of the large herbivores on the plains with average densities of over 173.3 animals/km² in several parts of the ecosystem (Fig. 5.10). High concentrations occurred in the Kitengela and west towards the escarpment in the Oloyiangelani area. This part of the system is high, cold, and has short grasses and forbs. Sheep were more numerous here. Unlike cattle, 'shoat' distribution did not seem to be affected by that of wildebeest in the wet season.

5.3.6.1 Cattle

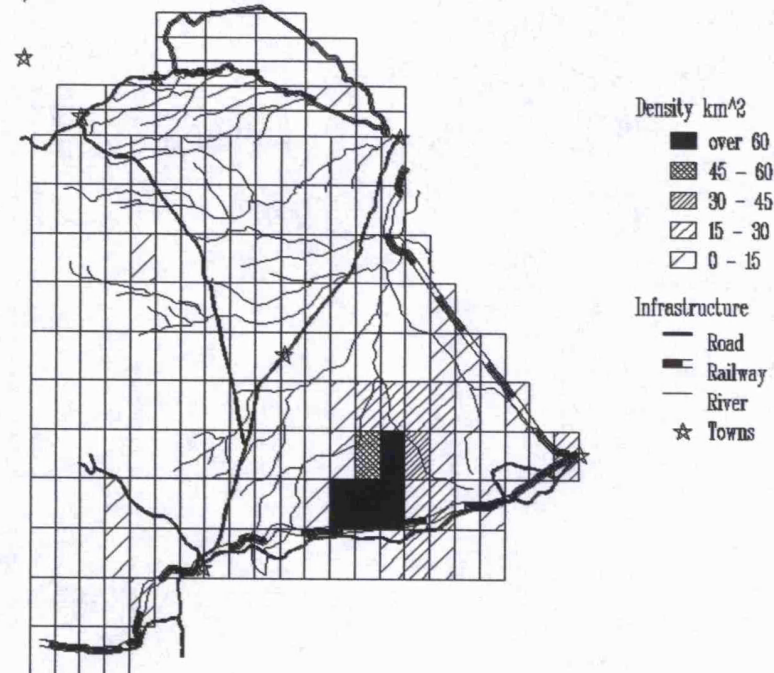
The density distribution of cattle was high in the wet season (Fig. 5.11a) compared to the dry. Cattle were however absent from areas of wildebeest calving, also areas of highest wildebeest density in the wet season (see Fig. 5.6). During the dry season areas of high density were fewer and did not correspond to those of the wet season. Former high wildebeest concentration areas were utilized by cattle (Fig. 5.11b). One of the grids devoid of cattle in the wet season had an average density between 27 to 53 cows/km² in the dry.

5.3.7 Ostrich

The density of ostrich in the ecosystem was generally at densities of between 0-15 birds/km² (Fig. 5.12), quite widespread but absent from the northwestern end of the ecosystem. In October 1992 a large number of ostrich was counted in an ostrich farm in the Kitengela. As a result the ostrich population in the ecosystem was overestimated. The farm had a density > 61 ostrich/km². When this estimate was removed, the density distribution returned to 0-15 per km².

Fig 5.6
Mean density distribution of wildebeest
in the Athi-Kapiti Plains

a) Wet season



b) Dry season

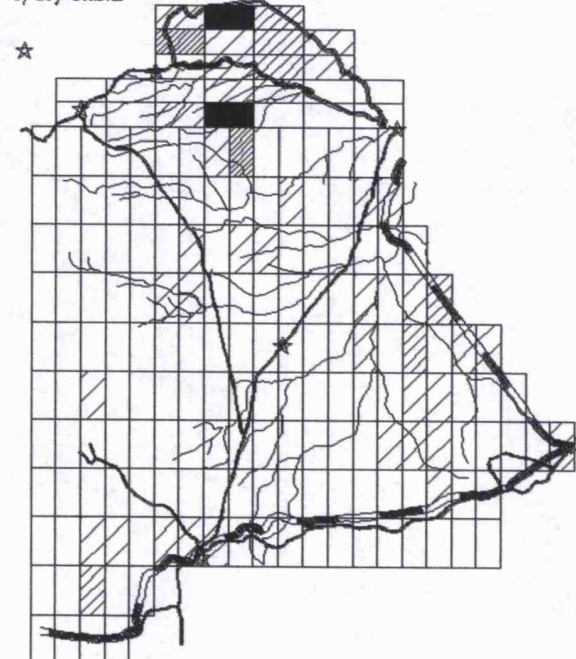
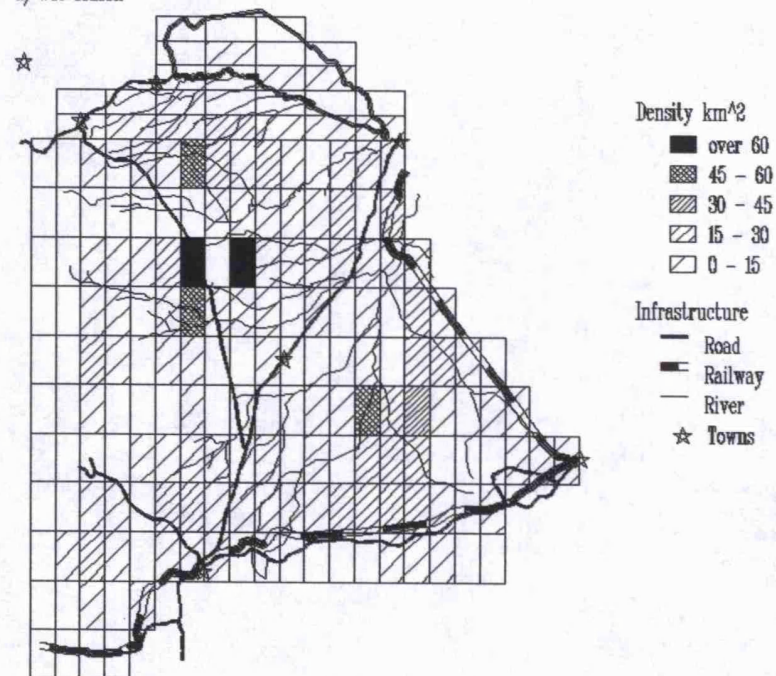


Fig 5.7
Mean density distribution of zebra
in the Athi-Kapiti Plains

a) Wet season



b) Dry season

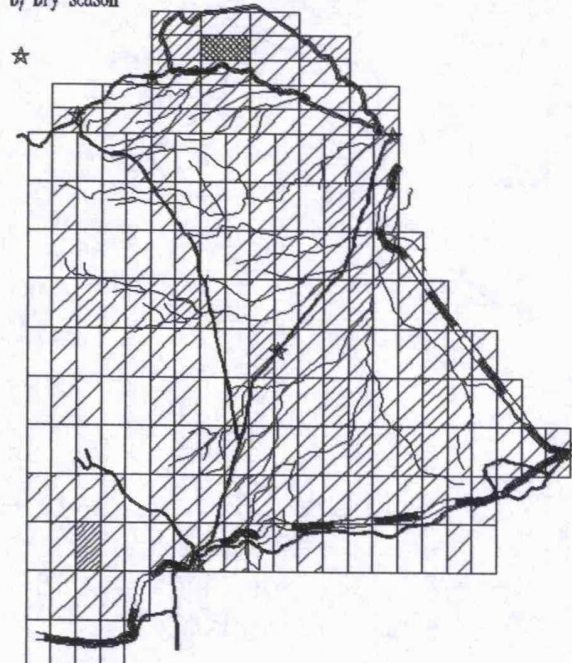
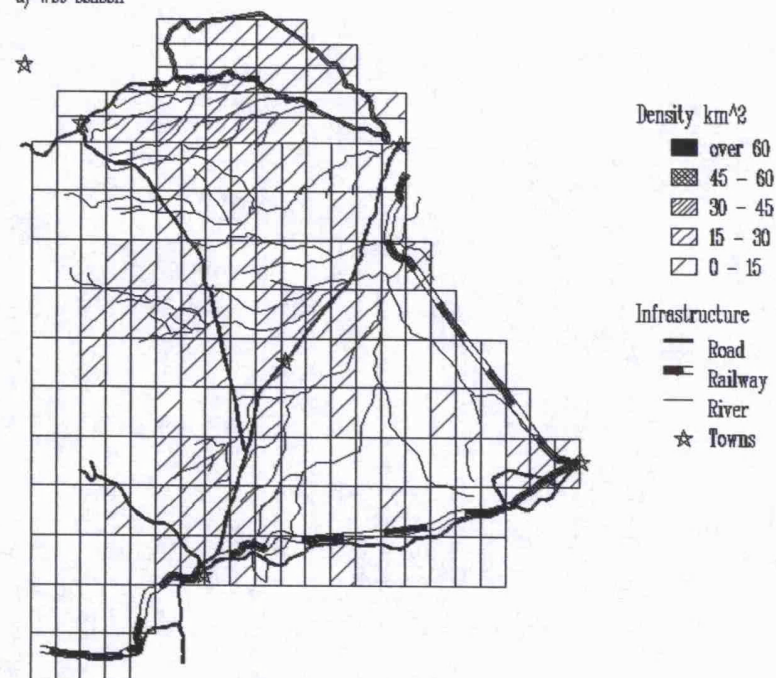


Fig 5.8
Mean density distribution of Coke's hartebeest
in the Athi-Kapiti Plains

a) Wet season



b) Dry season

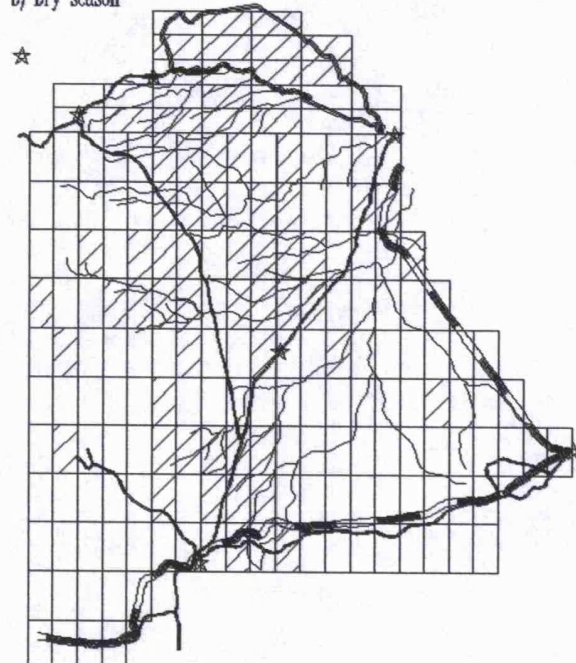
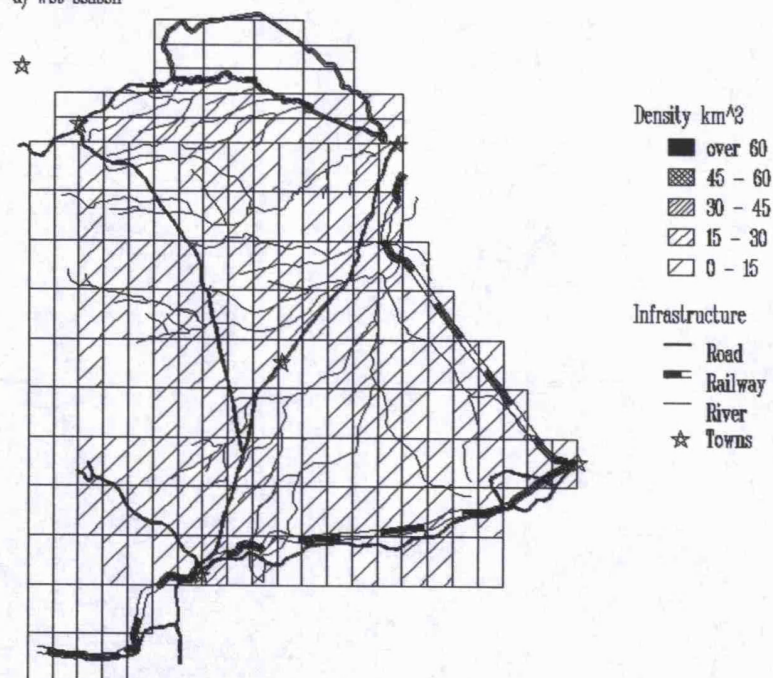


Fig 5.9
Mean density distribution of Thompson's gazelle
in the Athi-Kapiti Plains

a) Wet season



b) Dry season

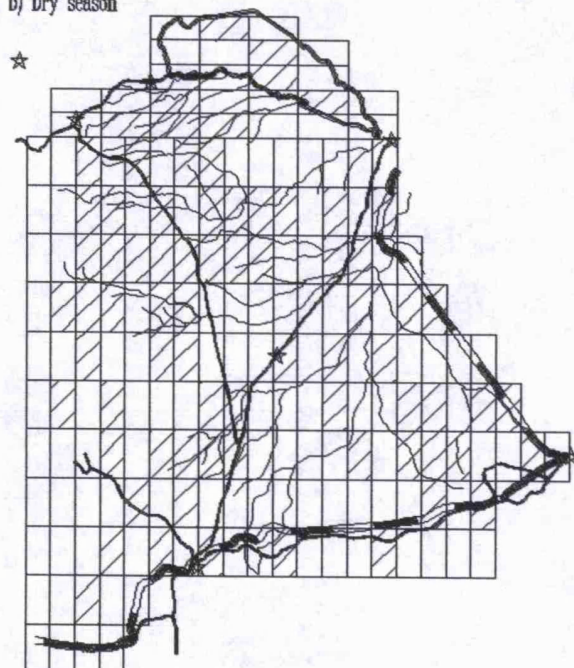
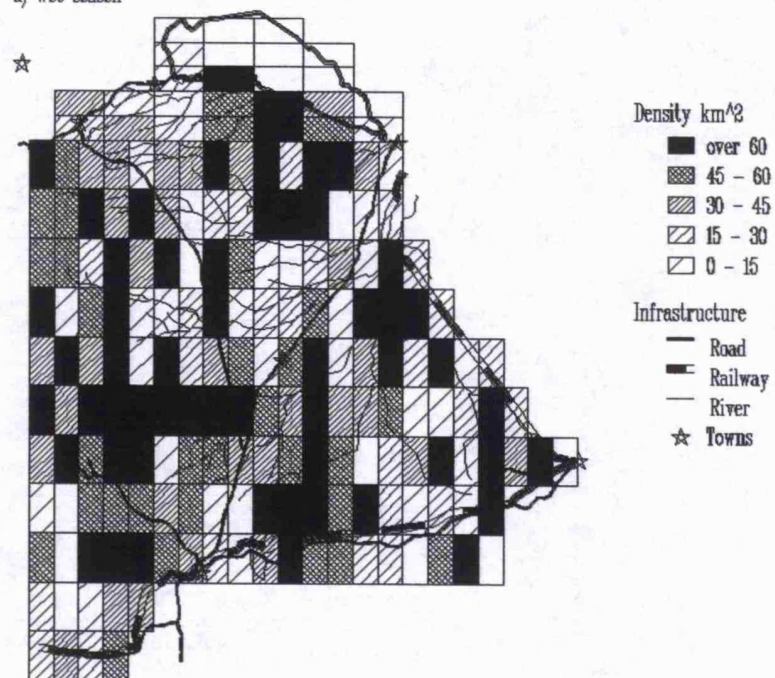


Fig 5.10
Mean density distribution of Shoats
in the Athi-Kapiti Plains

a) Wet season



b) Dry season

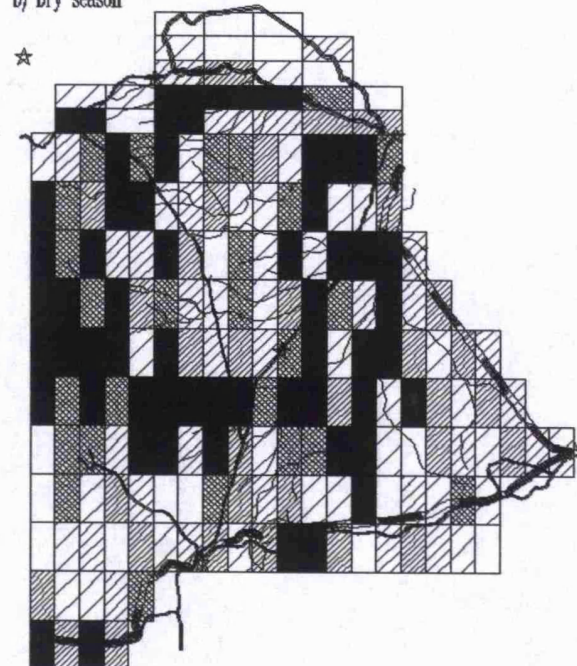
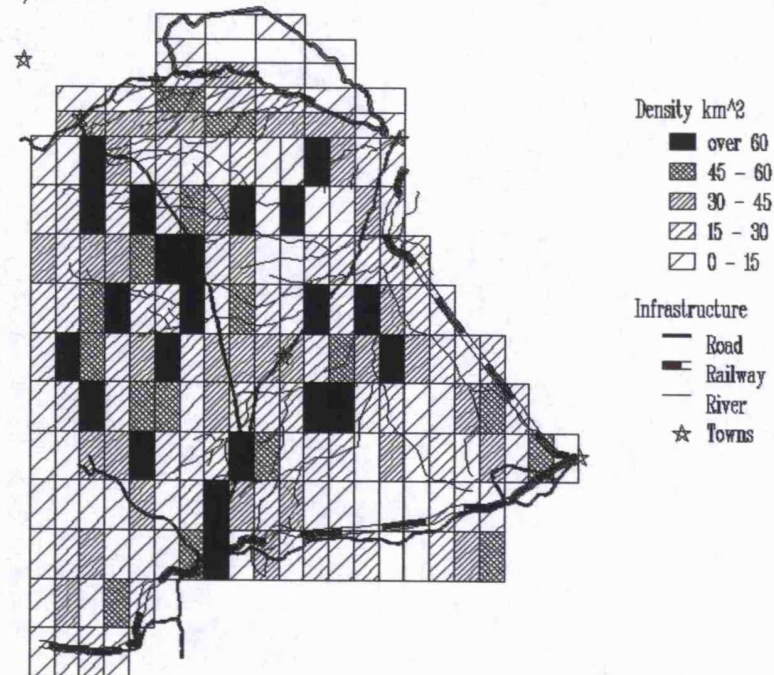


Fig 5.11

Mean density distribution of Cattle
in the Athi-Kapiti Plains

a) Wet season



b) Dry season

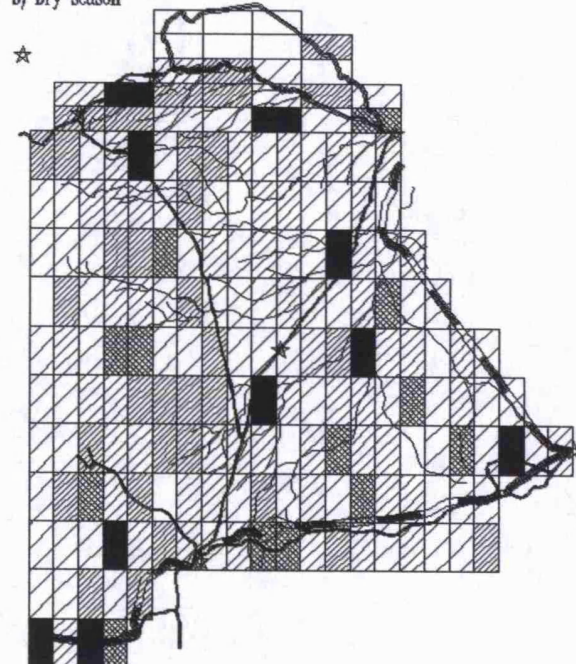
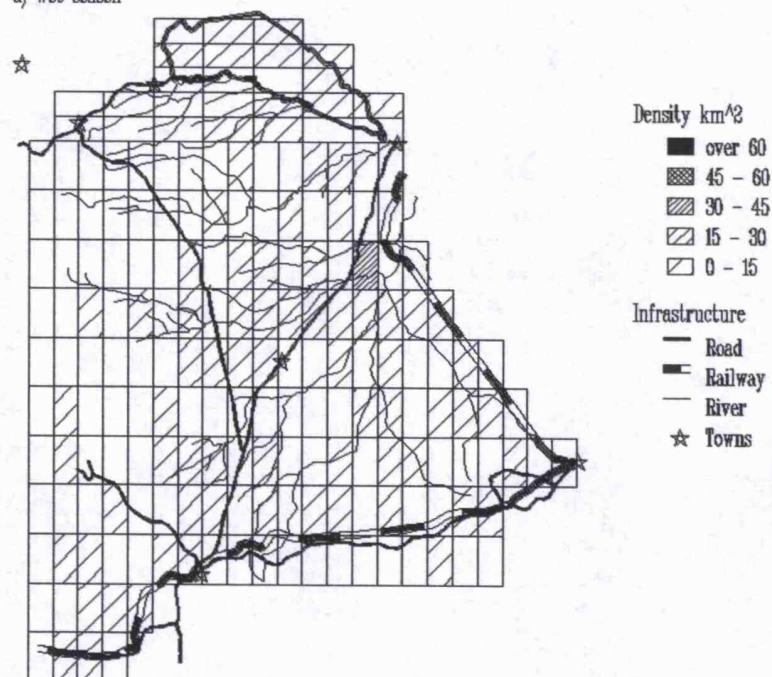


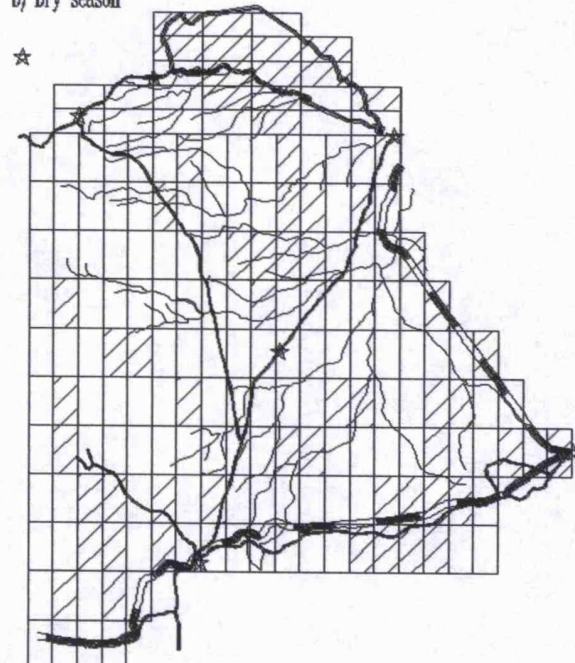
FIG. 5.12

Mean density distribution of Ostrich
in the Athi-Kapiti Plains

a) Wet season



b) Dry season



5.4 Nairobi National Park ground counts

Wildlife in the Park oscillated between very high peaks in the dry season and low numbers by comparison in the wet season. These marked fluctuations resulted from an influx of migrants into the park during dry conditions and their exodus at the beginning of the wet season. Wildebeest and zebra constituted the largest herbivore numbers and both moved in and out seasonally.

The numbers of wildebeest, zebra, eland and Coke's hartebeest were significantly higher in the wet season (table 5.2). The movements of wildebeest and zebra were large scale, those of eland and Coke's hartebeest less distinct. These movements resulted in overall seasonal changes of several orders of magnitude. The wet season average for 10 most numerous herbivore species was 183.83 ± 33.40 . Their dry season average rose by over five-fold to 991.37 ± 213.06 as the migrants returned.

At the beginning of the wet season, wildebeest moved out of the park and stayed out until the dry season. Their mean numbers in the park were low. Historically there was a small population of resident wildebeest in the park but during this study most wildebeest left for the plains during the wet seasons.

In the dry season wildebeest returned and were the most numerous ungulates. The largest concentration of this species was 8,243 in October 1991. The general seasonal cycle was that of intense use of the park in the dry season followed by an exodus to the Athi-Kapiti plains in the wet season (Fig. 5.13a). The average number of wildebeest using the park in the dry season over the study period was 5600.86 ± 701.05 and 29.33 ± 11.26 in the wet season.

Zebra behaved in a similar way with peaks in the dry season and troughs in the wet season. The migration cycle typically coincided with that of the wildebeest (Fig. 5.13a). However, the exact timing of the inward and outward movements differed between these two species. Wildebeest left the park earlier than zebra, and returned later. In total the migrant group of zebra spent more time in the park than the wildebeest.

The movements of hartebeest and eland were similar (Fig. 5.13b), but very small compared to the other two species. Though not obvious their movements can be inferred from the differences in seasonal averages. Dry season average was three times more for eland and 1.5 for hartebeest than the wet season. Eland demonstrated small scale migrations in the past, and the variation in seasonal means indicate that they may still take place. Grant's, Thomson's gazelle, warthog (Fig. 5.13c), impala, giraffe (Fig. 5.13d) and buffalo (Fig. 5.13e) are traditionally non-migrating and had constant numbers in the park throughout. Wet season variation for Thomson's gazelle was unusually high. Several reasons may have accounted for this but the most probable was that grasses

were too tall and the species may have been missed due to its small size. Wet season variance for eland was also high.

Buffalo do not normally go out of the park. The dry season mean was lower but not significantly so. These animals retreated to the forest when conditions were dry and this could explain the lower count.

Table 5.2 Seasonal means for 11 most common ungulates of Nairobi National Park.

SPECIES	Mean Number		Test Statistic	Sign. Level
	WET n=3	DRY n=7		
Grant's gazelle	98 ± 32	129 ± 15	0.6363	0.43
Thomson's gazelle	147 ± 50	98 ± 12	1.5714	0.21
Waterbuck	27 ± 9	33 ± 8	0.1169	0.73
Impala	625 ± 45	596 ± 47	0.0130	0.91
Wildebeest	29 ± 11	5601 ± 701	5.7273	0.02*
Giraffe	92 ± 7	97 ± 9	1.5714	0.21
Kongoni	352 ± 29	521 ± 51	4.6883	0.03*
Eland	62 ± 31	160 ± 18	4.6883	0.03*
Warthog	122 ± 31	82 ± 14	0.3267	0.57
Zebra	91 ± 46	2446 ± 113	5.7273	0.02*
Buffalo	220 ± 56	164 ± 36	1.5714	0.21

* Significant at $p \leq 0.05$

5.4.1 Comparisons of proportion of animals using the park

Based on the ground and aerial counts, a larger proportion of animals used the park in the dry compared to the wet season (table 5.3 & 5.4). Over half of the wildebeest population (52.35%) moved into the park in the dry season compared with only 0.31% in the wet season. Only 17.55% of zebra used the park in the dry season. Eland was the only other species that displayed large variation in the seasonal park to plains ratios. Of the total wildlife in the ecosystem, only 3.61% used the park in the dry season compared to 24% in the wet.

Aerial counts underestimated the numbers of both buffalo and warthog. In the wet season for example, the ecosystem's average (including NNP) based on aerial counts was lower than the population of NNP (table 5.3). This is of course not possible since NNP is contained within the Athi-Kapiti ecosystem. What this does show is that the ground counts gave better population estimates for these 2 species than the aerial counts. Both species are confined to the park; warthog are small and difficult to count and buffalo tend to move in large groups and the problems of clumping may affect this species. Both are confined to the park where their numbers were constant seasonally. The ground counts

gave a better estimate of their population.

Table 5.3 Average percentage of wildlife in the ecosystem occurring in the park in the wet season.

Species	Mean Number		% ratio park/plains
	NNP n=3	Athi-Kapiti n=3	
Wildebeest	29 ± 11	9373 ± 1934	0.31
Zebra	91 ± 46	16173 ± 3877	0.56
Thomson's gazelle	147 ± 50	5125 ± 1163	2.87
Kongoni	352 ± 29	6441 ± 424	5.46
Impala	625 ± 45	5746 ± 1021	10.88
Grant's gazelle	98 ± 32	7922 ± 2212	1.24
Giraffe	92 ± 7	649 ± 138	14.18
Eland	62 ± 31	967 ± 322	6.41
Warthog	122 ± 51	83 ± 29	*
Ostrich	136 ± 17	2208 ± 289	6.15
Buffalo	220 ± 56	68 ± 32	*

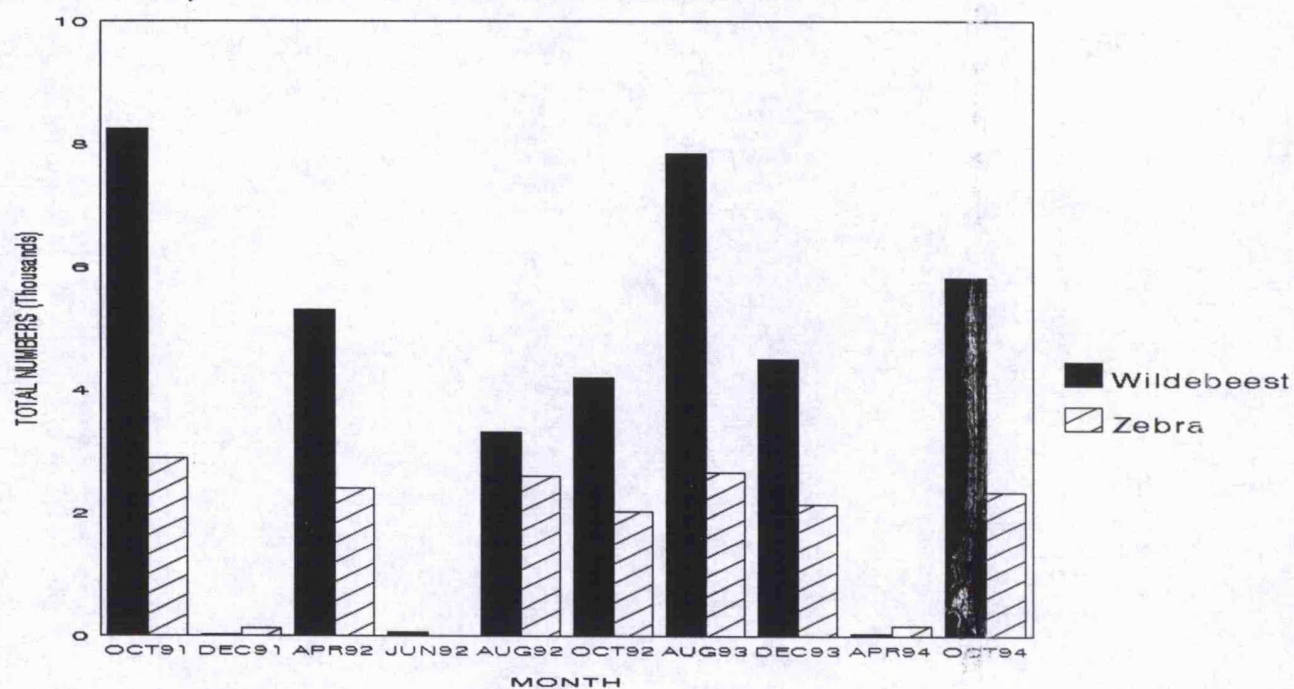
* error in aerial counts makes percentage too unrealistic to count

Table 5.4 Average percentage of the ecosystem totals occurring in the park in the dry season.

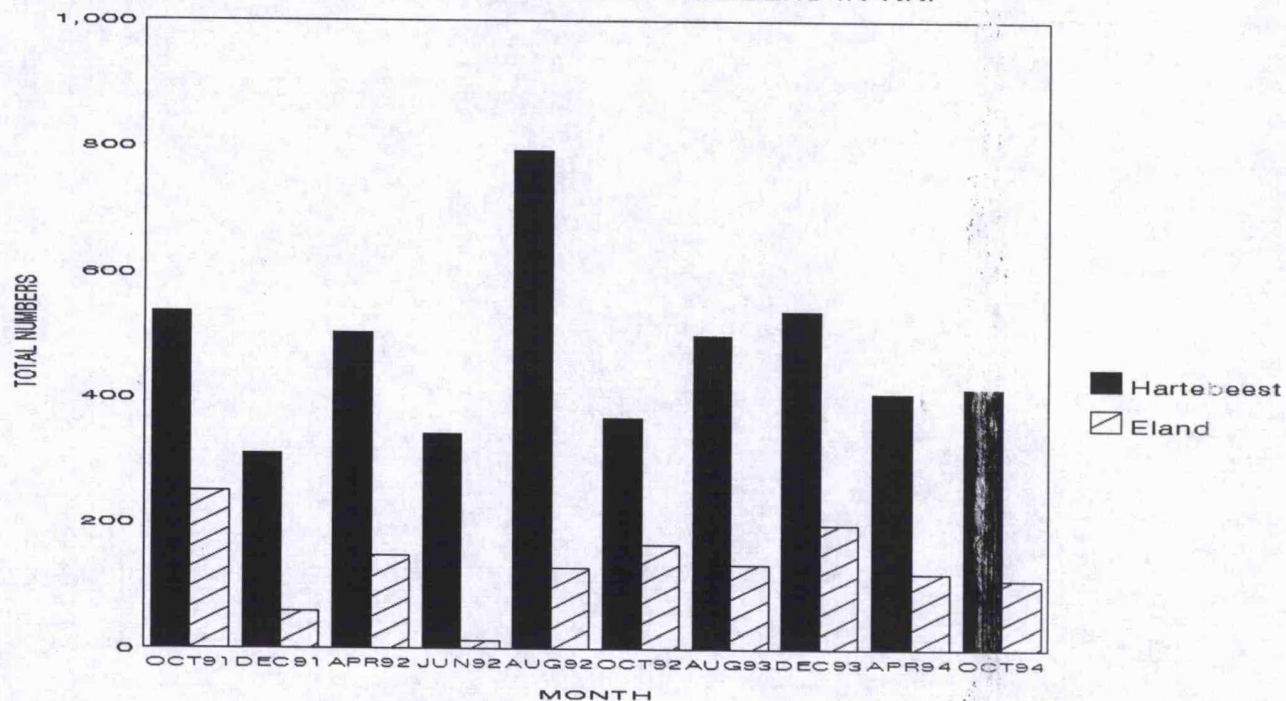
Species	Mean Number		% ratio park/plains
	Nairobi Park n=7	Athi-Kapiti n=3	
Wildebeest	5601 ± 701	10699 ± 3165	52.35
Zebra	2446 ± 113	13937 ± 923	17.55
Thomson's gazelle	97 ± 12	1766 ± 610	5.43
Kongoni	521 ± 51	4519 ± 722	11.53
Impala	596 ± 47	2712 ± 280	21.97
Grant's gazelle	129 ± 15	4752 ± 1493	2.72
Giraffe	97 ± 9	544 ± 80	17.83
Eland	160 ± 18	524 ± 152	30.59
Warthog	82 ± 14	115 ± 37	70.98*
Ostrich	220 ± 13	2330 ± 960	9.45
Buffalo	184 ± 36	290 ± 182	63.52*

* error in aerial counts, in reality 100% of the population is found within the park (pers. obs.)

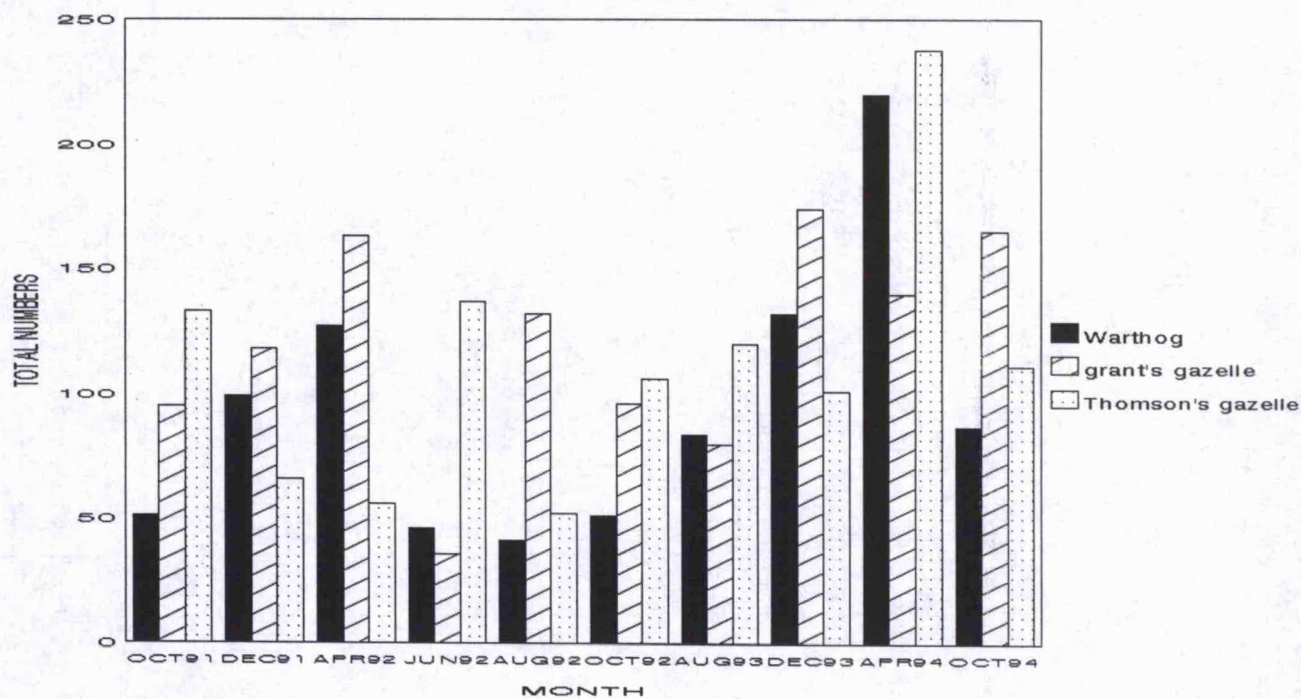
FIG 5.13
a) WILDEBEEST AND ZEBRA NUMBERS IN NNP



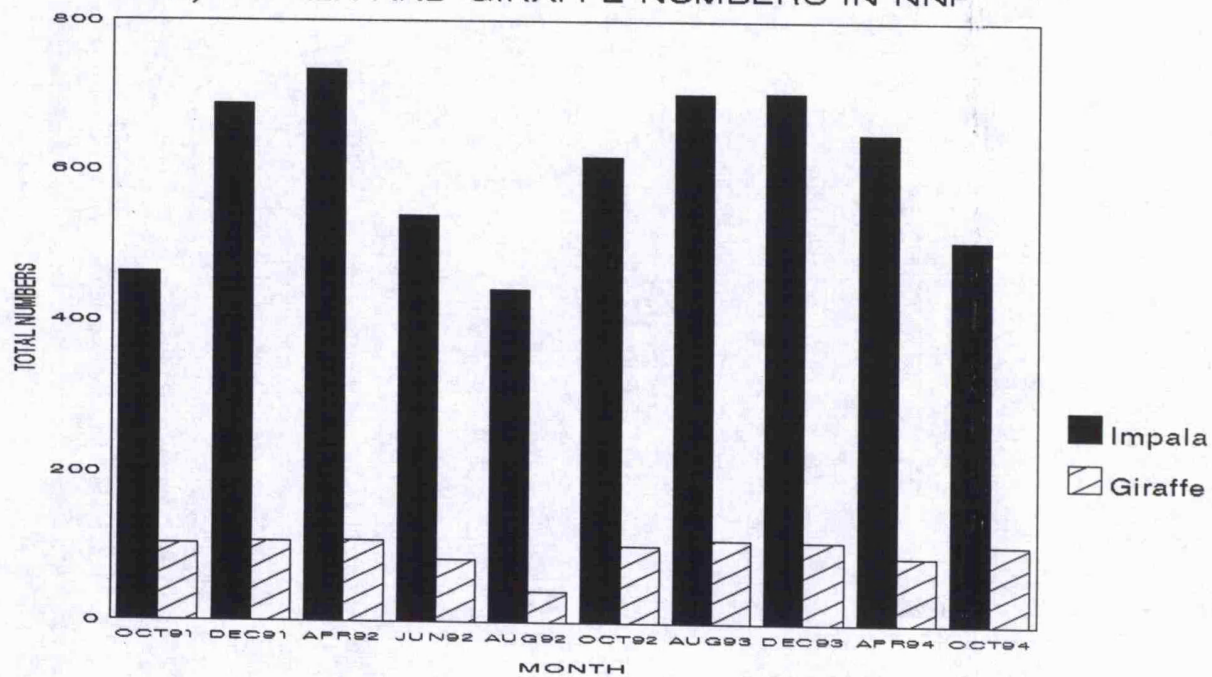
b) HARTEBEEST AND ELAND NUMBERS IN NNP



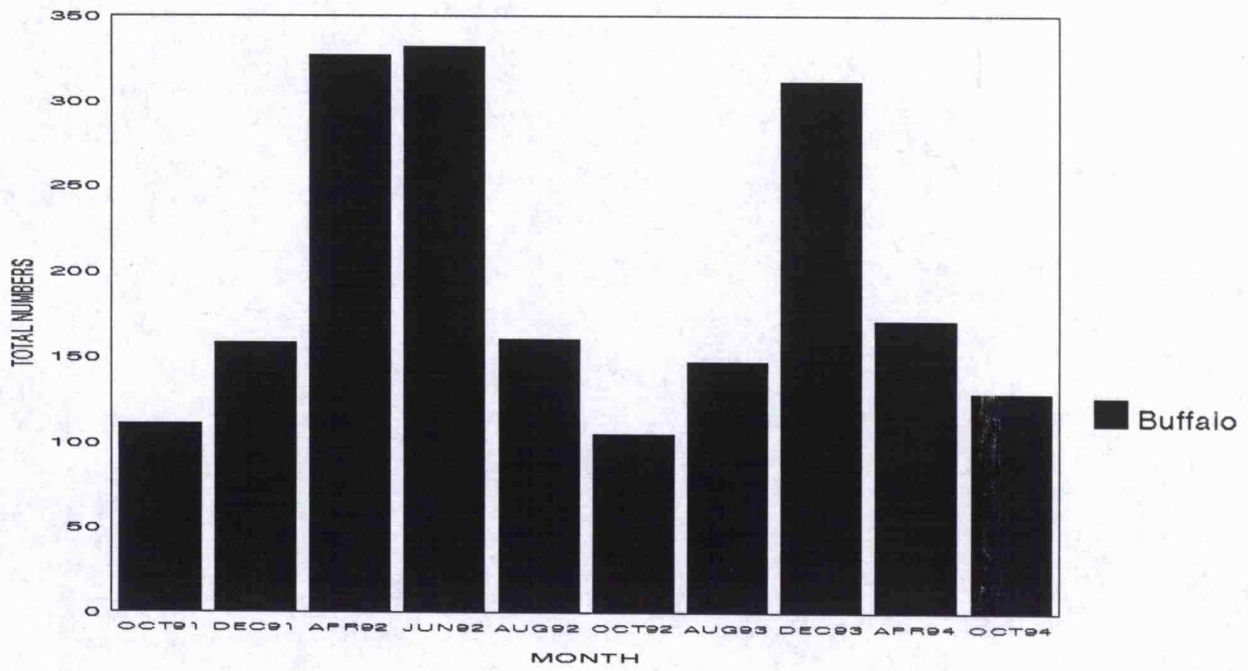
c) WARTHOG, GRANT'S AND THOMSON'S GAZELLE NUMBERS IN NNP



d) IMPALA AND GIRAFFE NUMBERS IN NNP



e) BUFFALO



5.5 Dung counting to estimate relative occupance patterns

5.5.1 Seasonal patterns in occupance over the Athi-Kapiti plains.

Herbivore distribution from dung deposition was similar to that detected by the aerial counts though the dung counts were on a finer and more localised scale. Animals could be grouped into categories of species that had obvious and distinct seasonal selection patterns such as wildebeest and zebra, those with less defined movements patterns and those that seemed to use the same areas over time. Wildebeest and zebra displayed the largest changes in occupance followed by hartebeest and eland on a smaller scale.

5.5.2 Wildebeest

Most wet season use by wildebeest was confined to the open plains to the south east of the ecosystem, around plot 10 (Fig. 5.14a). An average of 73.31 dung piles were counted in this plot. All other plots had lower occupance. The definite selection for these plains could be explained partly by vegetation quality (chapter 4), but that alone is not sufficient as other high quality plots such as 1, 12 and 13 were not selected in the same way. Plots 1, 8 and 13 were moderately used.

In the dry season, wildebeest concentrations shifted from plot 10 to 16 and 17 in the park (Fig. 5.14b). Average occupance increased from 4.13 and 1.94 respectively in plots 16 & 17 in the wet season to 50.88 and 68.92 in the two plots in the dry. Again the migrations were confirmed from these data. Plots 6, 11, 12 and 13 were moderately used during the dry season. Vegetation on plots 6 and 11 was of poorer quality than on plots 12 and 13. There was little wildebeest dung on plot 10 in the dry season, a dramatic change from wet season conditions.

Analysis of average dung over time showed shifts in habitat use patterns. During the early part of the study, for example, wildebeest dung was sampled in the western part of the ecosystem in plot 1. The average count in February was 5.37. By June 1992 however, the species did not occur in that part of the study area (Fig. 5.15).

5.5.3 Zebra

Zebra dung was abundant and the species most widespread of the wild herbivores in its ranging patterns. They were well distributed over the plains (Fig. 5.16a). Plot 4, located on a high altitude area bordering the escarpment had the lowest wet season average. This area is open and dominated by very short grasses. Very few wild herbivores used this plot though it was heavily used by sheep and goats (see Fig. 5.23 a & b).

The dry season use was also widespread, but there were areas of definite concentration. The highest dung counts were on plots 17 in the park followed by plots 1, 2, 5, 13 and 16 (Fig. 5.16b).

5.5.4 Coke's hartebeest

This species preferentially used plots 1, 8, 12 and 17. Plot 12 had large herds throughout the year (Fig. 5.17 a & b). Again, the selection was difficult to explain on the basis of nutritional requirements alone. Plots 1 and 12 had low biomass, high quality vegetation while 8 and 17 were areas of coarse grass. The one possible explanation for selection of plots 1, 12 and 8 on the plains may be the relative absence of settlement around these sites. Plot 8 for example is in an open area of black cotton soil where rain water sometimes accumulates during very wet years, perhaps a deterrent to construction of houses. Here, vegetation is coarse and of low quality, very unlike plots 1 and 12. Plot 12 is also very open and until very recently (about the middle of 1994) was totally devoid of settlement, most being confined on the eastern side of the Nairobi/Namanga road and northwest at the Athi river and Kitengela townships.

Dry season occupancy remained relatively similar though plots 1 and 12 were used more and plot 8 less. Use of plot 17 did not change.

5.5.5 Gazelle species

Thomson's gazelle seemed to have well defined habitat occupancy patterns (Fig. 5.18a) and were generally widespread outside the park. Plots 1, 10 and 12 had the largest numbers of dung piles counted. These three plots also had very high quality vegetation in the wet season (see chapter 4) which may explain this preference. The dry and wet season patterns were very similar. Occupancy peaks occurred in the same plots i.e. 1, 10 and 12 (Fig. 5.18b).

Grant's gazelle occupancy patterns were similar, though their use of plots 1, 10 and 12 was marginally higher (Fig. 5.19 a & b).

5.5.6 Buffalo

During the wet season, grass was tall and buffaloes ranged widely. Plots 16 and 17 were used more in the wet than dry season (Fig. 5.20 a & b). In the dry season when migrants returned from the plains outside the species seemed to have retreated to swamp edge habitat, forest glades and forest edge, all tall grass habitat (see block map for NNP).

5.5.7 Browsers

The distributions of the major browsing species; giraffe and impala are directly associated with the presence of woody vegetation, although on occasions, their dung was noted in open grass areas close to woodlands. Giraffe were common on plots 1, 2, 6, 3, 15 and 16 (Fig. 5.21 a & b). Plots 1, 2, 6 and 16 are *Acacia drepanolobium* woodland plots while 3, 15 and 10 have woodlands close by. Dung was counted in plots 4 where few *Acacia xanthophloea* and *A. tortilis* trees occurred in surrounding valleys. Giraffes may have defecated on this plot as they moved between the tree stands located on both sides of the plot.

Impala dung was found on plots 10, 11, 12 and 13 (Fig. 5.22 a & b) plots with, or surrounded by, large patches of *Acacia drepanolobium* woodlands.

5.5.7 Livestock

5.5.7.1 Sheep and Goats

Evidence of occupancy was found in a wide range of habitats across the ecosystem except plots 15, 16 and 17. Seasonal distribution patterns showed extensive use of plots 4 at Oloyiungalani and 14 at Naiserian (Fig. 5.23 a & b).

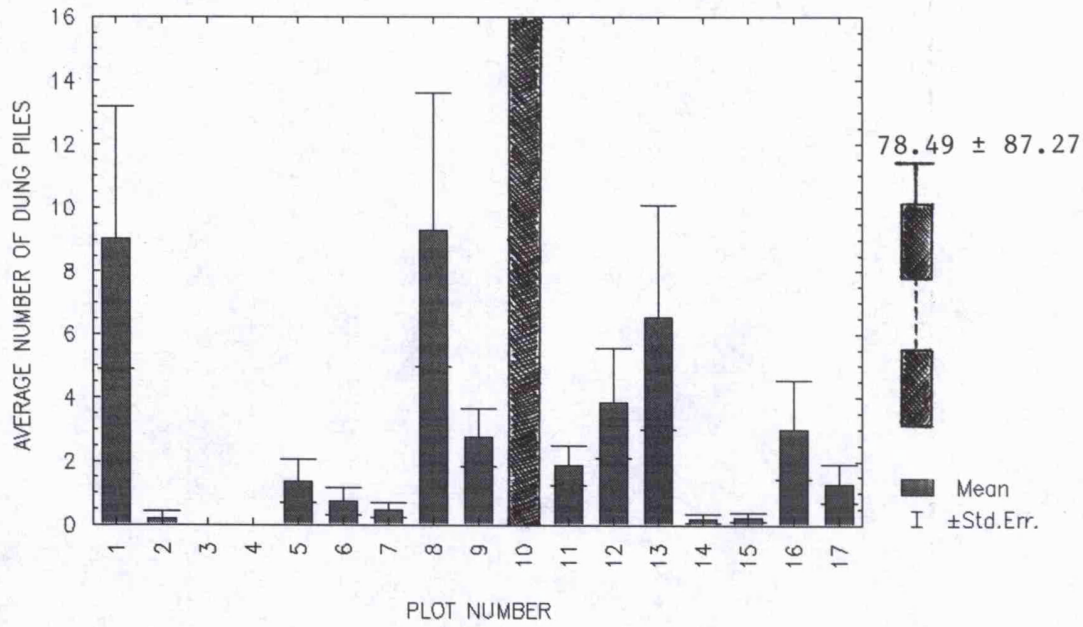
5.5.7.2. Cattle

Their distribution was as extensive as that of 'shoats' but they occurred in most of the ecosystem. Their dry and wet season use patterns were not too varied though use of plots 1 and 2 declined in the dry season while that of plots 8, 5 and 15 increased (Fig. 5.24 a & b). Pasture in these plots was normally depleted by wildlife which crowded here during the dry season. Many Maasai families usually responded by moving their cattle to better pasture, as they did during the drought of 1993.

Fig 5.14

TRENDS IN WILDEBEEST OCCUPANCE ACROSS PLOTS IN THE ATHI-KAPITI PLAINS

A) WET SEASON (n=12). LINE FOR PLOT 10 GOES TO A MAXIMUM OF 78 DUNG PILES. THIS IS NOT DRAWN TO SCALE



B) DRY SEASON (n=36)

LINE FOR PLOT 17 GOES TO A MAXIMUM OF 69 DUNG PILES. THIS IS NOT DRAWN TO SCALE

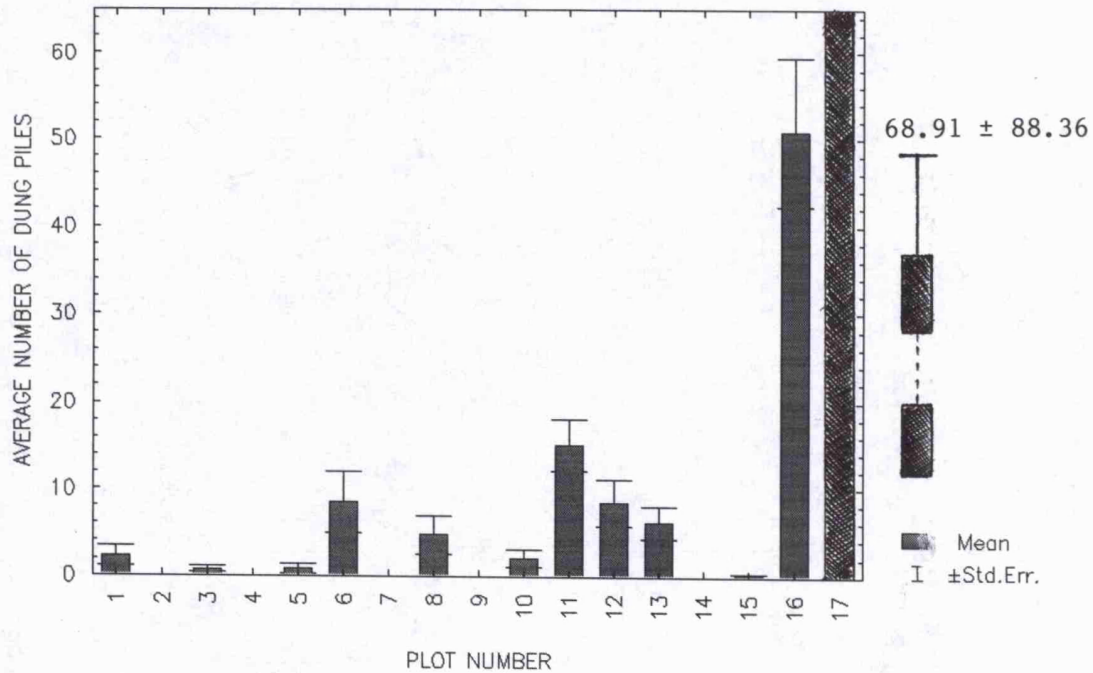


FIG 5.15
TRENDS IN WILDEBEESTE OCCUPANCE OVER TIME
FOR PLOTS 1 - 5 IN THE ATHI-KAPITI PLAINS

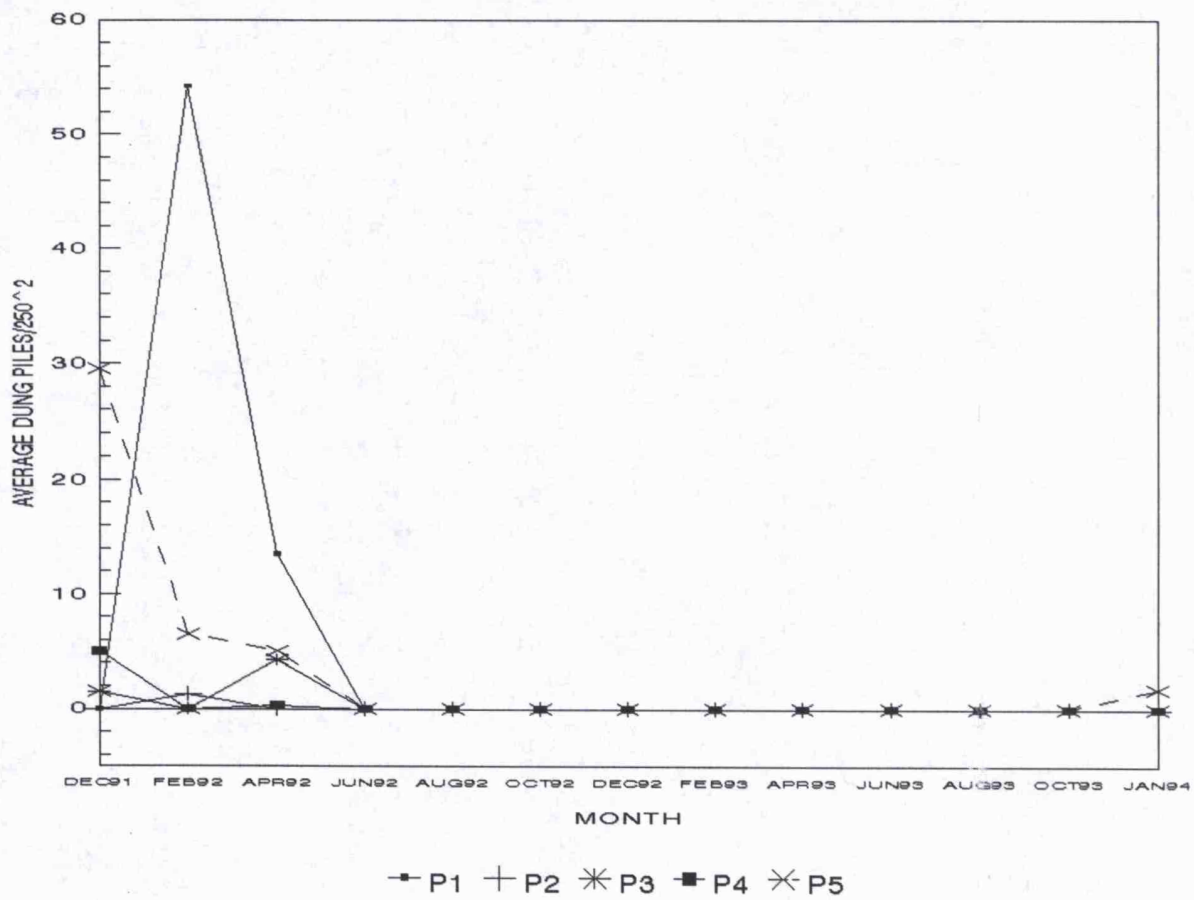
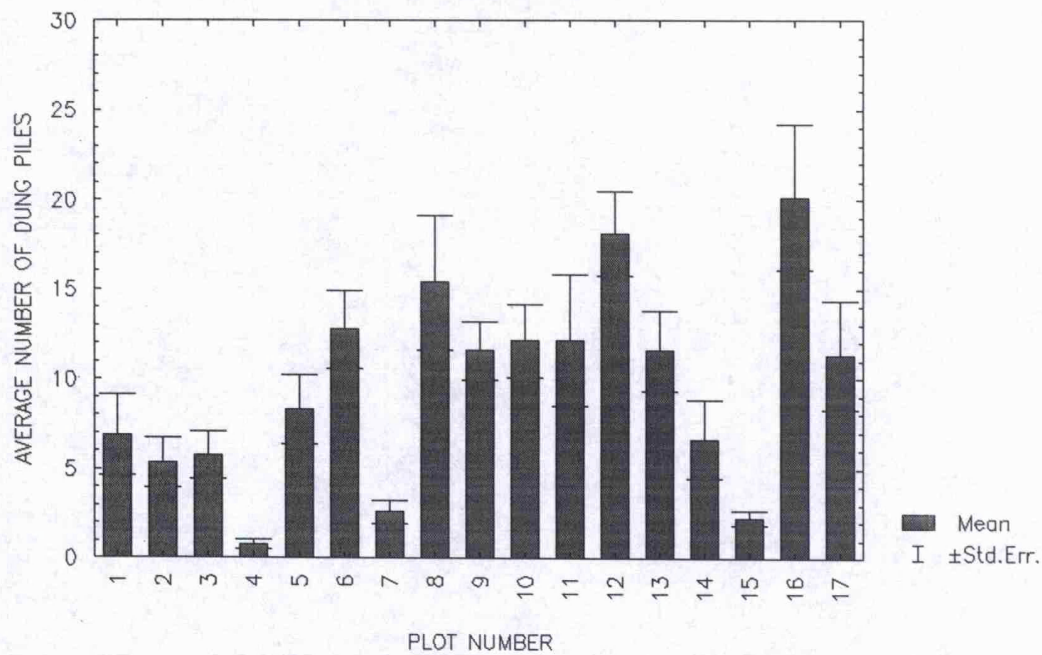


FIG 5.16
TRENDS IN ZEBRA OCCUPANCE ACROSS PLOTS
IN THE ATHI-KAPITI PLAINS
A) WET SEASON (n=12)



B) DRY SEASON (n=36)

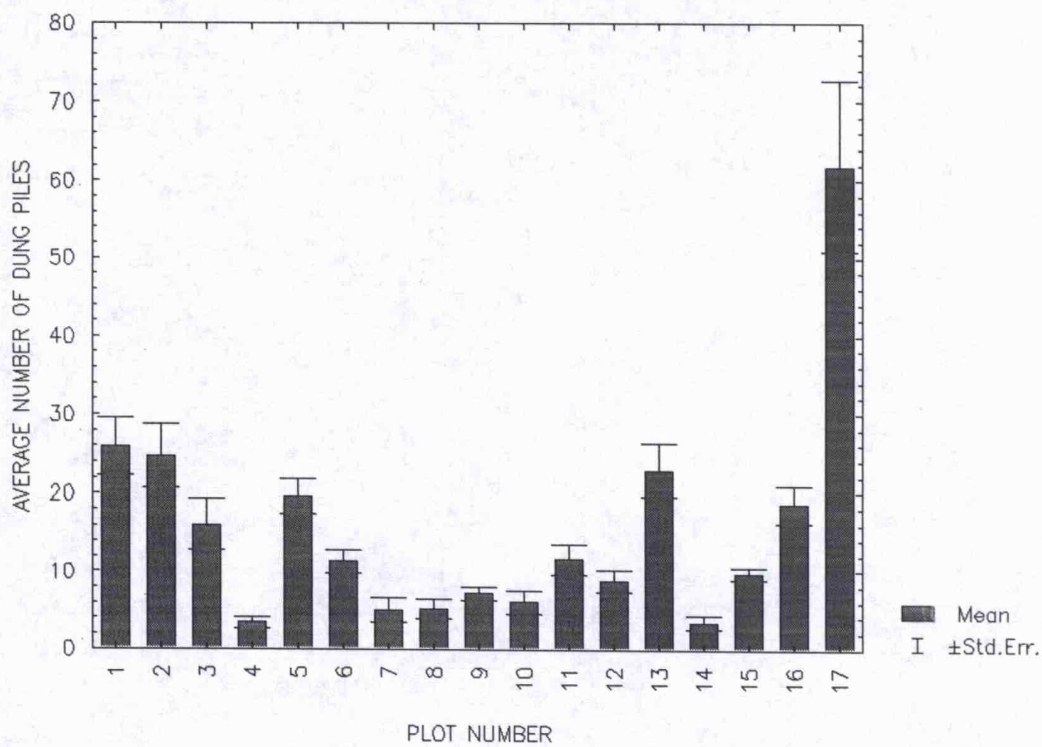
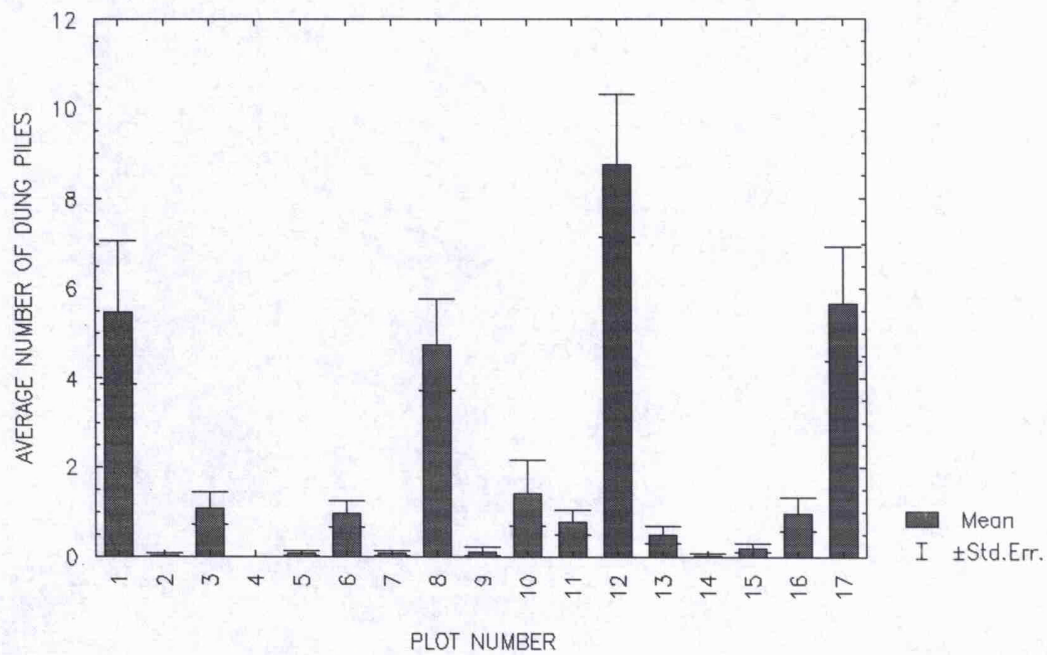


FIG 5.17
TRENDS IN COKE'S HARTEBEEST OCCUPANCE ACROSS PLOTS
IN THE ATHI-KAPITI PLAINS
A) WET SEASON (n=12)



B) DRY SEASON (n=36)

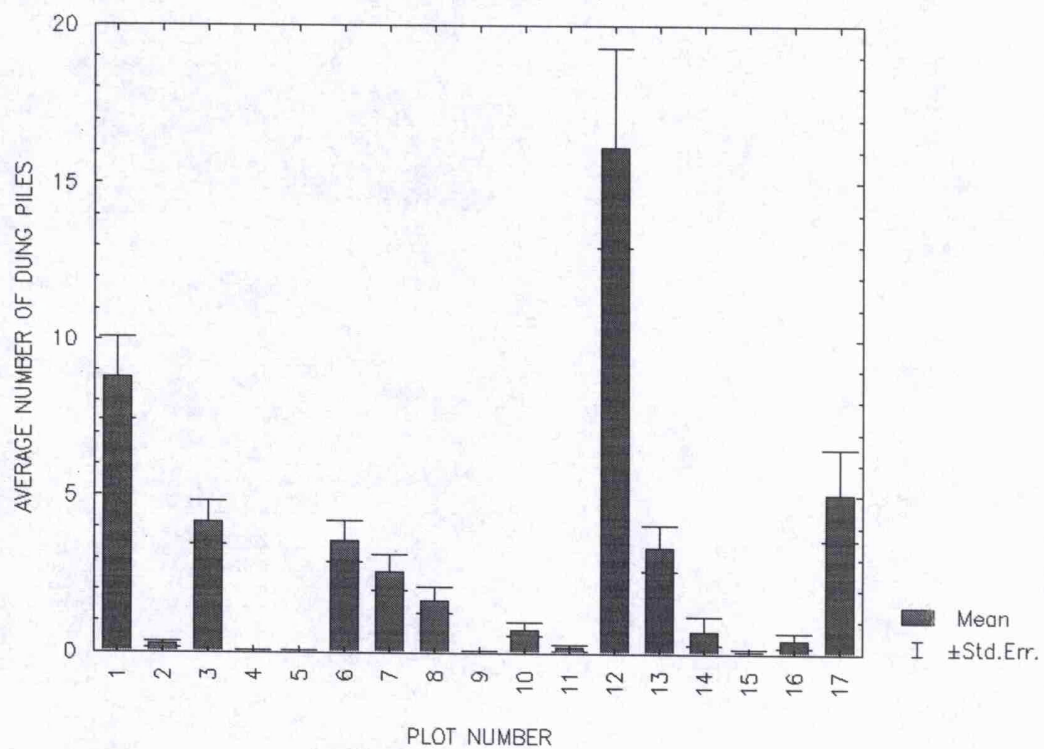
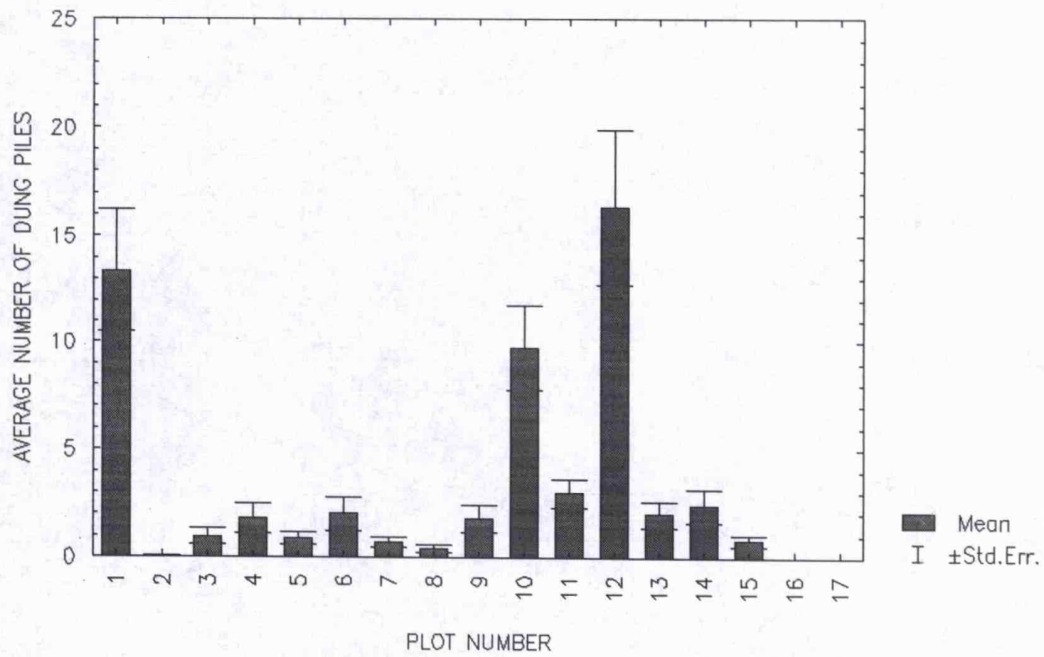


FIG 5.18
TRENDS IN THOMSON'S GAZELLE OCCUPANCE ACROSS PLOTS
IN THE ATHI-KAPITI PLAINS
A) WET SEASON (n=12)



B) DRY SEASON (n=36)

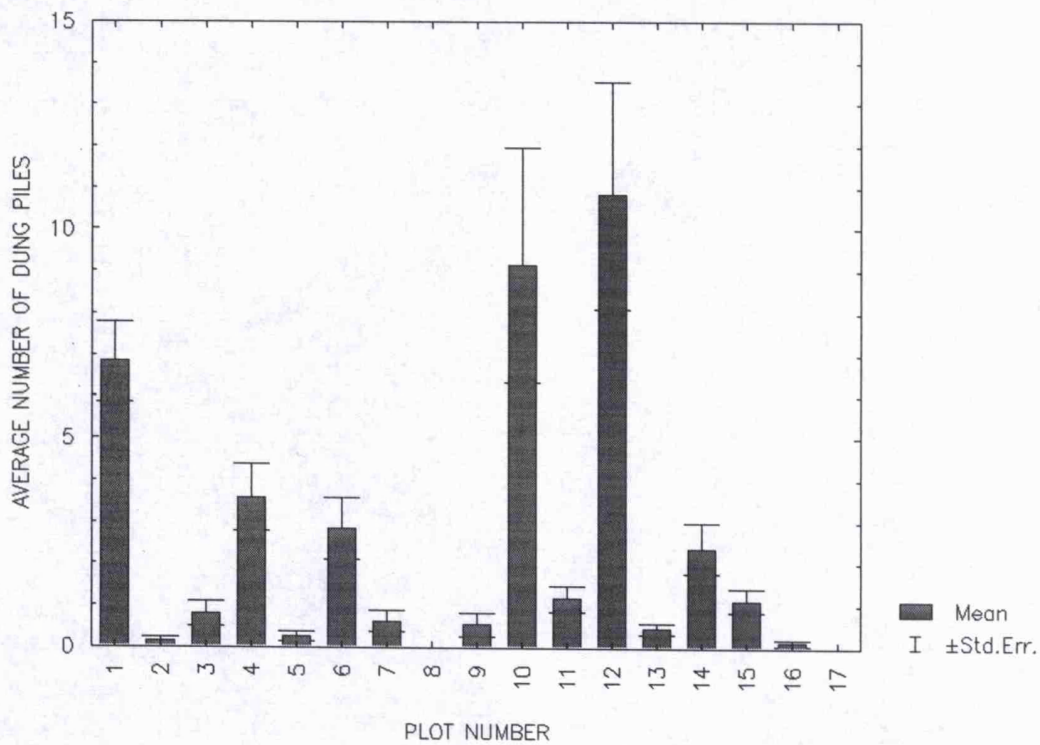
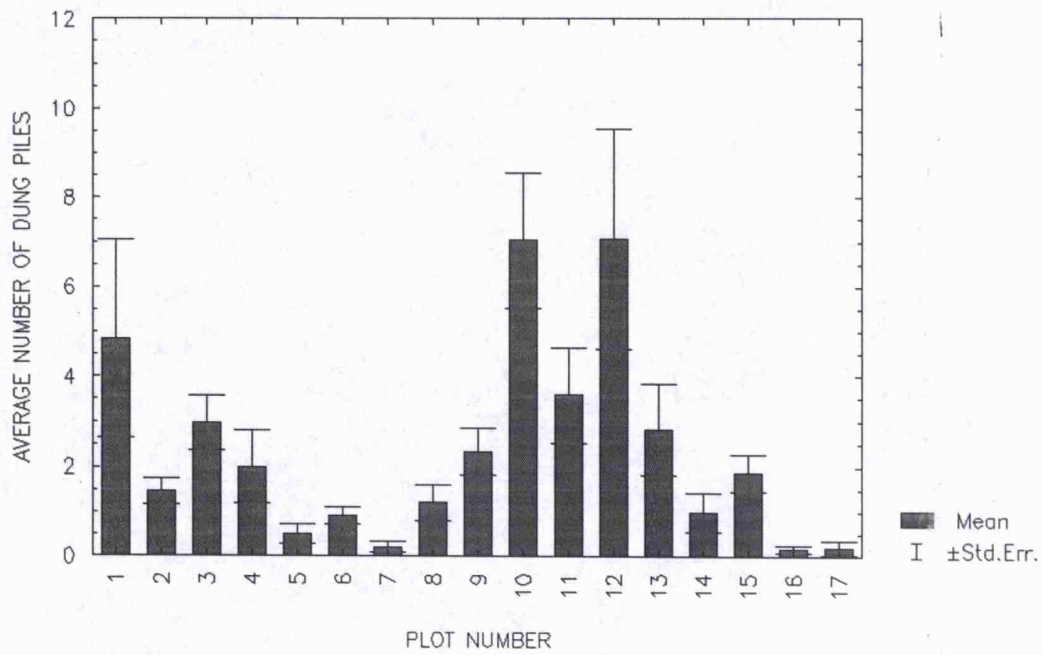


FIG 5.19
TREND IN GRANT'S GAZELLE OCCUPANCE ACROSS PLOTS
IN THE ATHI-KAPITI PLAINS
A) WET SEASON (n=12)



B) DRY SEASON (n=36)

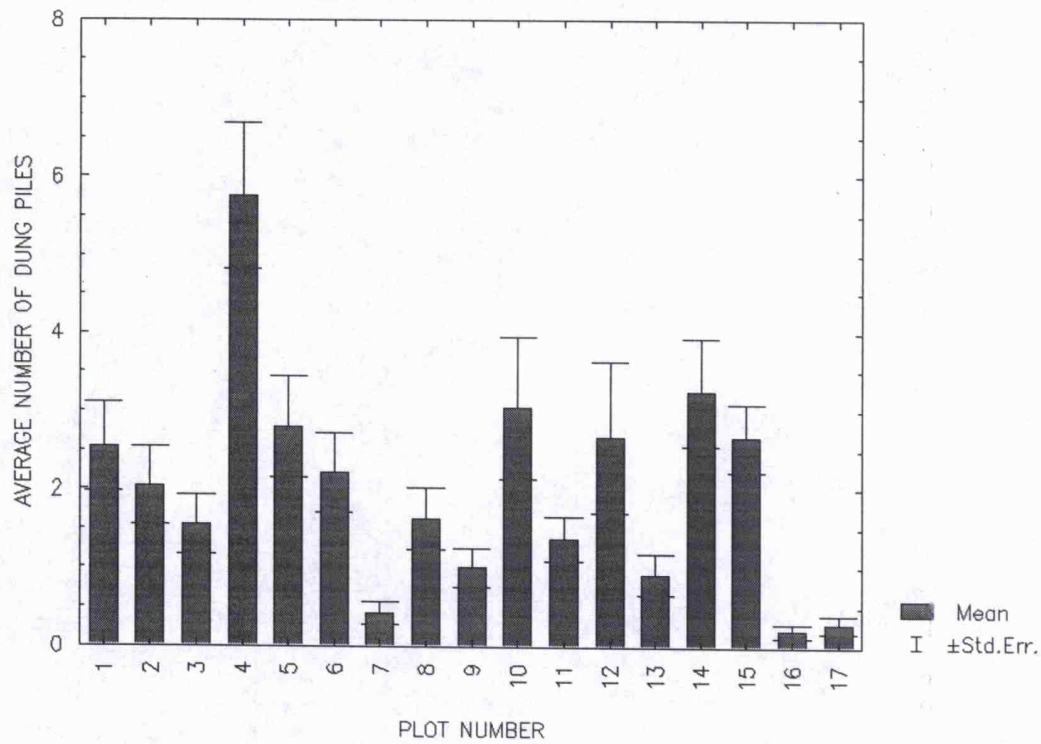
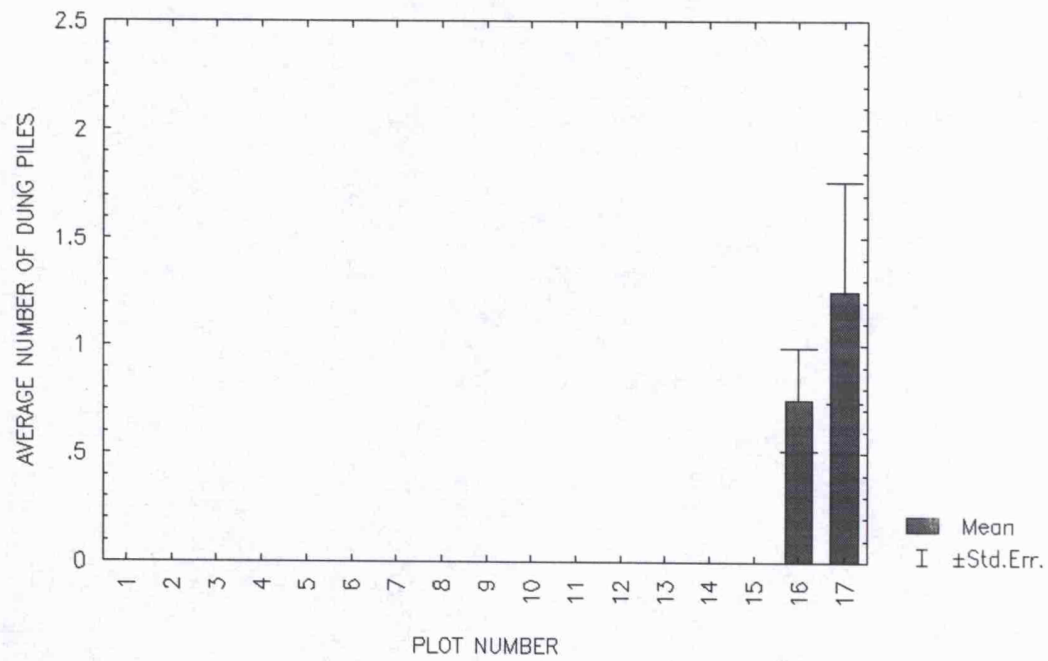


FIG 5.20
TRENDS IN BUFFALO OCCUPANCE ACROSS PLOTS
IN THE ATHI-KAPITI PLAINS
A) WET SEASON (n=12)



B) DRY SEASON (n=36)

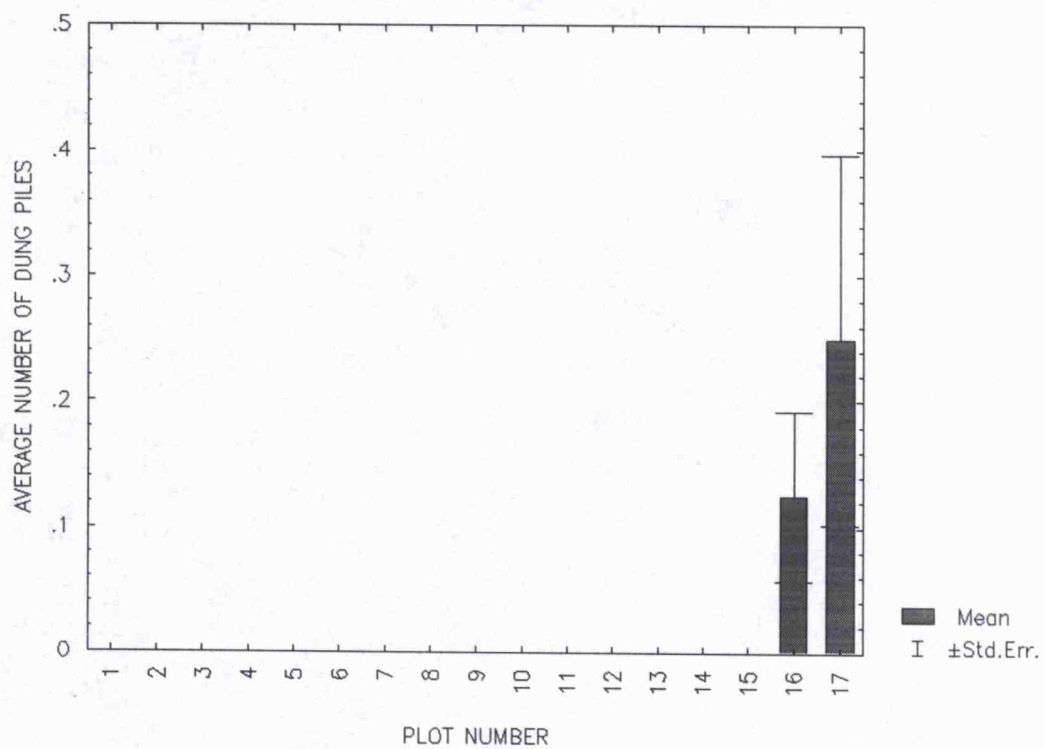
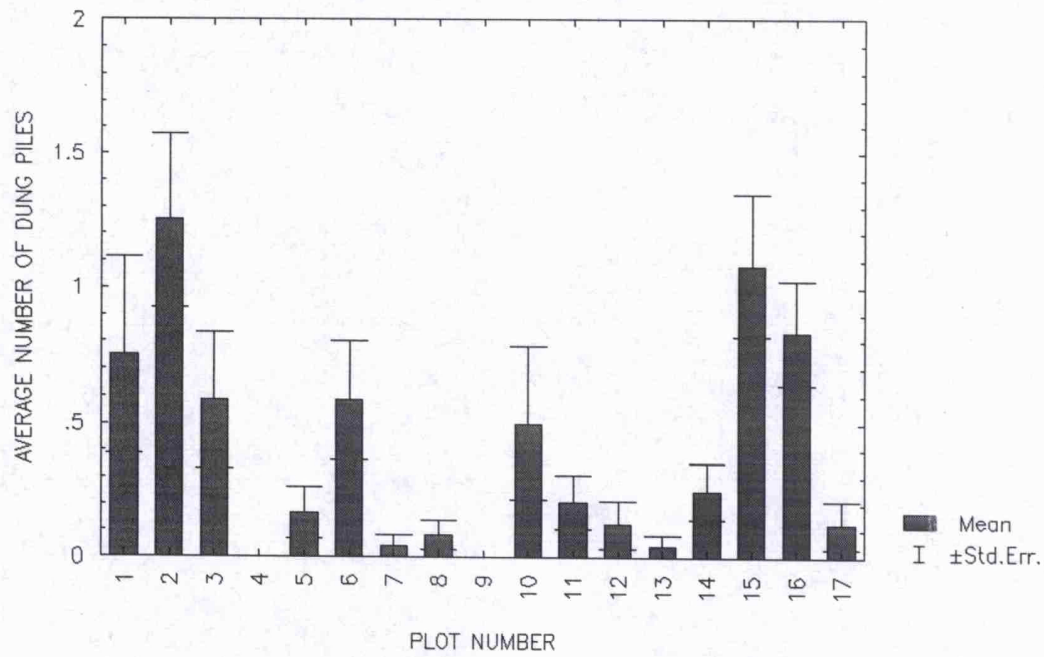


FIG 5.21
TRENDS IN GIRAFFE OCCUPANCE ACROSS PLOTS
IN THE ATHI-KAPITI PLAINS
A) WET SEASON (n=12)



B) DRY SEASON (n=36)

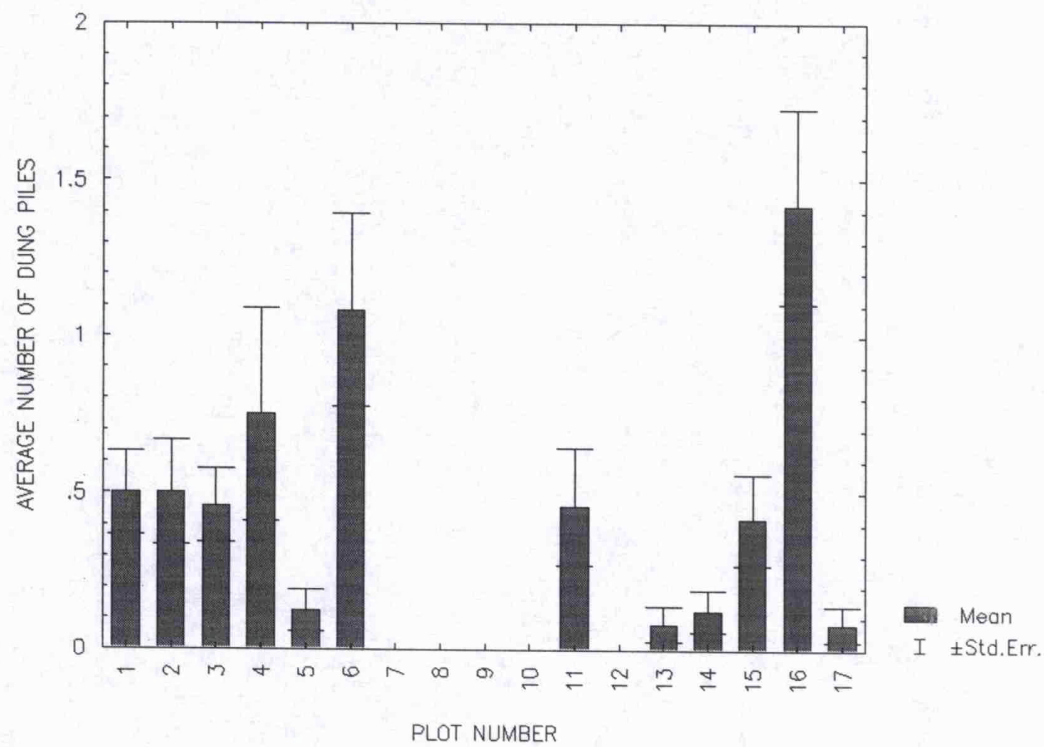
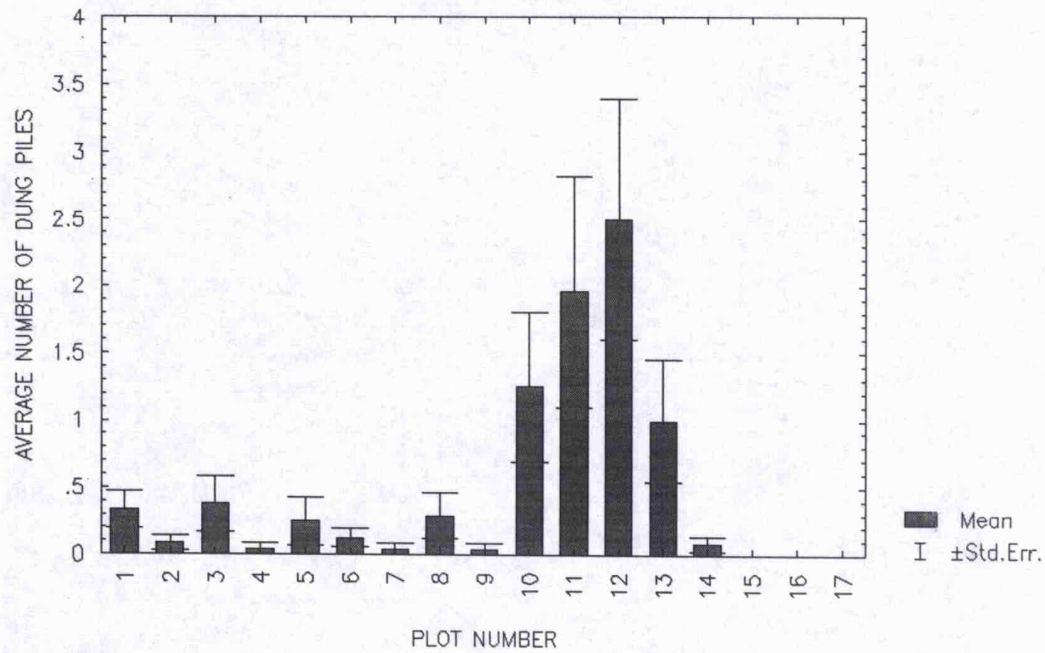


FIG 5.22
TRENDS IN IMPALA OCCUPANCE ACROSS PLOTS
IN THE ATHI-KAPITI PLAINS
A) WET SEASON (n=12)



B) DRY SEASON (n=36)

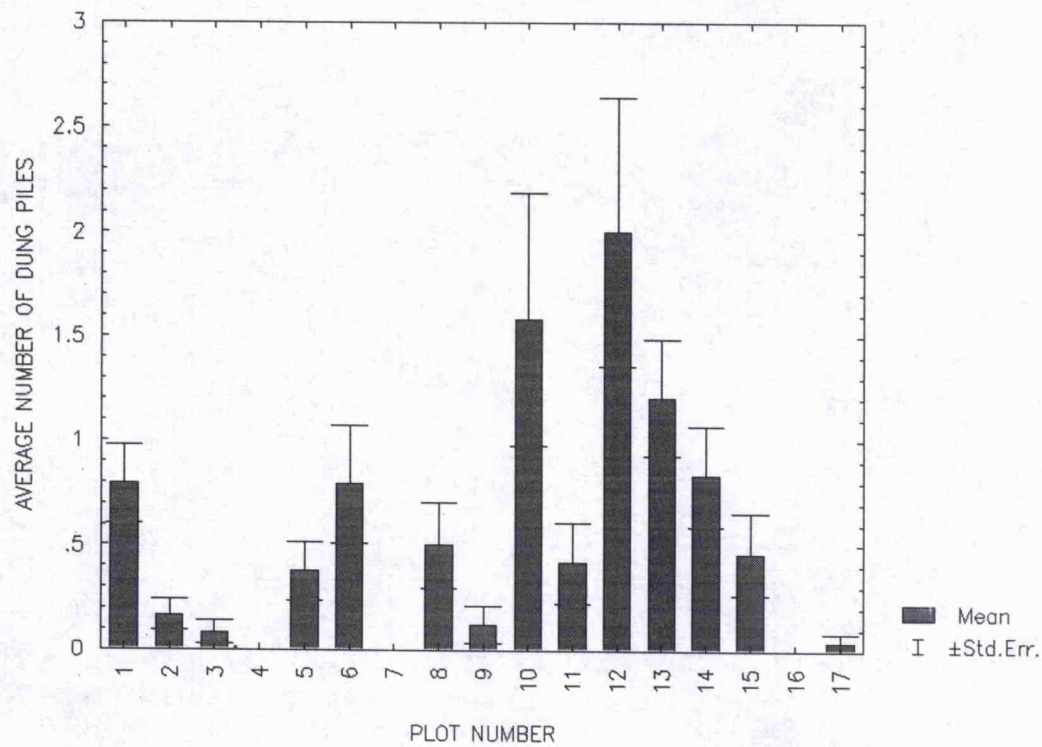
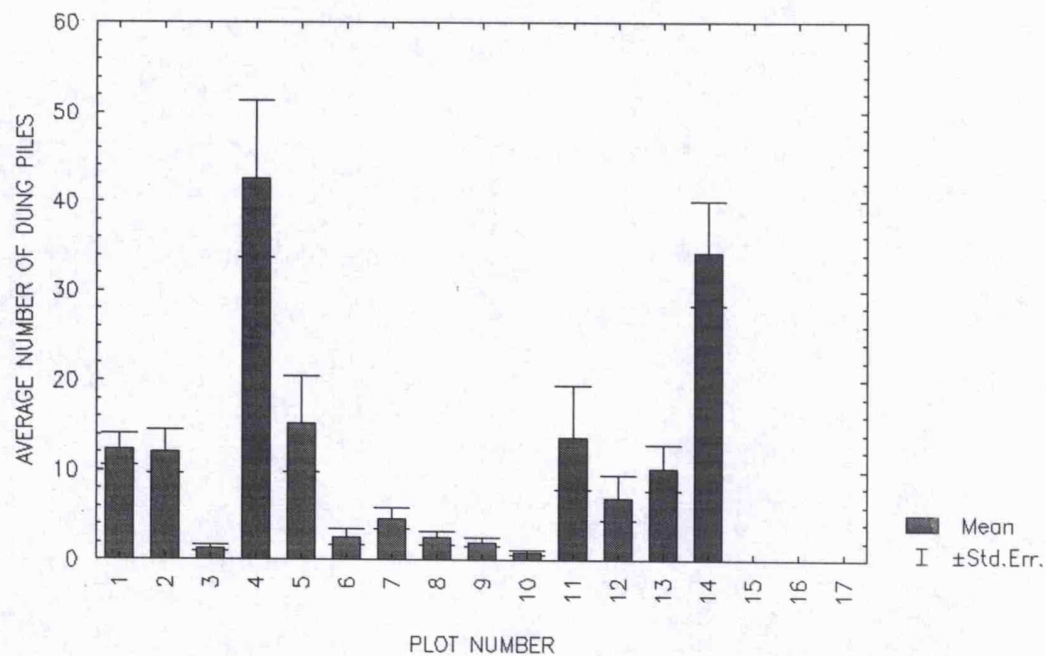


FIG 5.23
TRENDS IN 'SHOAT' OCCUPANCE ACROSS PLOTS
IN THE ATHI-KAPITI PLAINS
A) WET SEASON (n=12)



B) DRY SEASON

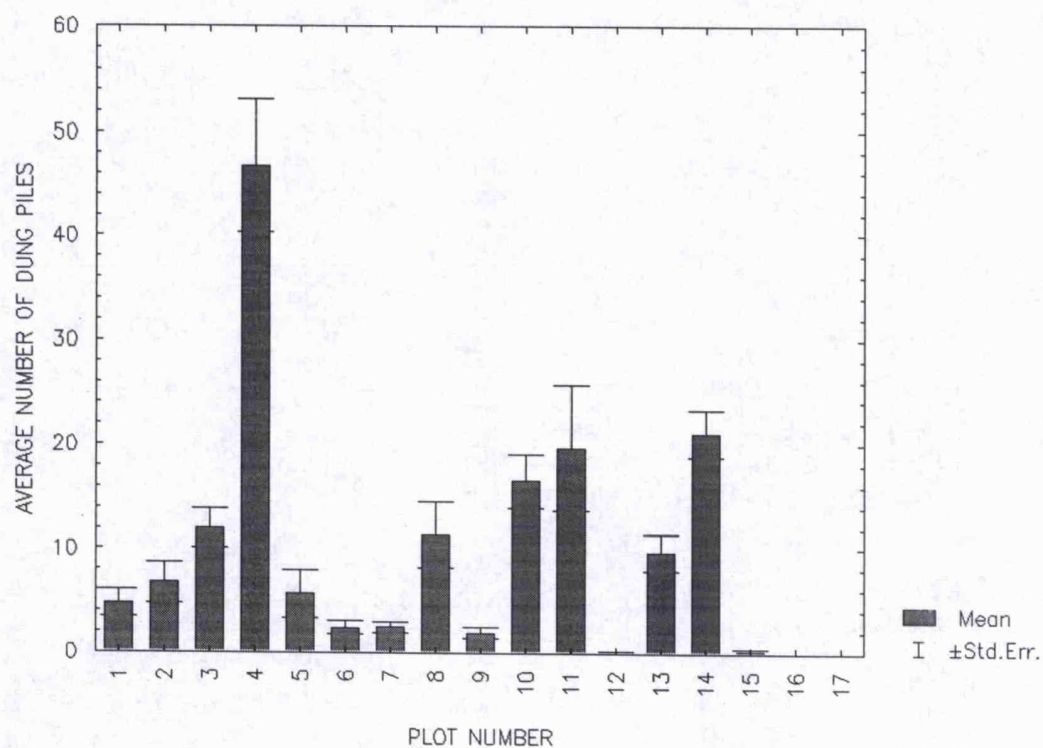
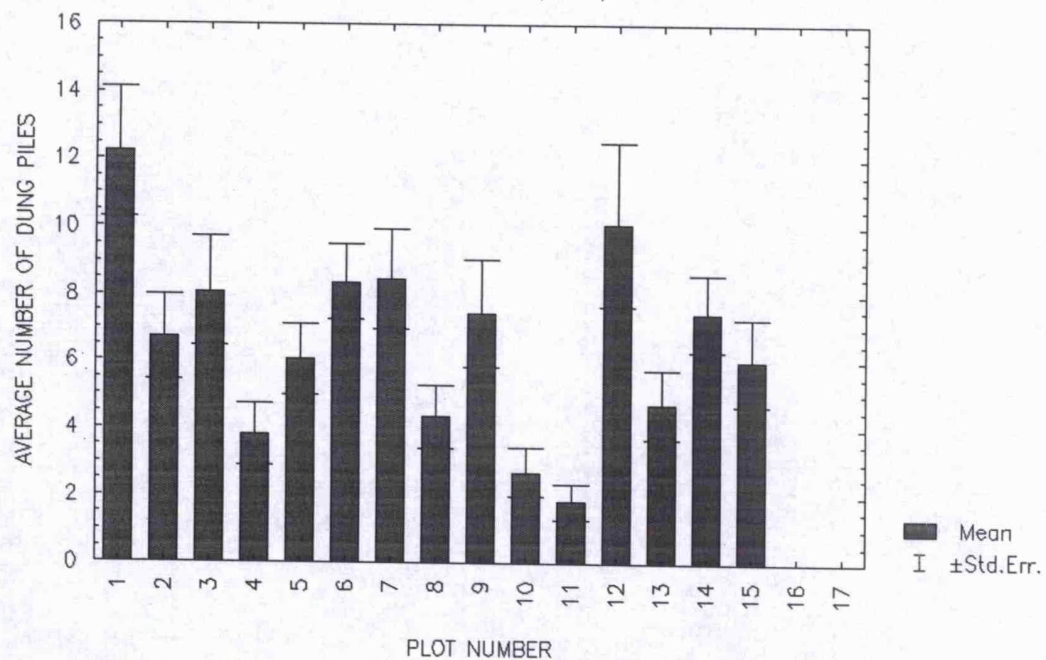
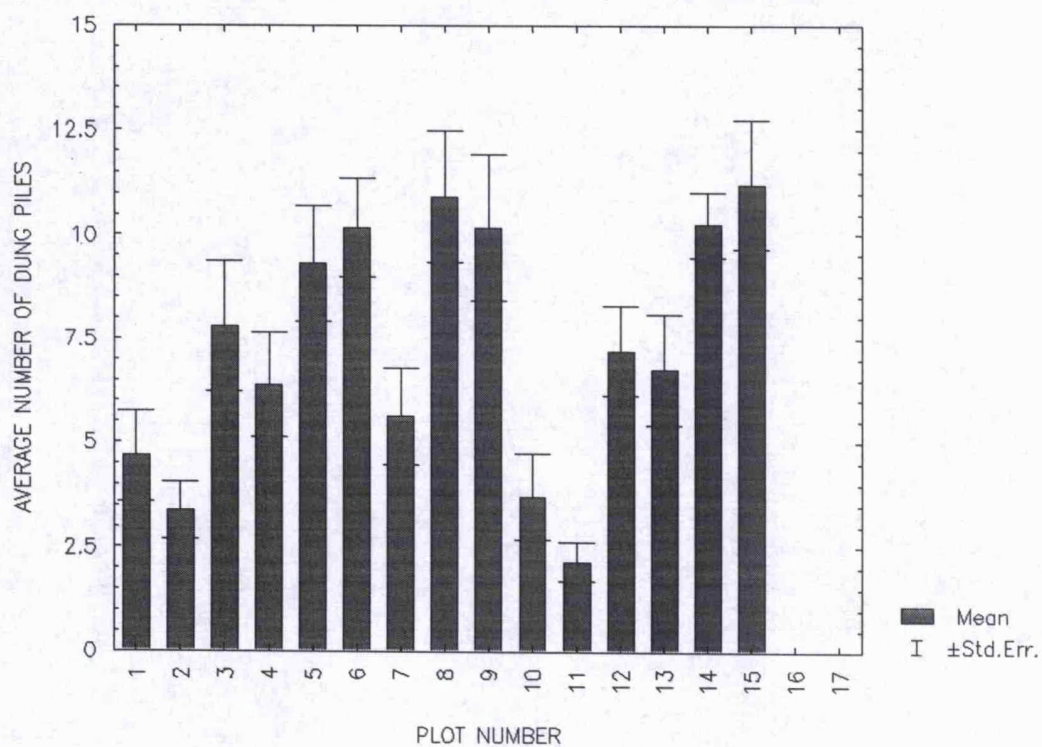


FIG 5.24
TRENDS IN CATTLE OCCUPANCE ACROSS PLOTS
IN THE ATHI-KAPITI PLAINS
A) WET SEASON (n=12)



B) DRY SEASON (n=36)



5.6 Interpretation

The Athi-Kapiti ecosystem is dominated by livestock but also has a large number of wild herbivores. Of the wild ungulates, wildebeest and zebra are the most numerous and constitute over half of the total wildlife population. The ecology of the park and plains is inextricably linked by the movement patterns of the migratory species. The migrations of wildebeest and zebra are large scale and conspicuous while those of eland and perhaps Coke's hartebeest are not obvious. The seasonal changes of eland and Coke's hartebeest though small were significant enough to suggest such movements. The non migrating species on the other hand displayed local shifts in distribution within the plains.

Aerial surveys showed definite movements and distribution patterns governed by seasonal climatic changes. During most years there were double movement cycles in and out of the park corresponding with the short and long rains. Outward movements for wildebeest were triggered by the rains and the return migrations by dry weather conditions (Fig. 4.20). Wildebeest filed towards the Athi basin crossing, the most fordable and open of the migration routes and other smaller routes as the rain clouds gathered and the first showers fell. The rainy season heralded a period of abundance when vegetation recovered from previous dry conditions and water resources became widely available. Migrants moved from their dry season range to the wet season dispersal areas. As the dry season progressed, water resources began to dwindle, vegetation growth stopped and senescence set in. For the water-dependant species such as wildebeest (Western, 1975) water began to become limiting. Animals had therefore to move to areas where water was readily available and food more plentiful. For wildebeest, this resulted in north westward movements into NNP. The movements took the animals along a rainfall gradient from the drier southeastern plains to the higher rainfall and better watered areas around the Park (Fig. 4.20).

Wildebeest traditionally used the Kapiti (Kaputei) plains in the wet season, in the triangle bounded by the Athi river-Namanga road, the Athi river-Konza and Konza-Kajiado railway line; in the sixties this was still the case (Peterson and Casebeer, 1972). Current distribution within this triangle in the wet season was very distinct but wildebeest use was confined mainly to the south on short open grasslands near the Konza-Kajiado railway line and around the Enkigirri school. Calving took place in this wet season range usually between March and April during the long rains. Some maasai families were forced to move their cattle to prevent them from feeding in areas where the calves had been dropped. Malignant catarrh fever (MCF), a fatal disease thought to originate from a virus associated with the wildebeests afterbirth, often kills their cows in large numbers.

Two factors may be responsible for some of these altered use patterns:

- Increased human settlement and numbers in the area making it difficult for continued use of much of the range by wildebeest due to their large numbers coupled with their herding behaviour.
- Shooting of the species for meat for police dogs. This is done in their wet season range, and increasingly the animals have come to associate vehicles with this activity. As a result they keep away from vehicle tracks and roads.

Despite these possible human-induced changes in distribution, the ecological explanation for selection of specific areas during the dry season cycles are similar to those proposed in other areas of wildebeest migration; high quality, mineral-rich vegetation (McNaughton, 1989) and the avoidance of muddy black cotton soil areas (Maddock, 1979).

Distribution maps from data by Casebeer (1969, unpublished data), Modha (1969), Casebeer (1967) and Peterson and Casebeer (1972) ranging from 1959 to 1971 however show more extensive use of areas to the south-west of the Kiserian/Isenya road in the dry season.

Unlike wildebeest, zebra were more widely distributed and in smaller groups. Zebra also converged towards the park in the dry season but on a smaller scale. Their movements were neither as conspicuous nor as spectacular as those of wildebeest partly because they were not as synchronised and far fewer individuals migrated. They also do not display herding behaviour like wildebeest. The majority of zebra remained on the plains in the dry season. Water was at this time confined to livestock troughs and pools on the Stony Athi, Senya river, Kisaju and the river valleys of many of the seasonal streams. Most of these dried up during extended dry periods. Animals that remained on the plains were therefore confined to variable distances along these points depending on each species' water requirements. Zebra were notorious for using water normally reserved for cattle in troughs and dams. Maasai hostility towards the species increased greatly with complaints that it was both depleting the resources and contaminating what little that was left.

Other species that had widespread distribution such as Grant's, Thomson's gazelles and Coke's hartebeest remained on the plains through the dry season. Stanley-Price (1974) showed that the hartebeest preferred the vegetation zones along the north and west sides of the plains. He showed that distribution patterns were different from those of migratory species in the wet season. Although there were hartebeest in the north and west, this study did not find such preference, and there was little distinction in

the range of the hartebeest and that of zebra, though the hartebeest was less widespread and occurred in smaller numbers. Stanley-Price (1974) also indicated that distribution of hartebeest was similar to that of cattle. This was also not clear from the results.

The ecological importance of NNP to the ecosystem has been questioned over the years. In the past, the park was dismissed as unimportant by arguments that the Ngong hills and its foot slopes were the key dry season areas. Other events that took place in the park in earlier years also made the park of little ecological importance. It was once a shooting range, was settled by the army and later by Somali herdsman (Cowie, 1961). Results from the old NNP game counts (Kenya National Parks unpublished reports) showed that there was little fluctuation in seasonal use of the park. As the higher rainfall areas around Ngong and Kiserian were progressively occupied by human settlement, a fence was constructed along the east, north and western boundaries and dams were constructed. The ecological importance of the park to the ecosystem increased. The present day characteristic concentrations did not begin until the severe drought of the 1973/1974. The present results show that the significance of NNP to the ecology of the Athi-Kapiti plains has increased. The park now acts as an important dry season concentration area for wildebeest and to a smaller extent zebra, eland and probably Kongoni too.

Despite this ebb and flow between the park and plains ungulate numbers in the ecosystems remained constant with the exception of cattle, impala and Thomson's gazelle which declined in the dry season. This constancy in numbers indicated one of two things, that the ecosystem is self contained and all the movements are within it, or that the variances due to the counting were so large that any movements out of the system would not have been detected.

Movement of the Maasai with their livestock out of the plains had been observed during all severe dry seasons. The moves were made in search of pasture to avoid mass mortality once grass was depleted. Many moved as far as Amboseli and areas bordering the Tsavo, others towards the Ngong hills and Nairobi city. Cattle were common around the city housing estates and open unsettled areas where grass had accumulated from lack of use.

In general, the Nairobi park ground counts, the aerial counts as well as the dung pellet counts all confirmed the seasonal distribution and use patterns. They also confirmed that some species preferred certain areas, e.g gazelles and hartebeest selected the short grassland areas both in the wet and dry season, while wildebeest selected short grass areas only in the wet season. Sheep, goats, cattle and zebra seemed less selective.

CHAPTER 6

EFFECTS OF VEGETATION IN STRUCTURING HERBIVORE COMMUNITIES

6.1 Introduction

The interaction between biotic and physical parameters in an ecosystem are important in determining large herbivore structure in an ecosystem. This chapter examines the relationship between vegetation condition and herbivore occupancy patterns in the Athi-Kapiti plains.

6.2 Grass height

Grouping of plots by grass height using Analysis of variance on wet season data produced five classes ranging from the shortest to the tallest in approximately 10cm intervals (table 6.1), ($F=131.35$, $df(4,187)$).

A one-way analysis of variance on grass height classes against herbivore occupancy by species groups for the wet season showed that the largest variation was in the distribution of small grazers and cattle. Overall, small grazers, cattle and medium-sized grazers showed distribution patterns that were height related. However occupancy along the height classes was different for each of these species groups (table 6.2).

The highest occupancy for small grazers occurred in grass height 1, the shortest grasses. Their occupancy declined progressively and inversely to grass height (Fig. 6.1a). As height increased the presence of small grazers declined to zero in the tallest grasses in the park. These differences in occupancy were significantly different (table 6.2). The shortest vegetation in height class 1 differed significantly from the other classes. The mean dung in height class 1 was 23.75 ± 4.045 compared to the next class with mean dung of 6.69 ± 1.90 . Plots with the shortest grasses were selected. These were plots 10,11 and 12.

Medium-sized grazer occupancy declined less systematically but as with the small grazers, occupancy in height class 1 was higher than the others. Mean dung in this height class was 46.61 ± 8.63 compared to 18.30 ± 3.86 in height class 3 (Fig. 6.1b). Height class 2 was used the least. Overall therefore, the differences relating occupancy along a vegetation height gradient were significant.

Cattle were absent from the park due to regulations that prohibit human activities. For this group therefore, there was no height class 5. The highest

occupance for cattle occurred in the height class 2 (10-20)cm with a mean dung of 11.17 ± 0.81 . Height class 4 also had high occupance. Although the differences in occupance were significant they did not follow the height gradient (Fig. 6.1c), and therefore factors other than height seemed more important in explaining the distribution patterns. 'Shoats' also did not show any height-related patterns (Fig. 6.1d) and (table 6.2).

Large grazers data could not be analysed as this group was confined to height class 5 only. Their preference for taller grasses has however already been demonstrated (chapter 5).

Dry season occupance patterns were different from the wet season. Small grazers still selected the shortest height class (Fig. 6.2a). There was significant variation in occupance along the height gradient (table 6.3). Although use varied significantly along grass height, both the wet and dry seasons, the mean occupance was lower in the dry season. The highest quantity of dung counted in height class 1 was only $7.22 \text{ piles} \pm 1.10$ in the dry season compared to 23.75 ± 4.04 in the wet season. Generally, there were relatively few individuals on the plains in the dry season.

The variation in distribution between height classes was more pronounced for medium-sized grazers and cattle. There were large shifts in occupance for medium-sized grazers in the dry season with the highest occupance in height class 5 (Fig. 6.2b) in the park. The analysis of variance gave significant variation (table 6.3) only between height class 5 and the other four classes. Differences in shoat and cattle occupance along height classes were also significant. Cattle had the highest occupance in height class 3 with a mean dung count of $9.54 \text{ piles} \pm 0.67$ (Fig. 6.2c & 6.2d).

During the field work it had been noted that there were variable movement patterns when rainfall was very patchy over the ecosystem. These distribution patterns did not follow the normal dry or wet months. For that reason, data collected in January 1994 were analysed alone (table 6.4). The distribution or occupance patterns for most species groups were different from the wet and dry season both inside the park and on the plains. Small grazers showed no variation along the height gradient (Fig. 6.3a). Medium grazers (which constitute the migratory groups) were evenly distributed between height class 1 which now had an average height of $4.89 \text{ cm} \pm 0.27$ and class 5 with an average of $16.43 \text{ cm} \pm 0.98$. The mean dung in height class 1 was $48.42 \text{ cm} \pm 18.40$ and in height class 5 was $40.63 \text{ cm} \pm 3.44$. These 2 means were not significantly different. The least amount of dung was found in height classes 2 and 4

(Fig. 6.3b). Compared to the wet season, the vegetation was short. Rain showers experienced in the month of January were the first after a long dry spell in the previous year. What is evident from these results is that when the rains fell, the animals did not leave the park as they did under normal rainfall conditions.

Cattle were concentrated mostly in height class 3 which had an average grass height of $13.90 \text{ cm} \pm 1.92$ (Fig. 6.3c). This height class had the lowest occupancy in the wet season. The patterns of "shoat" distribution followed the height gradient increasing with height to a maximum in height class 4 (Fig. 6.3d). This class had a mean height of $10.73 \text{ cm} \pm 0.85$, the equivalent of mean for height class 1 in the wet season. The occupancy pattern was statistically significant (table 6.4).

A regression analysis on the percentage cumulative dung proportions against average height for medium-sized grazers gave a high correlation, $r^2=0.987$ and $r^2=0.973$ for dry and wet seasons respectively. Of interest were the differences in the slopes (b) of the regression (Fig. 6.4). The wet season regression was at its steepest in the shorter height classes. The slopes of the seasonal data for the small-sized grazers were not too different (Fig. 6.5). Again, the regression slopes seemed steeper in the wet than dry season.

Table 6.1 Groupings of plots using grass height classes derived using wet season data.

Height Class	Plot Number	Mean height for class (cm)
1 (0-10)cm	11, 12, 10	9.31 ± 0.64
2 (10-20)cm	3, 2, 7, 6, 1, 4	16.06 ± 0.87
3 (20-30 cm)	8, 9, 13, 14, 15	26.39 ± 1.10
4 (30-40 cm)	5	36.30 ± 4.08
5 (>40 cm)	16, 17	55.86 ± 2.33

Table 6.2 One-way analysis of variance of large herbivore species groups on grass height classes for the wet season.

Species Group	F-Ratio	df	P-Value
Large grazers	-	-	-
Medium grazers	7.96	4,199	0.0000
Small grazers	14.08	4,199	0.0000
Cattle	14.60	4,199	0.0000
Shoats	2.19	4,199	0.072 NS

Table 6.3 One-way analysis of variance of large herbivore species groups on grass height classes for the dry season

Species group	F-Ratio	df	P-Value
Large grazers	—	—	—
Medium grazers	35.82	4,403	0.0000
Small grazers	13.62	4,403	0.0000
Cattle	24.92	4,403	0.0000
Shoats	5.41	4,403	0.0003

Table 6.4 One-way analysis of variance of large herbivore species groups on grass height classes for the early dry season/patchy rainfall period (January 1994).

Species Group	F-Ratio	df	P-Value
Large grazers	—	—	—
Medium grazers	6.91	4,63	0.0001
Small grazers	1.32	4,63	0.272 NS
Cattle	19.99	4,63	0.000
Shoats	7.92	4,63	0.000

Fig 6.1
Occupance along a vegetation height gradient for large herbivores (wet season)

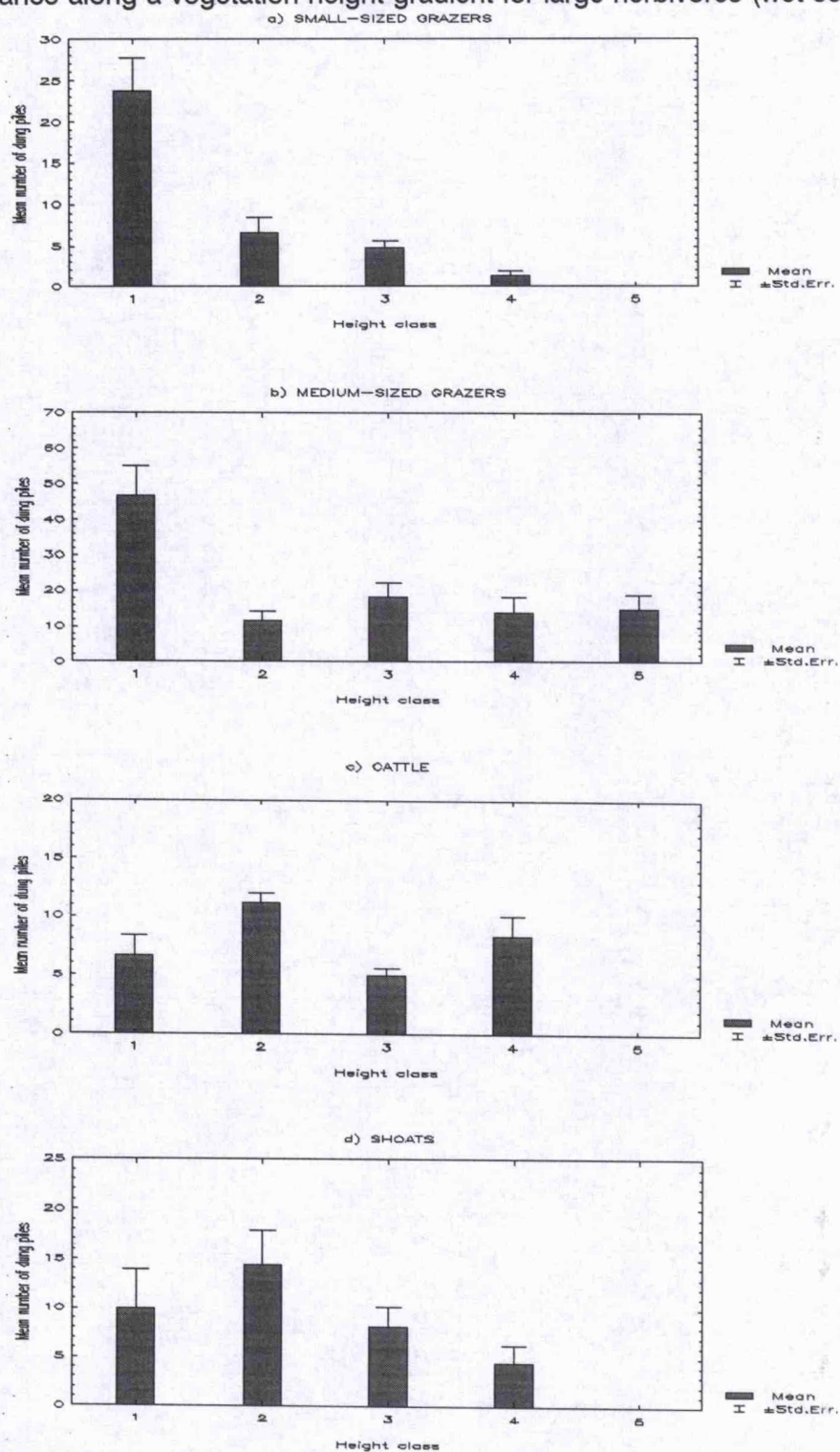


Fig 6.2
Occupance along a vegetation height gradient for large herbivores (dry season)

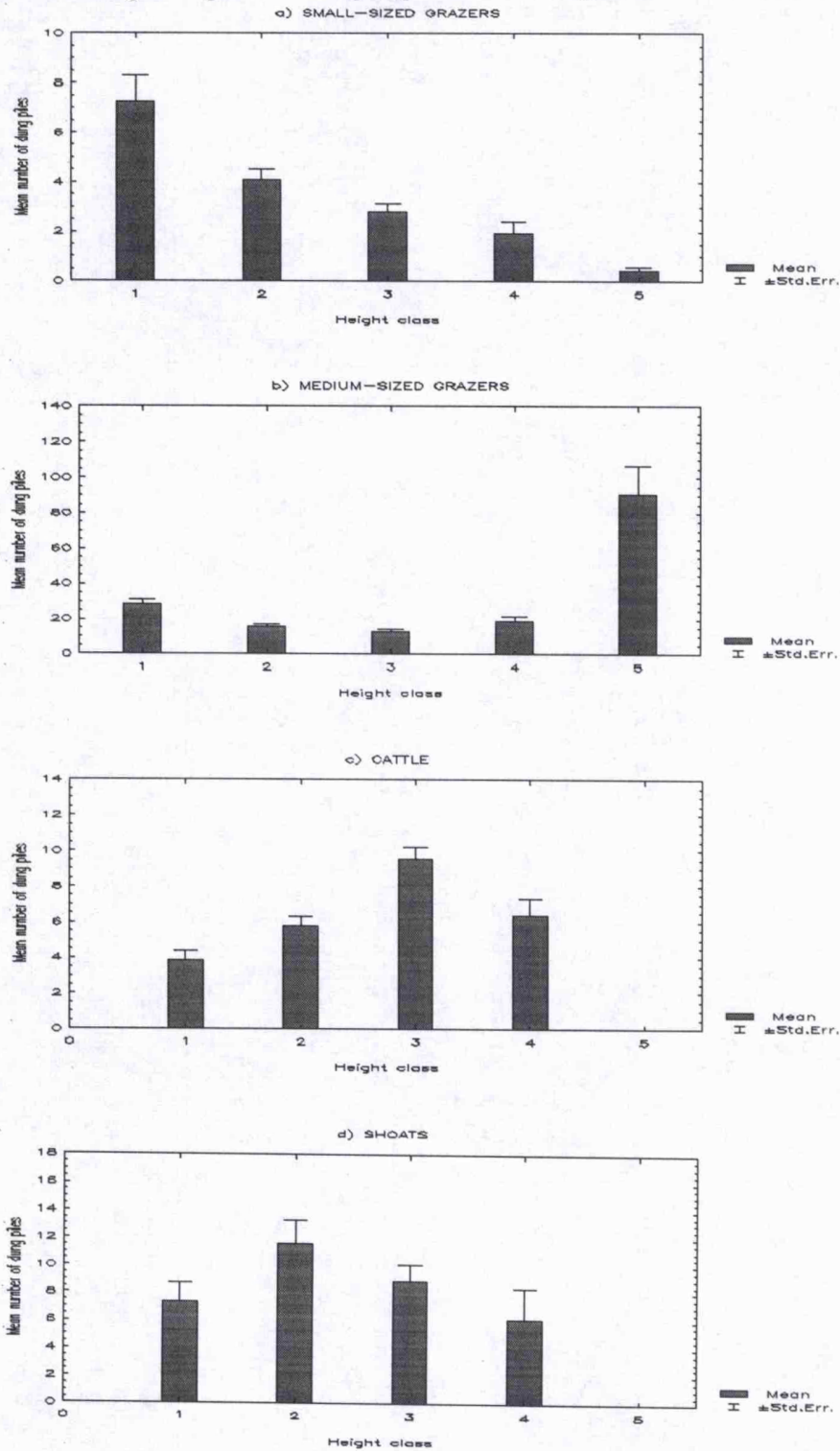


Fig 6.3
Occupance along a vegetation height gradient for large herbivores (January 1994)

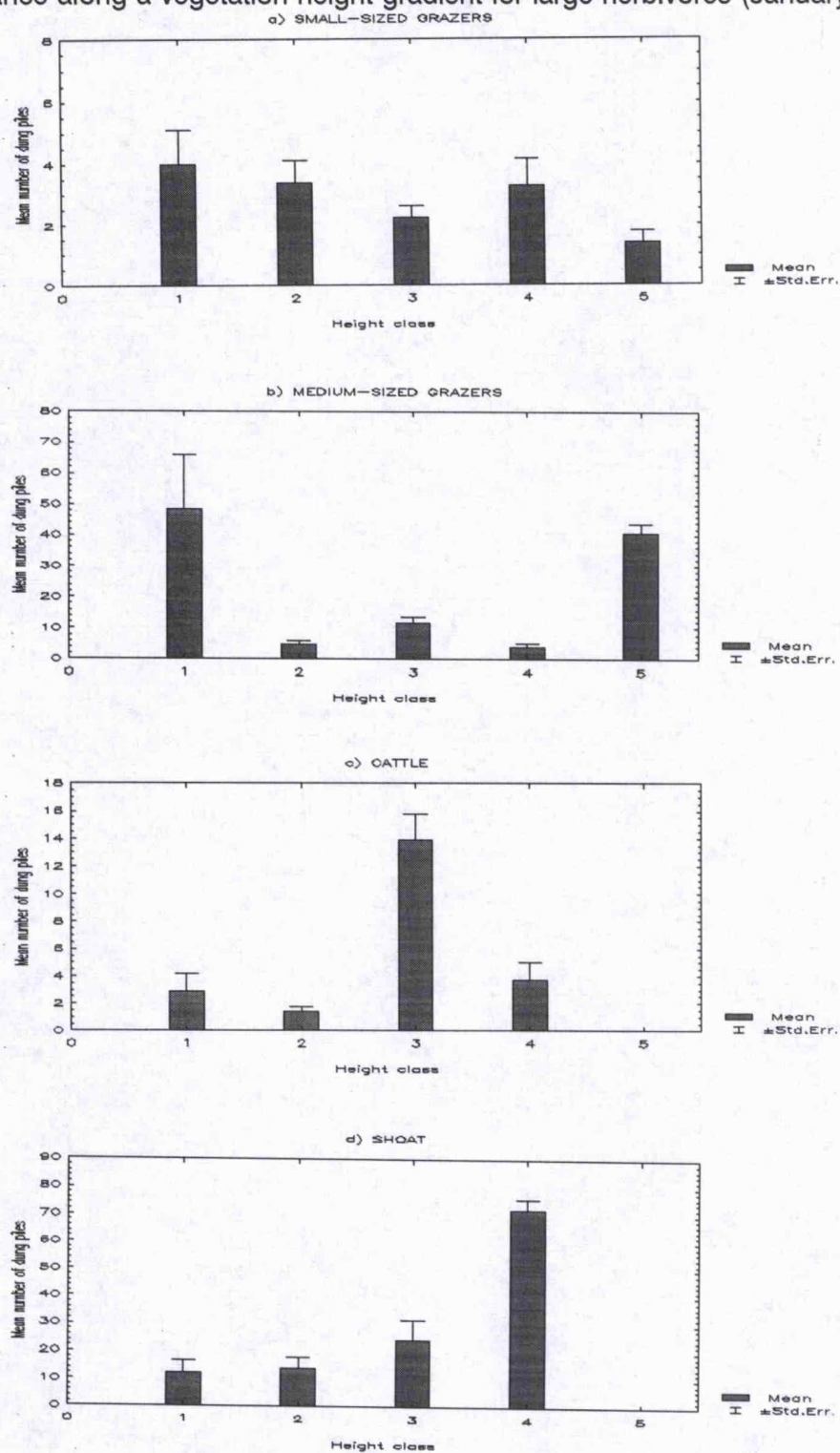


FIG 6.4 RELATIONSHIP BETWEEN DUNG PROPORTION AND AVERAGE GRASS HEIGHT
FOR MEDIUM SIZED GRAZERS

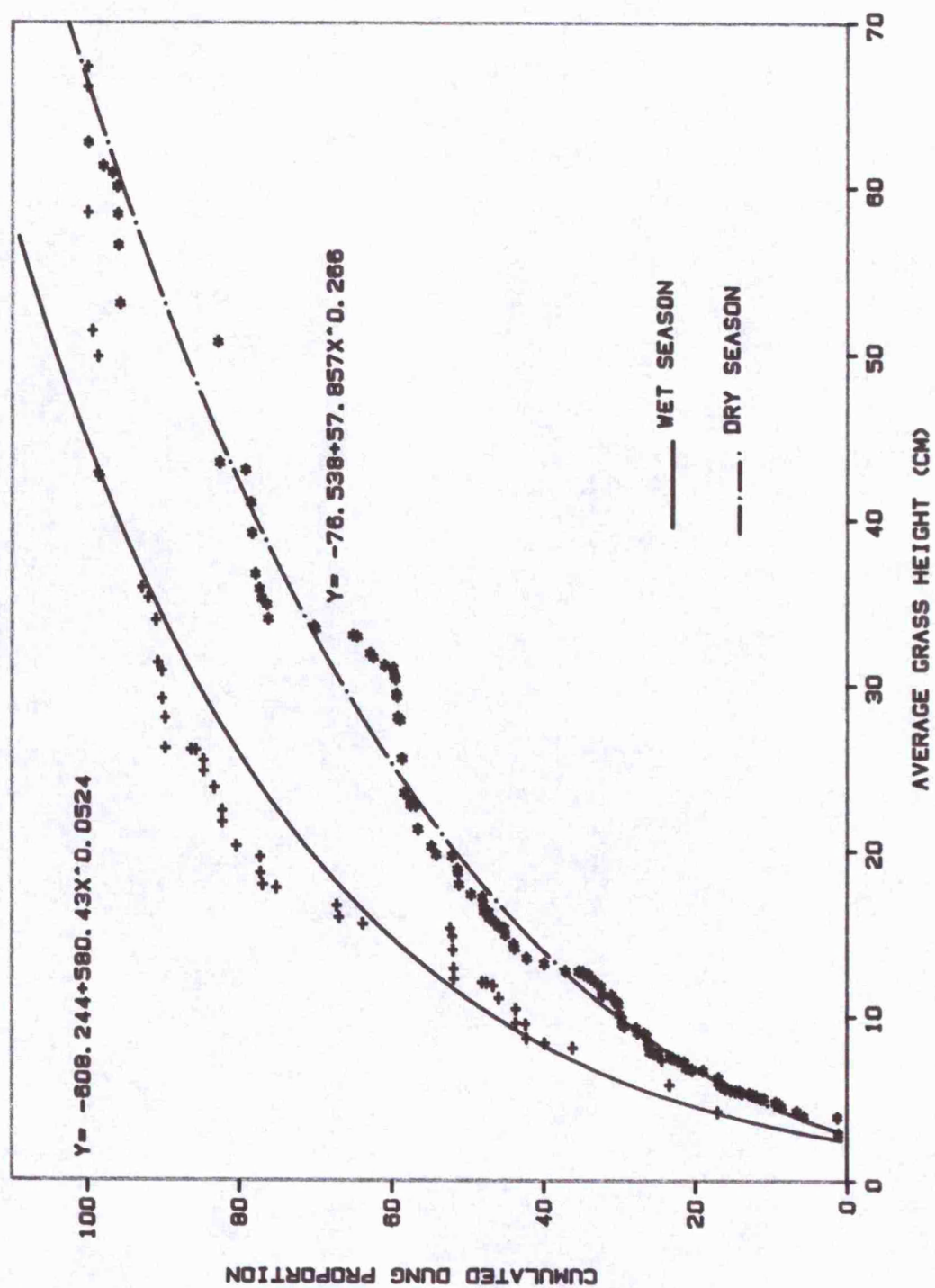
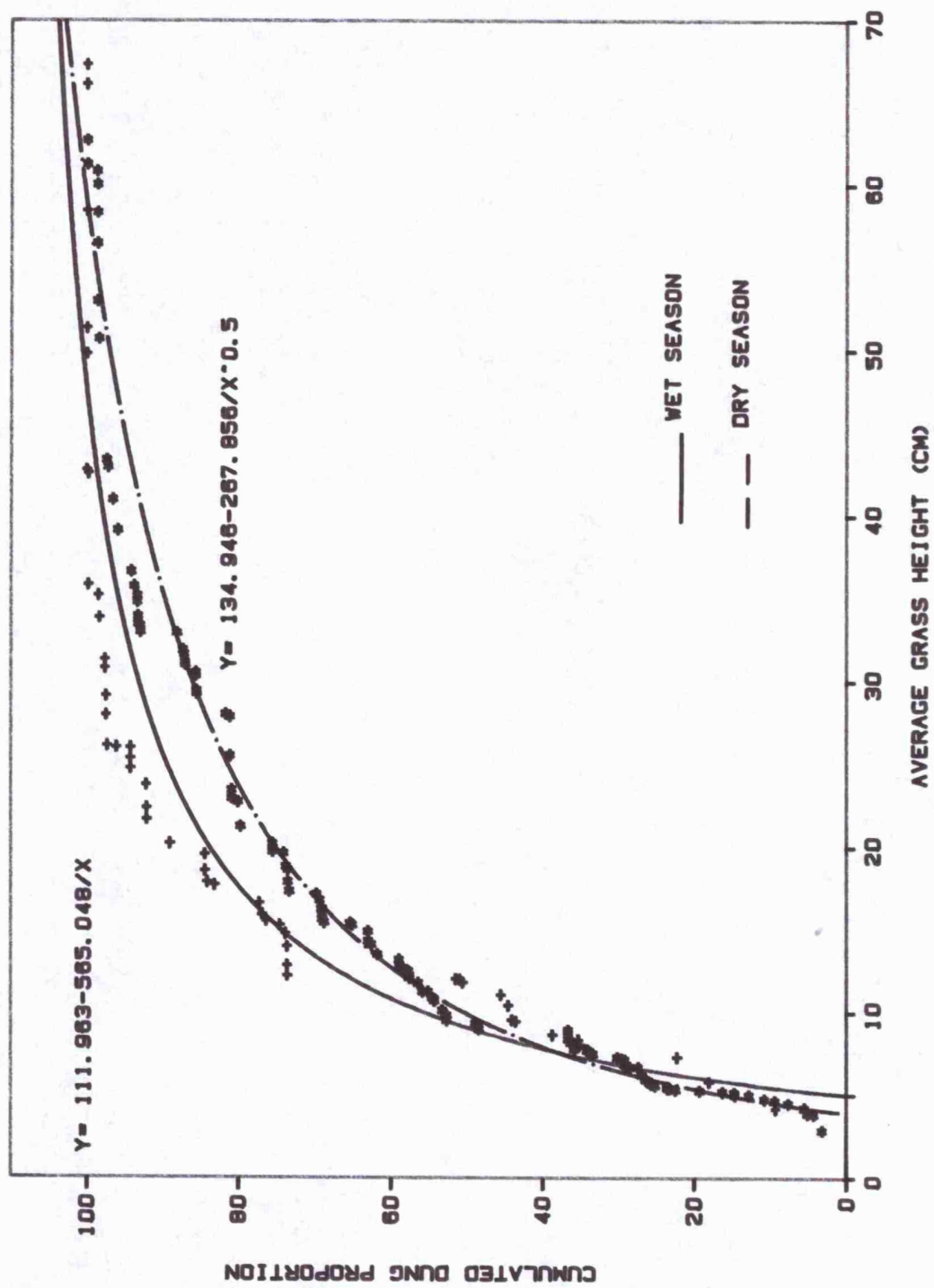


FIG 6.5 RELATIONSHIP BETWEEN DUNG PROPORTION AND AVERAGE GRASS HEIGHT
FOR SMALL SIZED GRAZERS



6.2.1 Vegetation quality as a factor influencing wildlife and livestock distribution patterns.

The highest occupancy for medium and small grazers occurred in plots of highest quality in the wet season. For example medium and small grazer occupancy was highest in plots 10 and 12, both with the highest vegetation quality (table 6.5).

Table 6.5 Large herbivore occupancy and vegetation crude protein for wet season.

Plot #	Veg. % Crude Protein	Herbivore Occupance		
		Small Grazers	Medium Grazers	Large Grazers
1	9.64 ± 0.74	4.25 ± 1.47	6.25 ± 2.26	-
2	8.93 ± 0.34	0.86 ± 0.28	1.75 ± 0.75	-
3	8.67 ± 0.68	3.75 ± 1.20	5.13 ± 1.34	-
4	8.29 ± 0.35	0.25 ± 0.23	0.13 ± 0.12	-
5	7.03 ± 0.42	0.00 ± 0.00	5.75 ± 0.79	-
6	8.78 ± 0.43	0.88 ± 0.48	18.63 ± 3.41	-
7	8.97 ± 0.55	0.63 ± 0.47	1.38 ± 0.47	-
8	8.09 ± 0.47	0.25 ± 0.23	6.25 ± 2.43	-
9	8.42 ± 0.46	5.13 ± 0.61	8.25 ± 3.42	-
10	10.48 ± 0.75	22.00 ± 7.93	69.75 ± 15.83	-
11	8.11 ± 0.67	9.00 ± 3.28	3.50 ± 1.56	-
12	10.05 ± 0.81	38.63 ± 12.82	27.13 ± 2.86	-
13	8.74 ± 0.44	2.88 ± 1.04	8.75 ± 0.88	-
14	7.79 ± 0.43	0.38 ± 0.25	0.75 ± 0.39	-
15	7.94 ± 0.41	1.50 ± 0.50	1.25 ± 0.58	-
16	6.34 ± 0.31	0.00 ± 0.00	0.00 ± 0.00	-
17	6.66 ± 0.12	0.00 ± 0.00	2.75 ± 1.422	7.53

There was a positive non-linear relationship between average occupancy by both small grazers and medium-sized grazers and vegetation quality in the wet season. Small grazers had a significant relationship ($r^2=0.61$ $p<0.05$). Occupancy increased with increasing grass quality. There were no small grazers at quality levels below 7.5 % crude protein in plots 16 and 17 in the Park and plot 5 on the plains (Fig. 6.6).

A similar significant relationship was found for medium-sized grazers ($r^2=0.81$ $P<0.05$). Like small grazers, medium-sized grazer occupancy increased with increasing grass quality. There was no evidence of dung below 6.5% crude protein (Fig. 6.7). In complete contrast, large grazer occupancy evidently decreased with increasing grass quality (Fig. 6.8) despite a small sample in the wet season ($r^2=0.90$, $p<0.05$). This confirms the selection of low quality taller grasses by the large grazers, specifically

buffalo. Correlations between cattle and shoats with grass quality were poor in the wet season ($r^2=0.30$). The best fit gave a correlation of $r^2=0.30$ and $r^2=0.08$ for cattle and shoats respectively.

In the dry season only large grazers demonstrated occupancy patterns that were similar to the wet season. These had a significant correlation ($r^2=0.65$, $p<0.05$), (Fig. 6.9). Occupancy by medium-sized grazers, small grazers, cattle and shoats were not correlated to vegetation quality. Although there were concentrations of medium grazers in the park, these were not related to vegetation quality but probably to the availability of forage and water. Water was readily available in dams inside the park but very scarce outside. Unfenced dams on the plains that still had water were guarded and except Mbagathi and few swamps outside, most rivers were dry.

6.2.2 Biomass and wildlife occupancy relationships

The data gave four biomass classes but these were not distinct enough for a gradient analysis. Instead the main distinctions seemed to be between the park and plains. Analysis for differences between these two are presented in section 6.2.5.

6.2.3 Wildlife selectivity patterns

Dung protein data indicated large differences in the means of various species in both the wet (June 1992 & February 1993), dry (October 1992) and early dry seasons (February 1992) (table 6.5, 6.6 & 6.7). In the dry season, giraffe and Thomson's gazelle had the highest mean dung protein and zebra the least (table 6.6). One way analysis of variance on dung protein by ranks and by species showed significant differences between species, ($H=41.7$, $df\ 8$, $p<0.0001$). Only giraffe and zebra, Thomson's gazelle and zebra were different (October 1992).

Analysis of the wet season sample also indicated larger differences ($F=28.1$; $df=7,81$; $p<0.0001$) and table 6.7. Comparison using Student-Newman-Keuls methods showed that there were more differences between individual species in this season: Grant's gazelle had higher dung protein than zebra, buffalo, Coke's hartebeest, cattle, wildebeest and shoats; Thomson's gazelle also had higher protein in their dung than zebra, buffalo, Coke's hartebeest, cattle and wildebeest. There was no difference between crude protein levels in the dung of zebras and buffalo, the two species with the least amount. Grant's gazelle and Thomson's gazelle were on the upper extreme.

Fig 6.6

Average dung of small grazers against average vegetation crude protein (wet)

$$Y = -1.638 + 2.175x^{8.961}$$

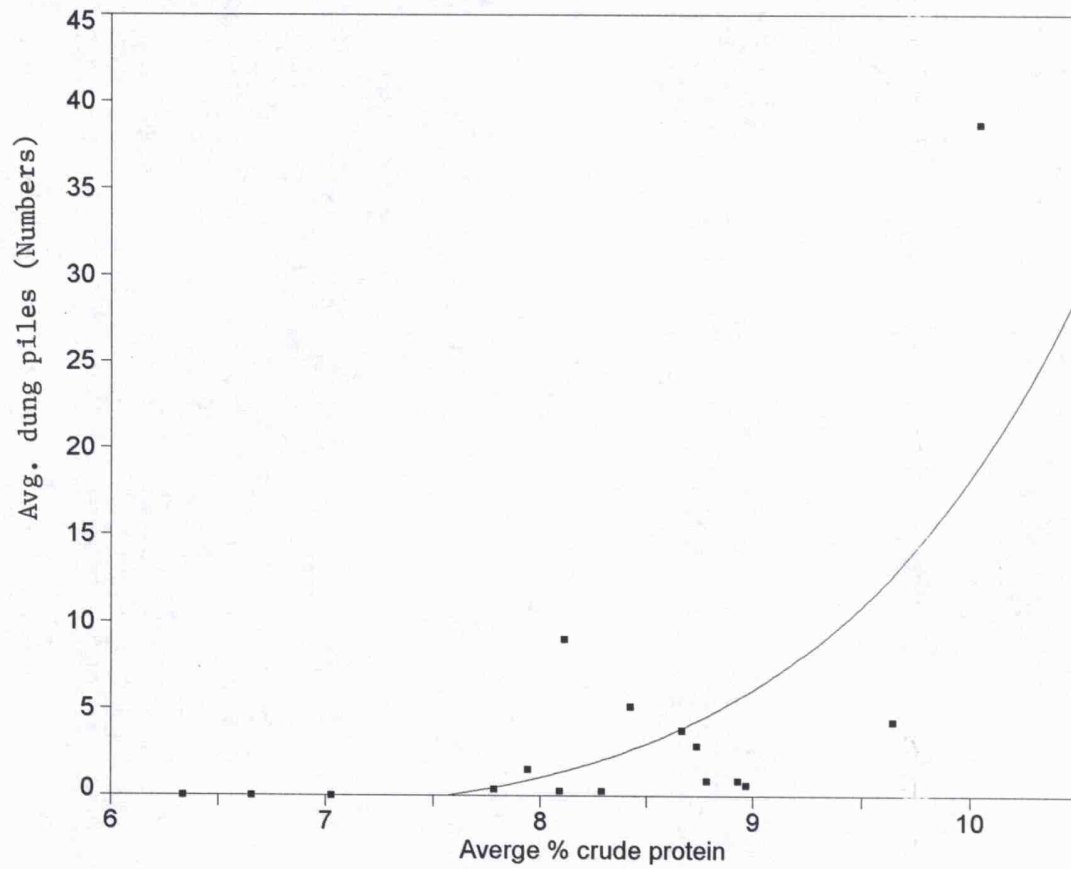


Fig 6.7

Average dung of medium grazers against average vegetation crude protein (wet)

$$Y = -2.978 + 0.00167e^x$$

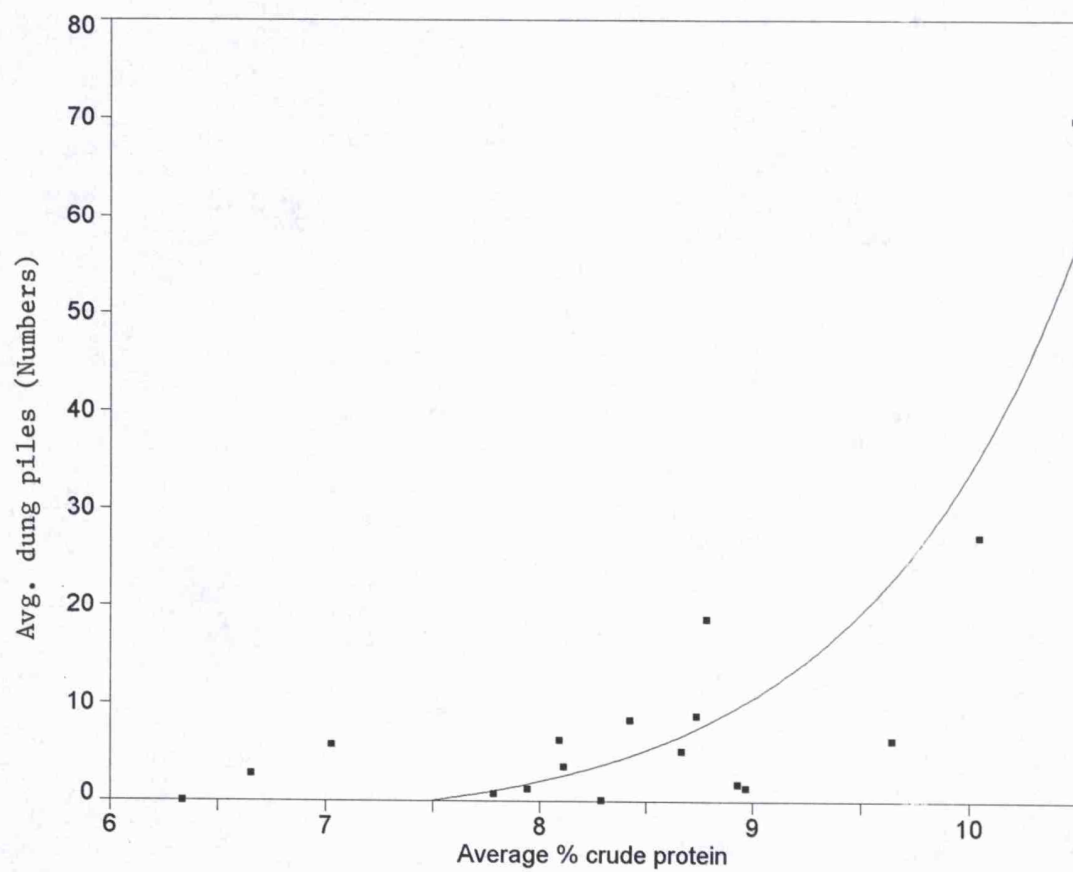


Fig 6.8

Average dung of large grazers against average vegetation crude protein (wet)

$$Y=1.792e+19 x^{-24.0715}$$

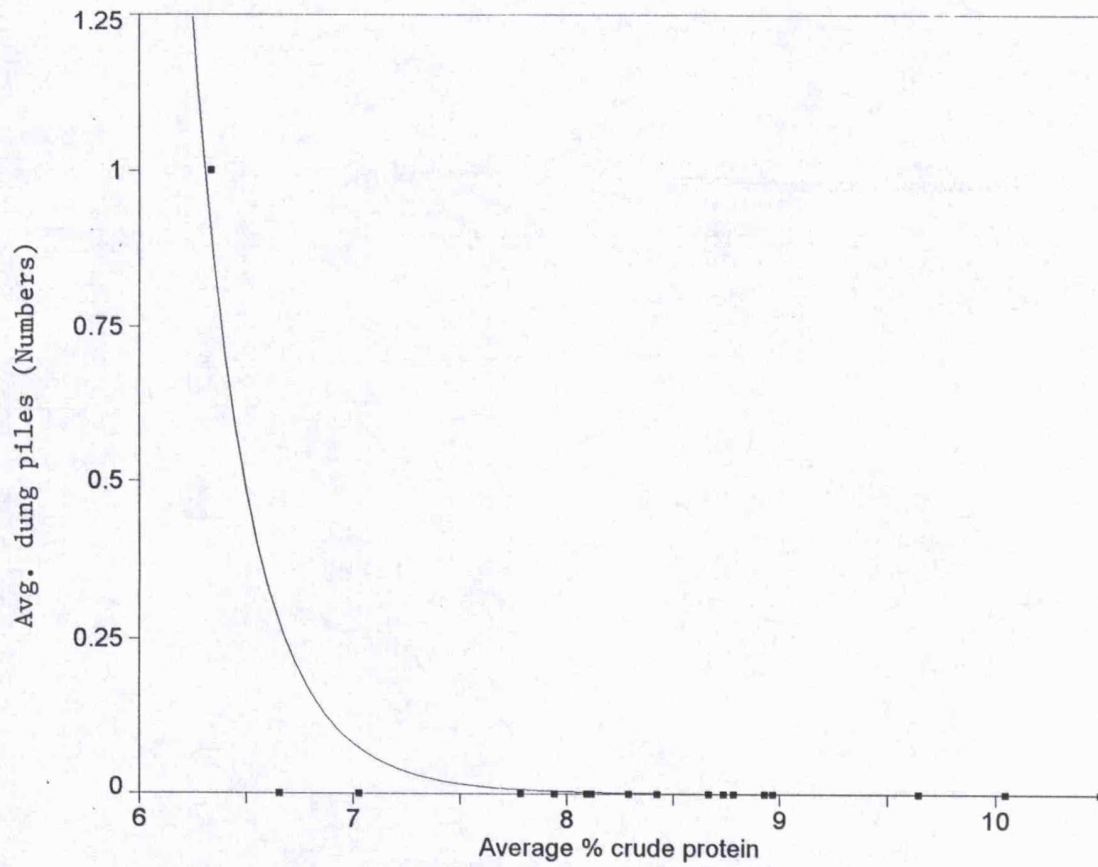
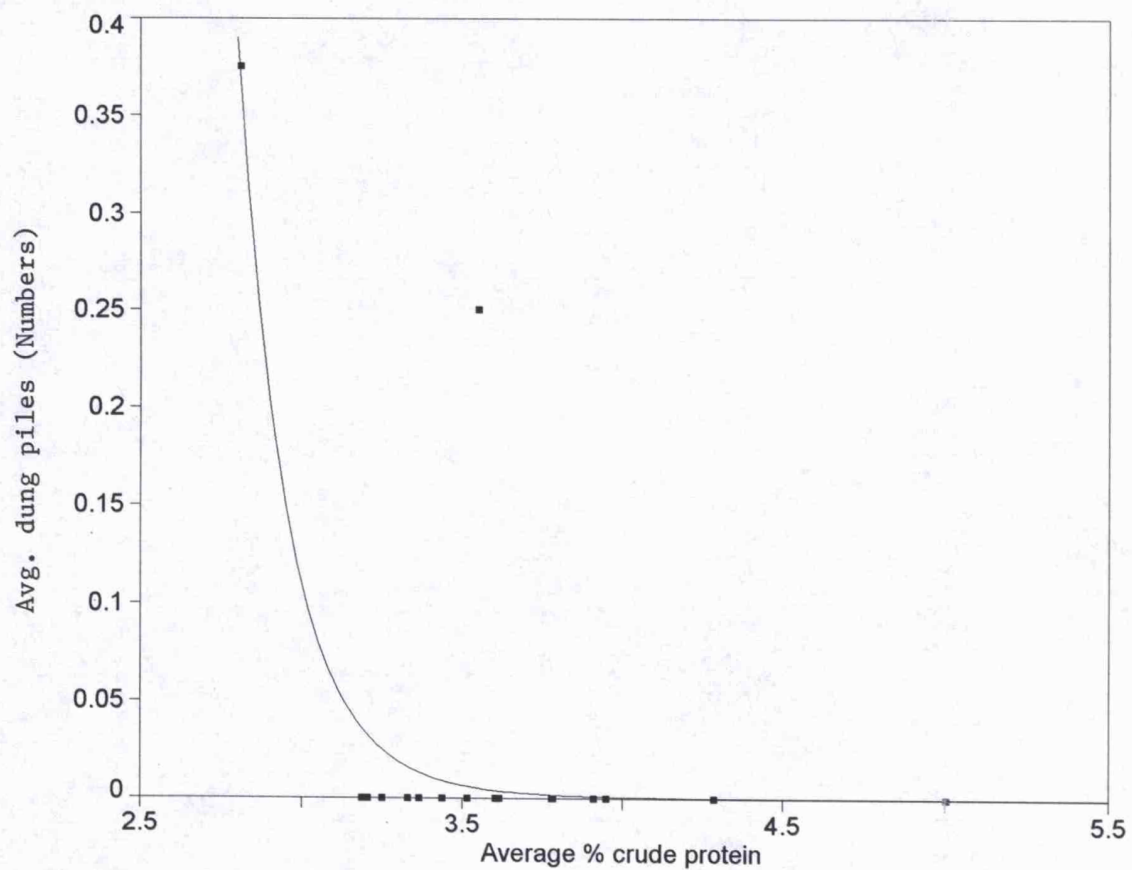


Fig 6.9

Average dung of large grazers against average vegetation crude protein (dry)

$$Y=72462187 x^{-18.492}$$



Among the grazing species, zebra had the lowest dung protein followed by buffalo, wildebeest, Coke's hartebeest and cattle in no specific order. The small grazers and the mixed feeders had the highest values. Buffalo were not different from cattle or wildebeest and 'shoat'.

Regression of body size against dung protein for the species sampled gave significant but negative correlations; as dung protein decreased, body weight increased. The dry season relationship (Fig. 6.10) was defined by the regression $Y = 43.66X^{-0.37}$, $r^2 = 72.1\%$. The Analysis of variance for the regression was significant ($F = 92.65$ df 1,44, $p < 0.05$).

In the wet season, the variation between dung protein was larger and averaged values were used for the 2 months in the wet season sample. The analysis also gave a significant regression defined by $Y = 19.74X^{-0.14}$, $r^2 = 59.95\%$ (Fig. 6.11). The correlation was similarly negative and the analysis of variance for the regression was significant ($F = 19.14$, df 1,14, $p < 0.05$).

Zebra, the only non ruminant in the group had the lowest dung protein. When excluded from the analysis in the dry season the new regression was marginally weaker; $Y = 5.09 + 103.7X^{-0.80}$, $r^2 = 70.2\%$. When zebra was removed from the wet season regression the correlation between body size and dung protein improved markedly, going up to $r^2 = 65.4\%$ from $r^2 = 59.95\%$. The new regression was $Y = -49.93 + 67.07X^{-0.023}$.

Comparisons of dung protein with the overall mean vegetation quality in the wet season showed that zebra had lower dung protein than the quality generally found in the vegetation. With the exception of Coke's hartebeest and wildebeest, dung from all the other species had higher crude protein than the general grass quality (table 6.8).

Further comparisons of dung protein and vegetation crude protein in specific plots where various large herbivore species had been sampled gave results that were similar to those of overall vegetation quality. In previous comparisons, dung protein of ostrich was higher than that in the vegetation. However, once specific plots were compared no significant differences were found between the two (table 6.9). In the dry season crude protein in the dung of all species was higher than the overall and selected plots vegetation quality (tables 6.10 and 6.11).

Fig 6.10

Relationship between dung crude protein and large herbivore body weight
in the dry season

$$Y=43.66x^{-0.371}$$

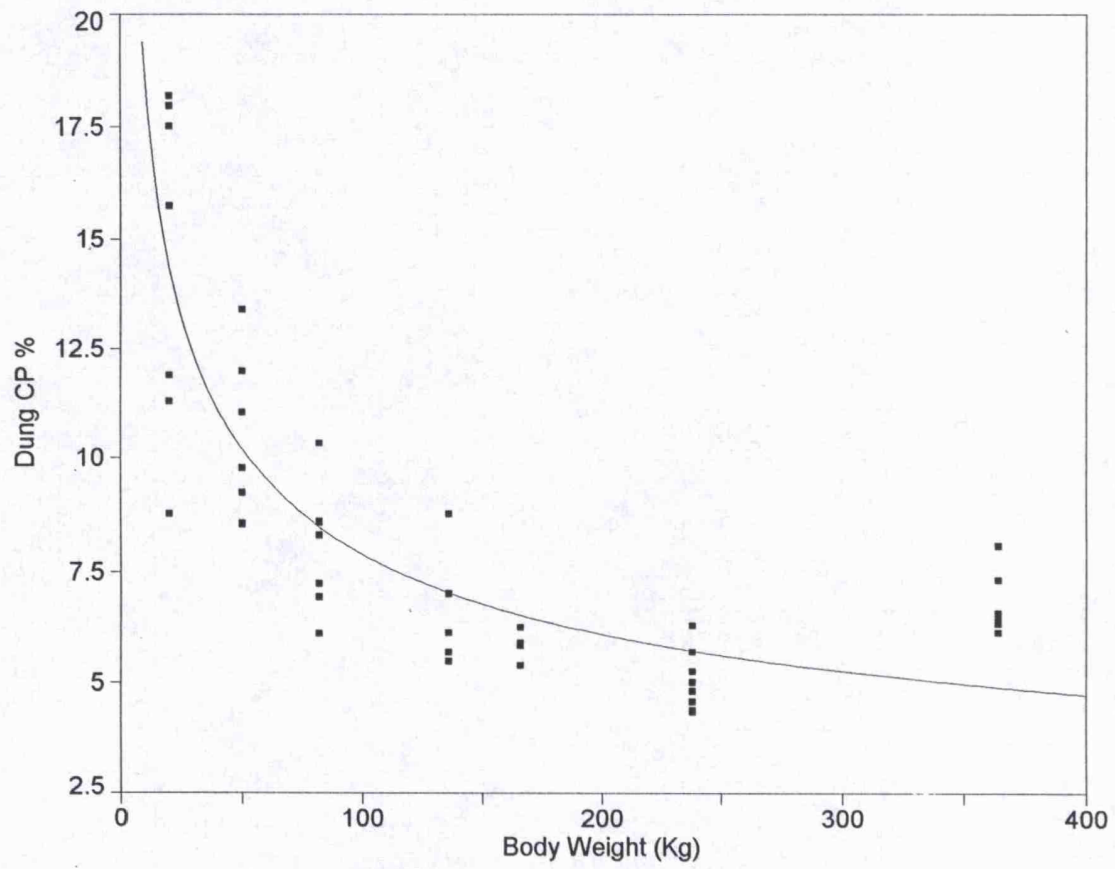


Fig 6.11

Relationship between dung crude protein and large herbivore body weight in the wet season

Data were averaged over two seasons.

Note that Zebra had the lowest crude protein at 7%

$$Y=19.74x^{-0.14}$$

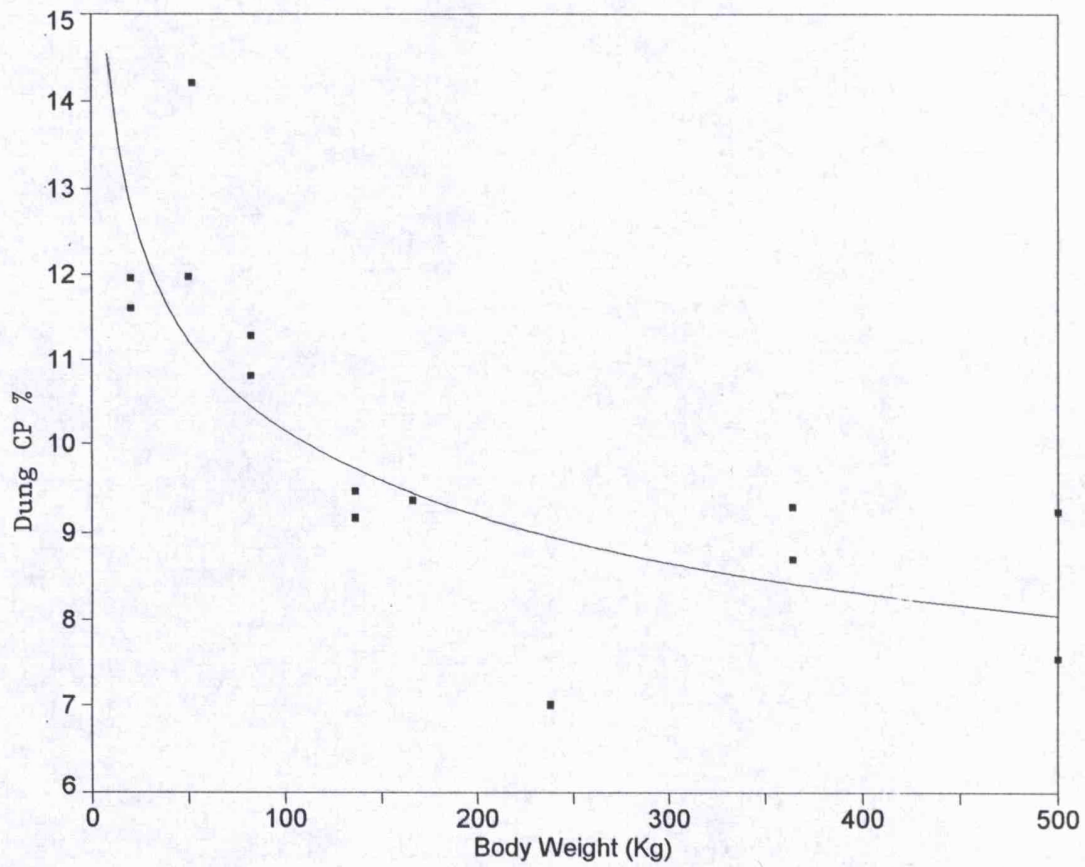


Table 6.6 Percent mean crude protein in the dung of various large herbivores in a dry season - (October 1992)

Species	% Mean crude protein	Sample size n
Giraffe	15.40 \pm 0.46	2
G. Gazelle	10.65 \pm 0.75	6
Impala	10.97 \pm 0.64	2
C. Hartebeest	6.60 \pm 0.42	7
Shoats	7.91 \pm 0.61	6
T. Gazelle	14.47 \pm 1.43	7
Wildebeest	5.84 \pm 0.18	4
Zebra	4.98 \pm 0.22	9
Cattle	6.75 \pm 0.26	7

Table 6.7 Percent mean crude protein in the dung of various large herbivores in the wet season - (February 1993 and June 1992)

Species	% Mean crude protein	Sample size n
G. Gazelle	14.20 \pm 0.50	12
C. Hartebeest	9.16 \pm 0.86	6
Shoats	11.28 \pm 0.37	4
T. Gazelle	11.60 \pm 0.55	8
Wildebeest	9.35 \pm 0.30	4
Zebra	7.00 \pm 0.24	14
Cattle	9.28 \pm 0.40	14
Ostrich	13.19 \pm 0.56	2
Buffalo	9.23 \pm 0.29	3

Table 6.8 Comparisons of % mean dung crude protein of large herbivores against overall grass quality (wet season).

SPECIES	% Dung crude protein	% Veg. crude protein	t-Value	df	p-Value
T. Gazelle	11.60 ± 0.55	8.41 ± 0.18	-5.82	74	0.00
G. Gazelle	14.20 ± 0.50	8.41 ± 0.18	-12.3	78	0.00
C. Hartbeest	9.16 ± 0.86	8.41 ± 0.18	-1.17	72	0.25 NS
Wildebeest	9.35 ± 0.30	8.41 ± 0.18	-1.28	70	0.21 NS
Zebra	7.00 ± 0.25	8.41 ± 0.18	3.46	80	0.00
Cattle	9.28 ± 0.40	8.41 ± 0.18	-2.03	80	0.05
Shoats	11.28 ± 0.37	8.41 ± 0.18	-3.88	70	0.00
Ostrich	13.19 ± 0.56	8.41 ± 0.18	-4.58	68	0.0001

Table 6.9 Comparisons of % mean dung crude protein of large herbivores against grass quality in selected plots in the wet season (February 1993).

SPECIES	% Dung crude protein	% Veg. crude protein	t-Value	df	p-Value
T. Gazelle	11.60 ± 0.548	9.56 ± 0.413	-2.91	22	0.0062
G. Gazelle	14.20 ± 0.496	9.20 ± 0.254	-9.99	34	0.0001
C. Hartbeest	9.16 ± 0.863	8.97 ± 0.428	-0.229	16	0.822 NS
Wildebeest	9.35 ± 0.304	10.19 ± 0.456	-1.21	10	0.254 NS
Zebra	7.00 ± 0.237	9.32 ± 0.259	5.75	40	0.0001
Cattle	9.28 ± 0.396	9.32 ± 0.259	0.084	40	0.934 NS
Shoats	11.28 ± 0.365	8.91 ± 0.354	-4.16	10	0.0019
Ostrich	13.19 ± 0.555	11.0 ± 0.653	-2.14	4	0.099 NS

Table 6.10 Comparisons of % mean dung crude protein of large herbivores against overall grass quality (Oct/Sept 1992 - dry season).

SPECIES	% Dung crude protein	% Veg. crude protein	t-value	df	p-value
T. Gazelle	14.47 ± 1.432	3.62 ± 0.111	-19.5	72	0.0001
G. Gazelle	10.64 ± 0.746	3.62 ± 0.111	-16.4	71	0.0001
C. Hartbeest	6.60 ± 0.422	3.62 ± 0.111	-8.07	72	0.0001
Cattle	6.75 ± 0.262	3.62 ± 0.111	-8.81	72	0.0001
Shoats	7.91 ± 0.607	3.62 ± 0.111	-10.5	71	0.0001
Wildebeest	5.84 ± 0.179	3.63 ± 0.111	-4.84	69	0.0001
Zebra	4.98 ± 0.220	3.62 ± 0.111	-4.34	74	0.0001

Table 6.11 Comparisons of % mean dung crude protein of large herbivores against grass quality in selected plots (Oct/Sept 1992 - dry season).

SPECIES	% Dung crude protein	% Veg. crude protein	t-Value	df	p-Value
T. Gazelle	14.47 ± 1.432	3.49 ± 0.143	-16.5	44	0.001
G. Gazelle	10.64 ± 0.746	3.62 ± 0.197	-13.2	38	0.0001
C. Hartebeest	6.60 ± 0.422	3.57 ± 0.218	-6.54	29	0.0001
Cattle	6.75 ± 0.262	3.61 ± 0.111	-8.30	33	0.001
Shoats	7.91 ± 0.607	3.62 ± 0.197	-8.73	28	0.0001
Wildebeest	5.84 ± 0.179	3.27 ± 0.183	-5.61	9	0.0003
Zebra	4.92 ± 0.220	3.37 ± 0.177	-5.11	34	0.0001

6.2.4 Comparisons of conditions between park and plains.

The plains generally had lower rainfall than the park (table 6.12 and see Fig. 4.20 - chapter 4) particularly in the South and East. Table 6.13 shows that in the wet season optimum conditions seemed to exist on the plains. Grass was short, green, of high quality and the ratio of green parts to brown was very high (table 6.13). The quantity of litter in the park was more than double that on the plains. Medium-sized grazers were more abundant in the plains than the park (table 6.14a). In most wet seasons there were no zebras or wildebeest in the park. During the dry season, conditions were poor in both the park and the plains. Quality was marginally lower in the park and herbaceous biomass was almost four times higher. Most parts of the plains were almost bare by this time. Despite the poor conditions, a very large proportion of medium-sized grazers still returned to the park (table 6.14b). Their density was extremely high at 75.16 animals/km² compared to only 7.32 animals/km² on the plains.

Table 6.12 Rainfall averages 1992 - 1993

Location	Average Rainfall (mm)
Park	53.65
Plains	41.385

Table 6.13 Ratio of plant parts sampled to total hits by season

		Green	Brown	Litter
Wet	Plains	65.83	24.51	8.65
	Park	56.97	25.39	17.62
Dry	Plains	8.20	66.59	25.21
	Park	9.28	55.42	35.29

Table 6.14 Comparison of average herbivore numbers and average vegetation conditions between park and plains.

a) Wet season

WET SEASON				
VEG. CONDITION	PARK	PLAINS	f-ratio	P-value
Grass Height	50.80 ± 2.33	19.74 ± 0.68	19.883	0.000
Grass Biomass	620.06 ± 45.26	165.25 ± 4.52	503.981	0.000
Grass Quality	6.48 ± 0.190	8.67 ± 0.172	22.57	0.000
DENSITY OF THE LARGE HERBIVORES (animals/km ²)				
SPECIES	PARK	PLAINS	t-value	p-value
Small Grazers	3.216	4.933	0.960	0.194 NS
Medium Grazers	4.111	11.559	2.53	0.032
Large Grazers	-	-		
Cattle	-	30.13 ± 3.29		
Shoats	-	49.77 ± 8.84		

b) Dry season

DRY SEASON				
VEG. CONDITION	PARK	PLAINS	f-ratio	P-value
Grass Height	37.89 ± 2.74	15.92 ± 0.586	135.44	0.000
Grass Biomass	352.69 ± 27.24	94.99 ± 2.76	158.69	0.000
Grass Quality	3.15 ± 0.167	3.68 ± 0.791	5.10	0.026
DENSITY OF HERBIVORES				
SPECIES	PARK	PLAINS	t-value	p-value
Small Grazers	2.703	1.569	2.258	0.027
Medium Grazers	75.609	7.316	6.517	0.0007
Large Grazers	1.933	---		
Cattle	-	21.80 ± 0.36		
Shoats	-	45.20 ± 1.39		

6.3 Interpretation

Vegetation height and quality were important in structuring the herbivore community in the Athi-Kapiti plains. The relationship between quality and wildlife selectivity, and between dung protein and body size was highly significant. This showed that the protein content in dung of large herbivores can be used as a measure of diet selectivity. It showed that as the body size of a herbivore increased, it became less selective in its diet. The smallest grazers were the most selective and the largest the least. There was a slight deviation to this pattern which could be attributed to the presence of zebra in the regression. Although zebra was not the largest grazer it did not follow the size relationship in the same way as the other grazers. It had the lowest dung protein in both the wet and the dry season. These are patterns that can perhaps be attributed to differences in digestive system (ruminants and non-ruminants).

Inside/outside park differences also confirmed some of the community structure patterns suggested by earlier analysis. Differences were mainly seasonal. The plains are selected in the wet season by all groups of large herbivores except large grazers. Rainfall, an important factor driving primary production in terrestrial ecosystems was a major factor influencing the movements of herbivores (McNaughton *et al.*, 1988). In the wet season they moved to the optimum sites while dry conditions propelled movements to other areas once forage was exhausted here. The rainfall gradient from park to plains may also have been a significant factor in the migration, but other vegetation conditions that result from the interaction of several factors may also have had some significance. The rainfall gradient also had certain influences on general vegetation conditions and in turn on the large herbivore populations (Stanley-Price 1974).

In summary therefore, among grazing species, Grant's and Thomson's gazelles were the most selective with highest crude protein in their dung. The order of selectivity emerging from the wet season analysis was Grant's gazelle - Thomson's gazelle - 'shoats' - wildebeest, Coke's hartebeest and cattle - zebra.

However, in the dry season Thomson's gazelle had higher dung crude protein than Grant's gazelle.

CHAPTER 7

LOCALIZED WILDLIFE UTILIZATION PATTERNS WITHIN NAIROBI NATIONAL PARK AND AROUND SETTLEMENTS IN THE ATHI-KAPITI PLAINS

7.1 Introduction

7.1.1 Habitat utilization in Nairobi National Park

Localized herbivore use of areas may arise from seasonal forage conditions and water distribution. Nairobi National Park is used by a large number of herbivores in the dry season compared to the wet (see chapter 5). A certain proportion of migrants return to the park during the dry season and stay until the beginning of the rains. Zebra and wildebeest (Chapter 5) return to Nairobi National Park in the dry season. This influx presents opportunities to study the utilization of grasslands in the park by the dominant grazing herbivores.

7.2 RESULTS

7.2.1 Vegetation patterns

Grass height and grass quantity in transects selected at the beginning of the study were variable (table 7.1). The variation was significant ($F=2.27$, $p<0.05$, $df\ 7,61$) for vegetation height and ($F=21.88$, $p<0.05$, $df\ 7,61$) for grass quantity. Differences in vegetation height were less profound. Vegetation biomass in transect 2 differed from transects 6.1, 5, 4 and 1. Transect 5 was different from 7 and 2, 4 from 7 and 2 ($p<0.05$). Transect 2 had the least biomass and 6.1 the most.

When vegetation height was used, differences between transects changed. Transect 4, 1 and 6.1 had the tallest vegetation. Other transects that were different include transect 5 from 2, transect 3 from 2 and transect 7 from 2. Pairwise comparisons of all these also gave $p<0.05$.

Vegetation height and quantity showed general decrease from June 1993 to December 1993 followed by an increase in 1994 (Figs. 7.1a & b; 7.2a & b). In general biomass declined from time 1 to time 9 in December 1993. After some showers in January 1994, biomass and height of vegetation increased. The maximum height and biomass for these samples was reached in June 1994 after which sampling stopped. The largest difference in grass height occurred in transect 2 where the mean height ranged between 4.30 ± 0.23 cm at the shortest height to 74.49 ± 2.21 cm in the late June 1994 sample, a change in several orders of magnitude. Transect 1 and 7 also had large

changes. An analysis of variance showed these changes in vegetation to be significant for both quantity and height (table 7.2 and 7.3) respectively.

Table 7.1 Average biomass and height for transects in NNP in June 1993 (1st sample)

TRANSECT	Mean biomass g/m ²	Mean grass height (cm)
1	444.24 ± 31.33	42.41 ± 1.98
2	79.33 ± 11.40	5.76 ± 0.24
3	338.47 ± 43.01	14.88 ± 1.91
3	498.30 ± 34.48	116.79 ± 57.23
5	577.63 ± 29.05	17.27 ± 2.01
6.1	605.65 ± 68.20	28.92 ± 4.60
6.2	209.38 ± 22.28	10.13 ± 2.81
7	260.90 ± 23.92	18.29 ± 1.50

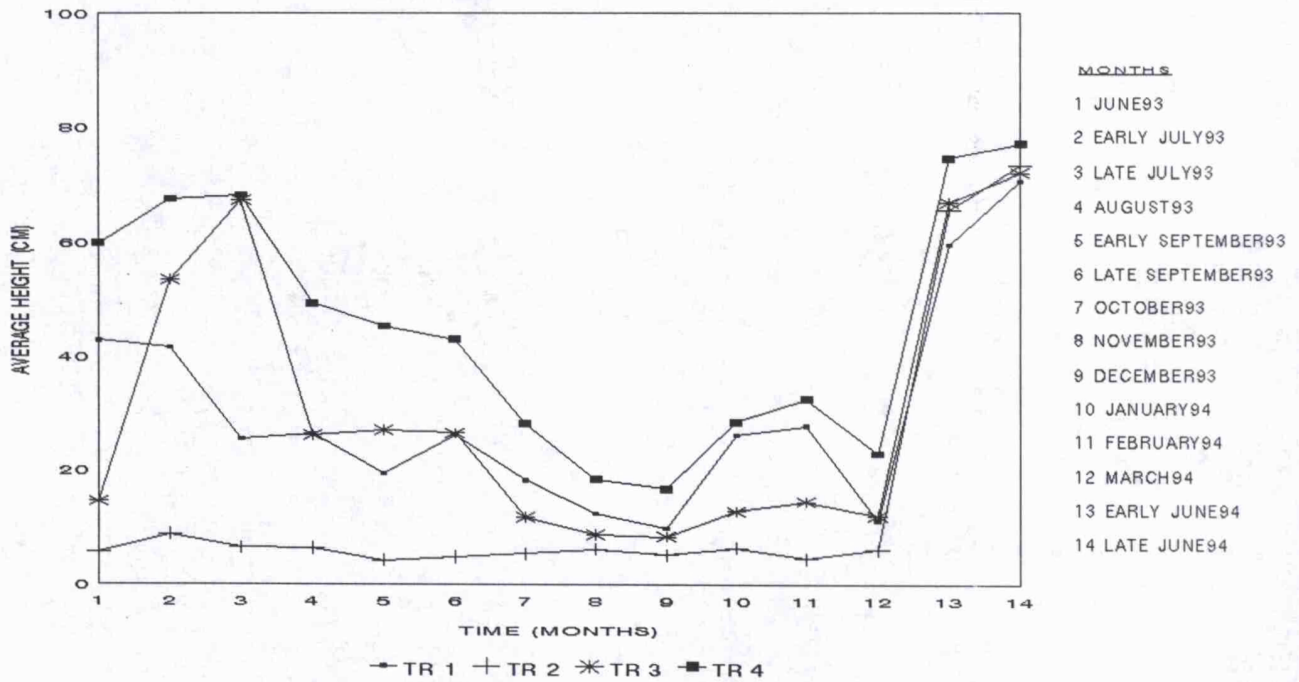
Table 7.2 Changes in vegetation biomass over time in the 9 transects sampled in Nairobi National Park.

TRANSECT	F-Ratio	P	df
1	16.894	0.000	13,140
2	49.302	0.0000	13,140
3	11.189	0.0000	13,140
4	26.863	0.0000	13,140
5	12.935	0.0000	13,70
6.1	11.241	0.0000	13,70
6.2	20.345	0.0000	13,14
7	19.061	0.0000	13,140
8	4.385	0.009	3,40

Table 7.3 Changes in grass height over time in the 9 transects sampled in Nairobi National Park.

TRANSECT	F-Ratio	P-Value	df
1	80.870	0.0000	13,140
2	510.677	0.0000	13,140
3	8.203	0.000	13,140
4	3.348	0.002	13,140
5	54.144	0.0000	13,70
6.1	32.907	0.0000	13,70
6.2	49.388	0.0000	13,14
7	57.306	0.0000	13,140
8	47.746	0.0000	13,40

FIG 7.1
a) Changes in vegetation height over time
in Nairobi National Park



b) Changes in vegetation height over time
in Nairobi National Park

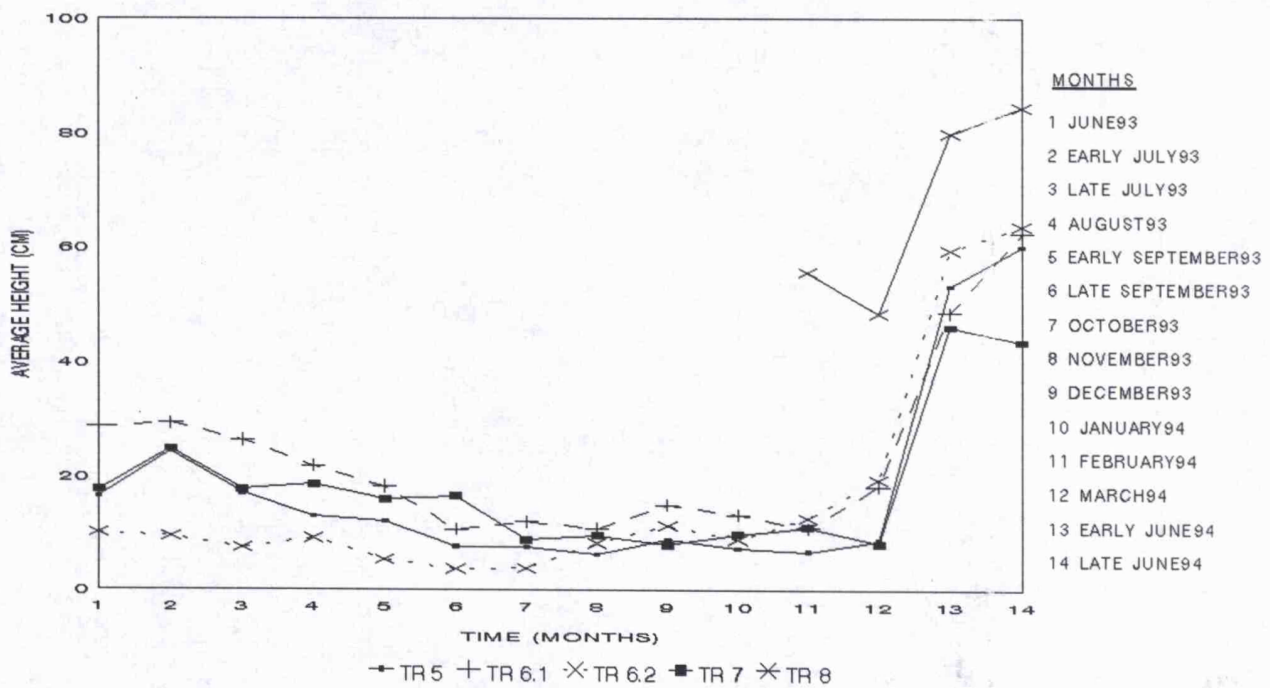
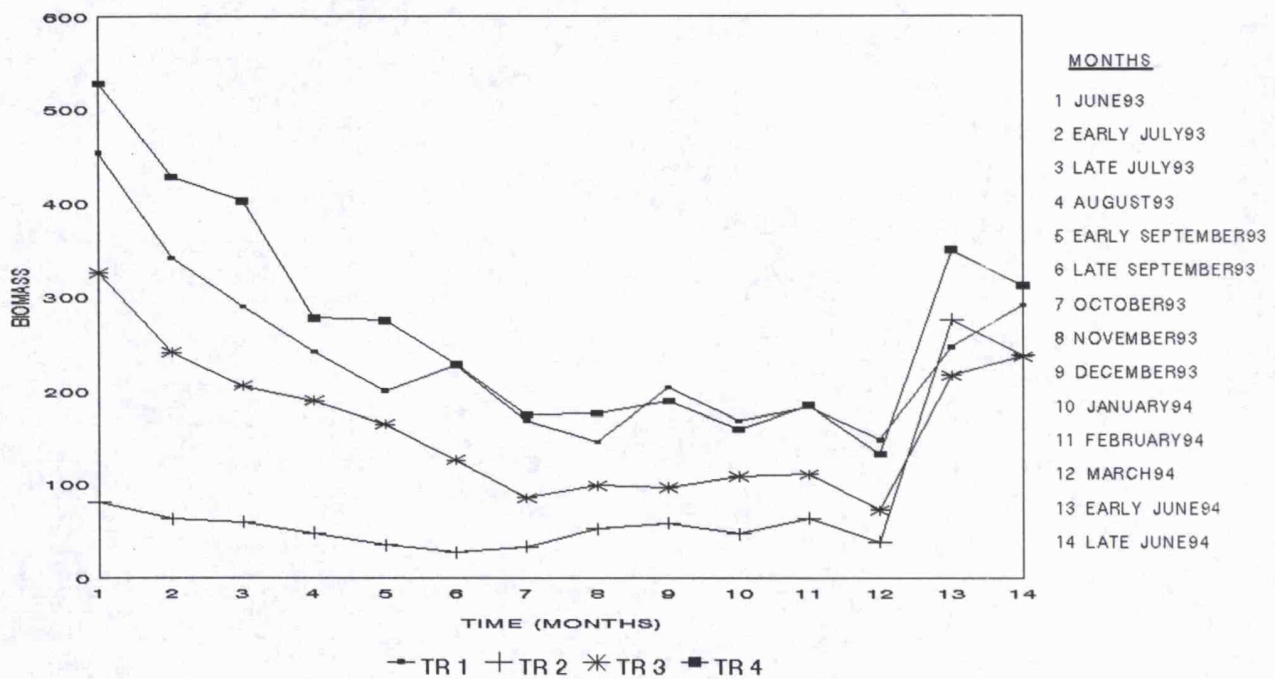
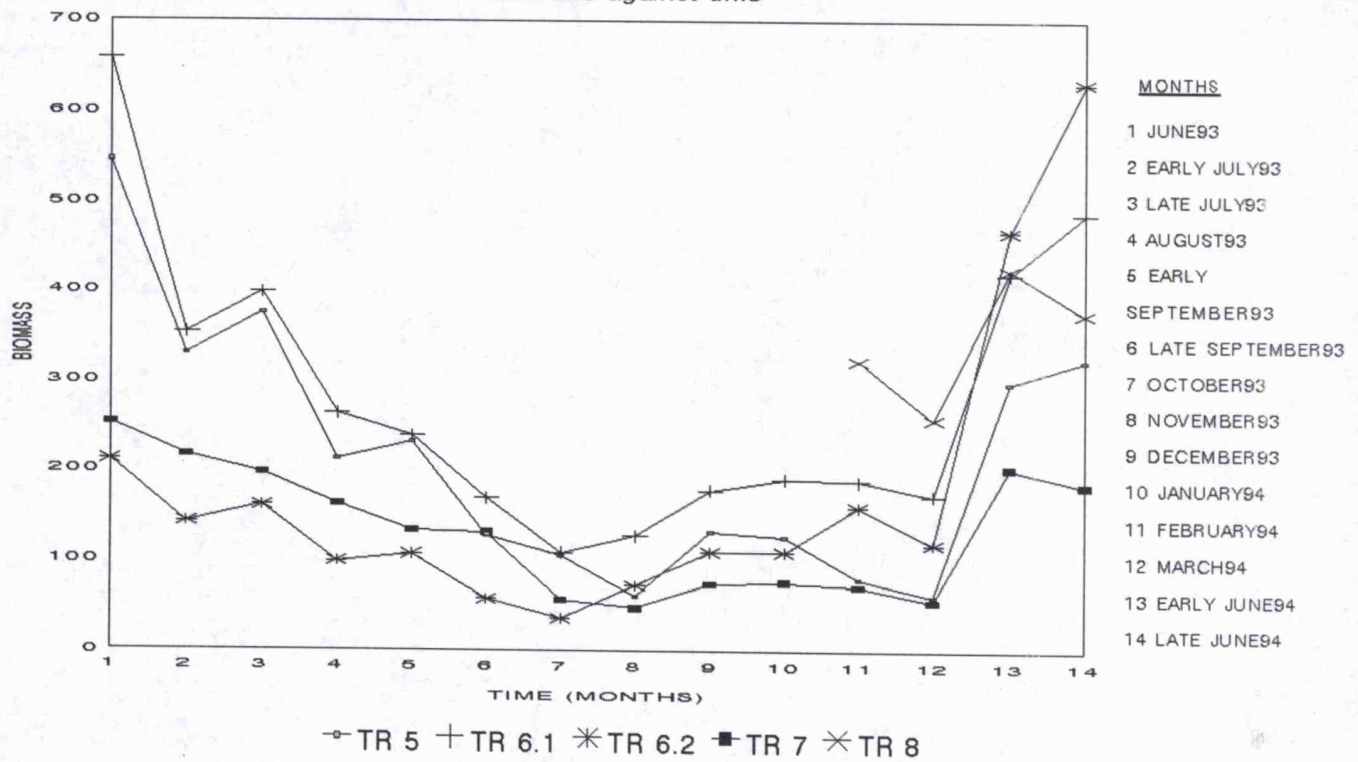


FIG. 7.2
a) changes in vegetation biomass over time in Nairobi National Park
Biomass against time



b) Changes in vegetation biomass over time in Nairobi National Park
Biomass against time



7.2.2 Distribution of wildlife in the park by blocks

Distribution of wildlife in the park by block revealed that some species had a favoured block both in the wet and dry season and depending on habitat type (Fig. 7.3). For example, in the wet season kongoni numbers were highest in block 2, impala selected blocks 9, followed by 6, 6a, 7a and 7b. These plots all had browse vegetation. Buffalo used plots 5b and 2 the most. In the dry season, most blocks were dominated by wildebeest and zebra. The blocks preferred by wildebeest were 5b, 2 and 1. Zebras preferred blocks 5b, 4, 5a and 8.

7.2.3 Wildlife distribution and use patterns along transects

The numbers of ungulates using the 8 transects selected in the park were averaged over the sampling period to give an indication of occupancy patterns (table 7.4).

Table 7.4 Average numbers of animals (by species groups) using the seven transects sampled in NNP and average grass height in each transect

Transect	Mean number of animals				Avg. height (cm)
	Small grazers	Medium grazers	Large grazers	Browsers	
1	0.30	37.70	0.00	0.00	23.36
2	25.00	12.00	0.00	0.00	5.90
3	3.40	119.50	0.00	0.00	25.96
4	0.10	17.60	0.30	0.30	40.29
5	6.70	11.90	0.00	0.00	11.16
6	14.00	123.90	0.00	0.00	13.03
7	3.80	43.40	0.00	0.00	14.14

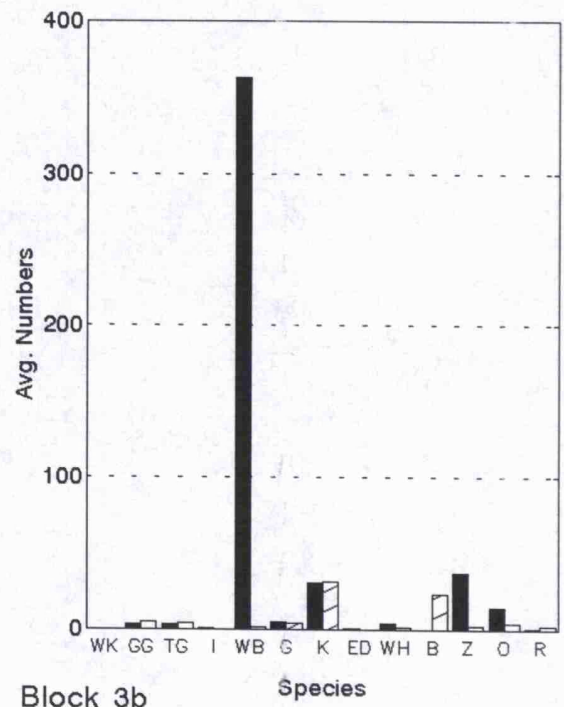
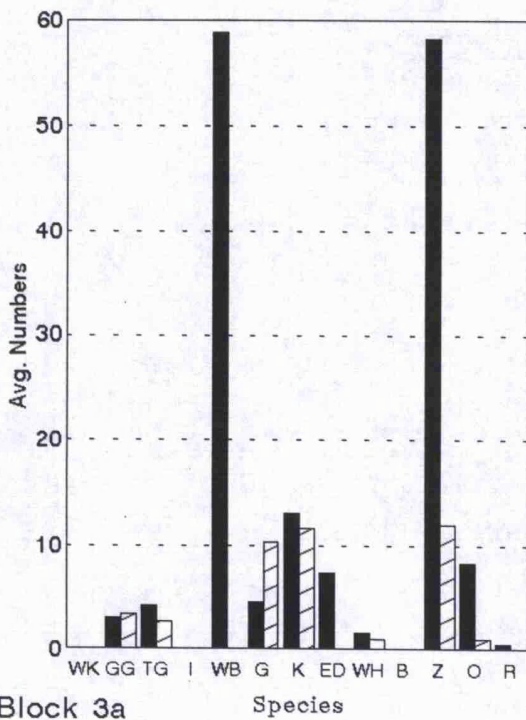
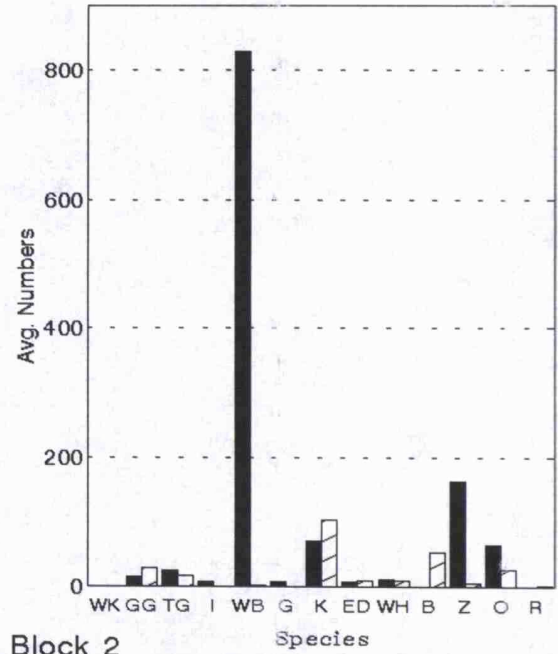
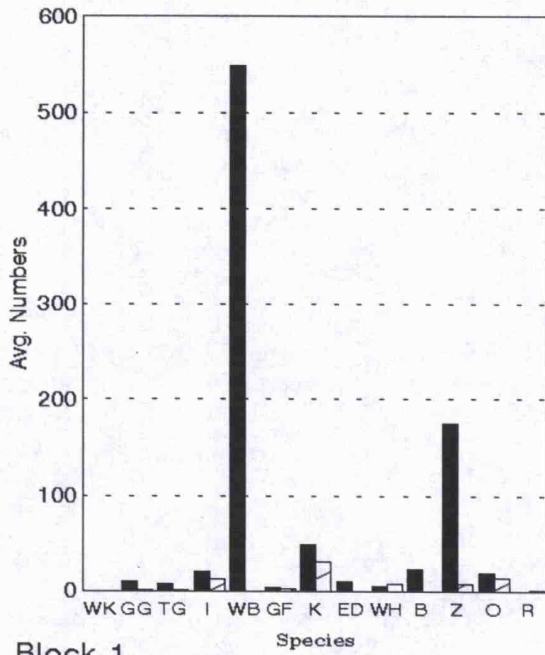
The largest numbers of small grazers were in transect 2 and of medium grazers in transect 6. Large grazers and browsers occurred in one transect only (table 7.4). Analysis of wildlife numbers against vegetation heights in the various transects over time showed the following:

There was no variation for large grazers due to vegetation characteristics of the transects over time. Numbers of large grazers counted were low and any patterns of use were difficult to detect.

Medium grazers which were most numerous showed significant variation due to time ($F=2.31$ $P=0.028$ df 9,6) but not due to transect and therefore height of the grasses ($F=2.10$ $P=0.07$ df 9,6). There was variation in use between time 6 and 12 (Late September 1993 and January 1994).

Fig 7.3

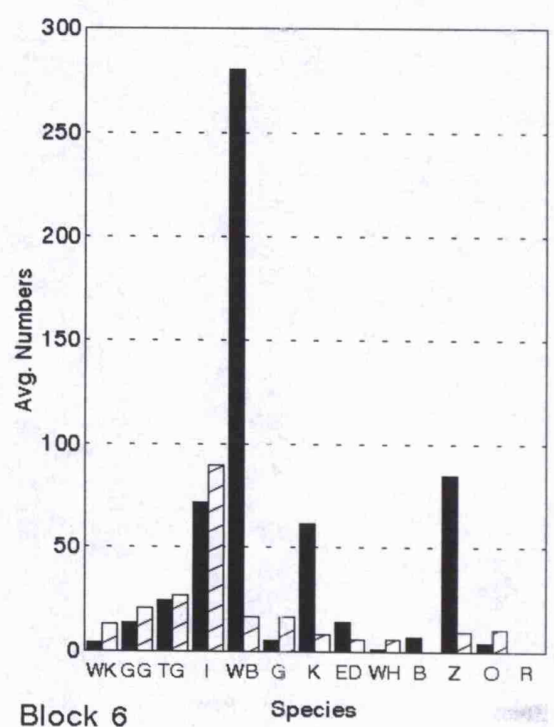
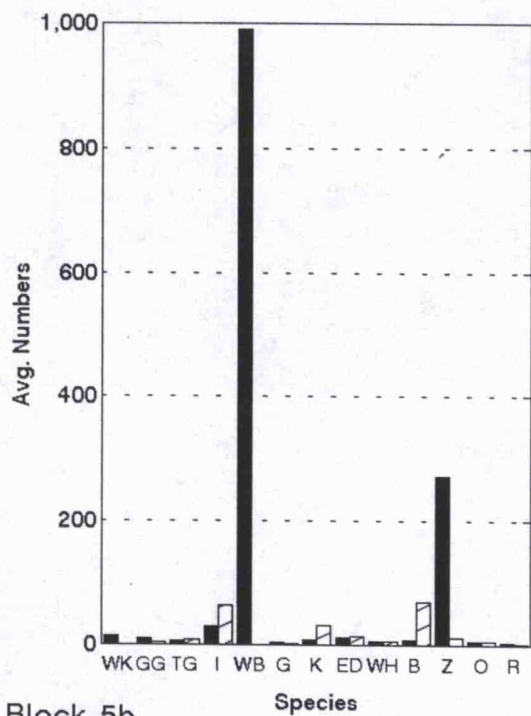
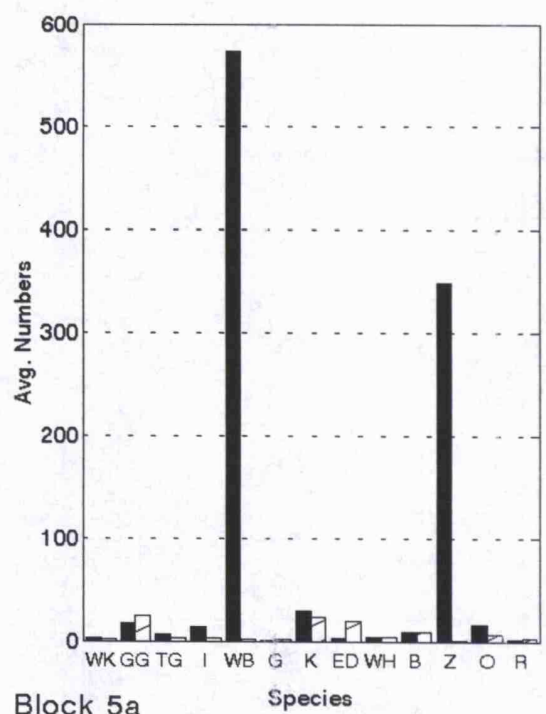
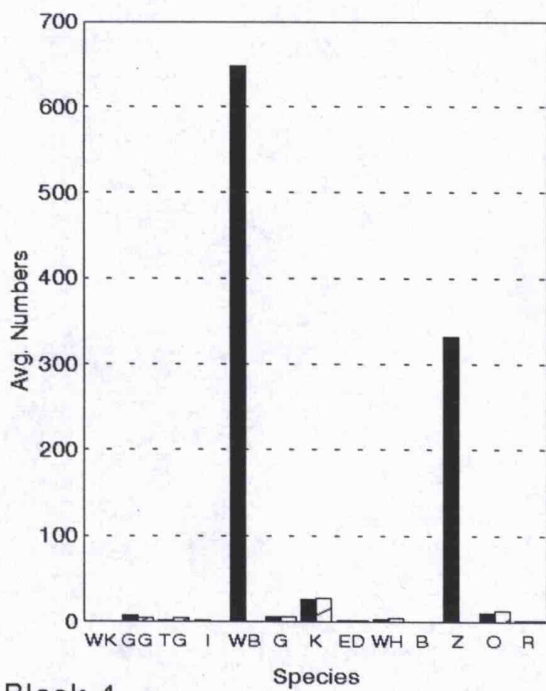
Distribution of wildlife in the park by blocks

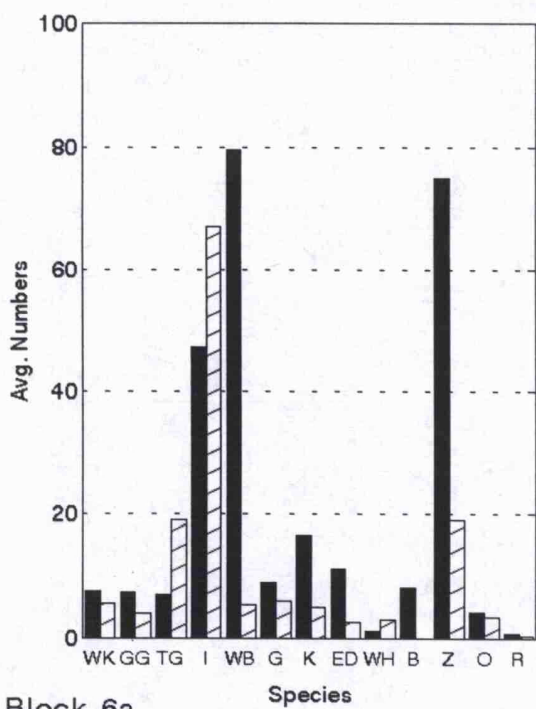


GG Grants gazelle
TG Thompson's gazelle
WK Waterbuck
I Impala
WB Wildebeest
GF Giraffe

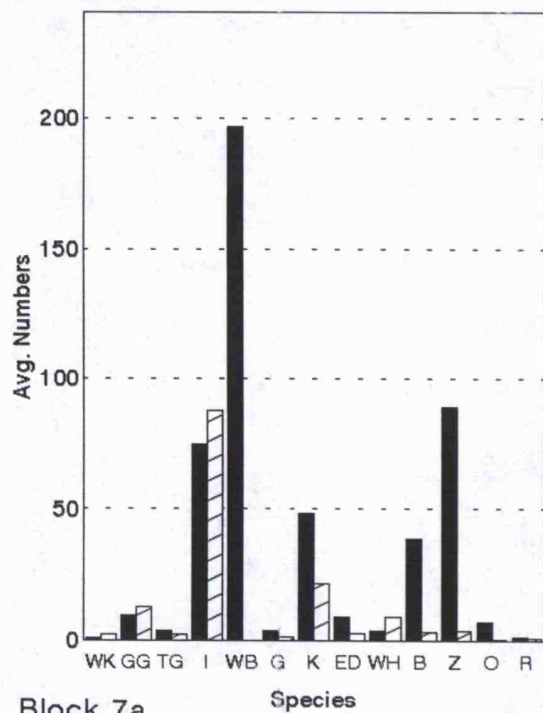
K Kongoni
ED Eland
WH Warthog
B Buffalo
R Rhino
Z Zebra
O Ostrich

■ Dry Season □ Wet Season

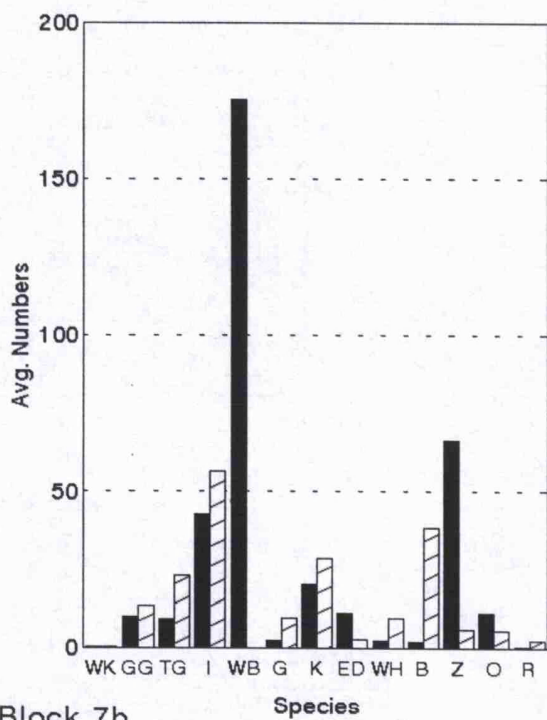




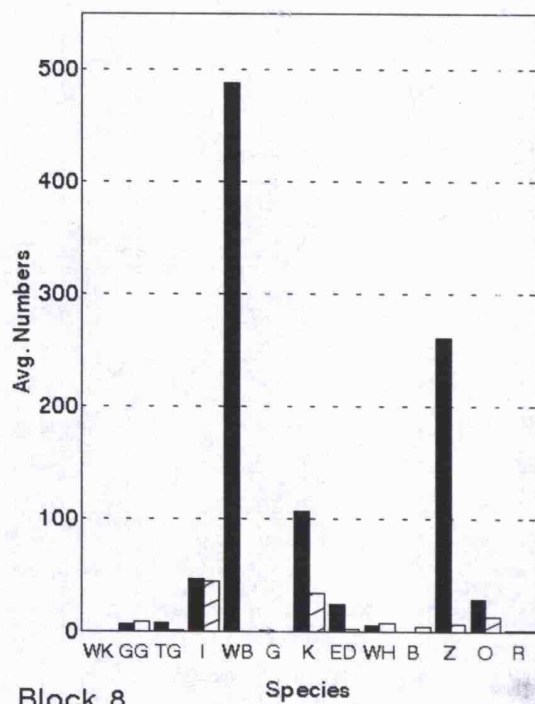
Block 6a



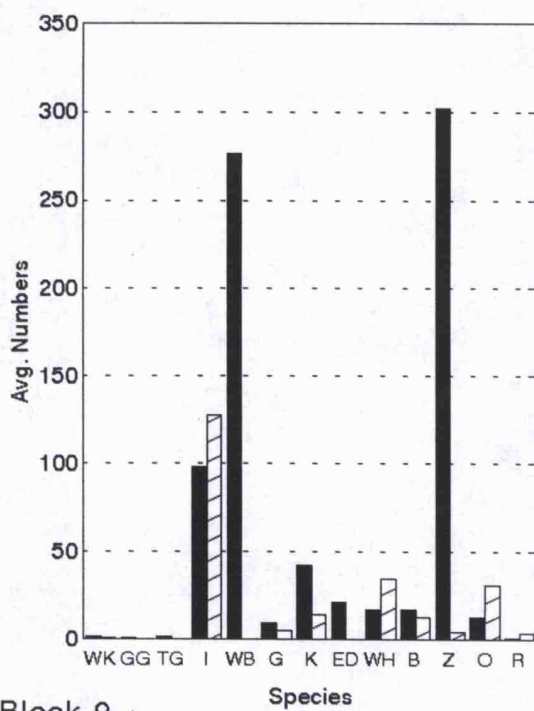
Block 7a



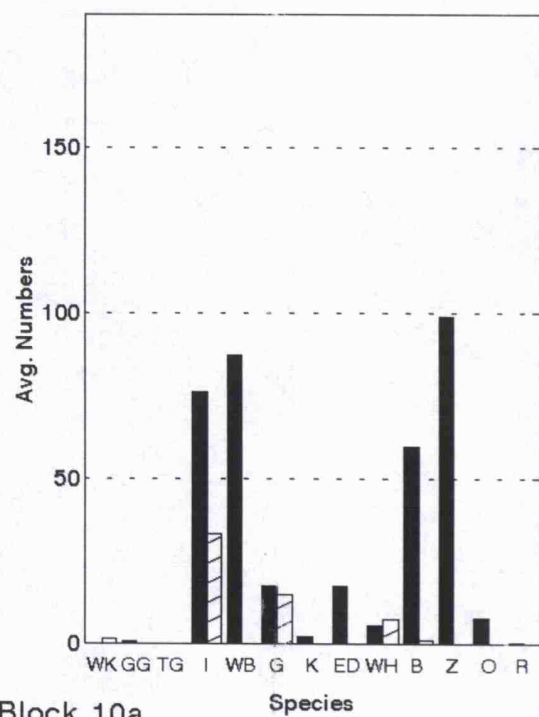
Block 7b



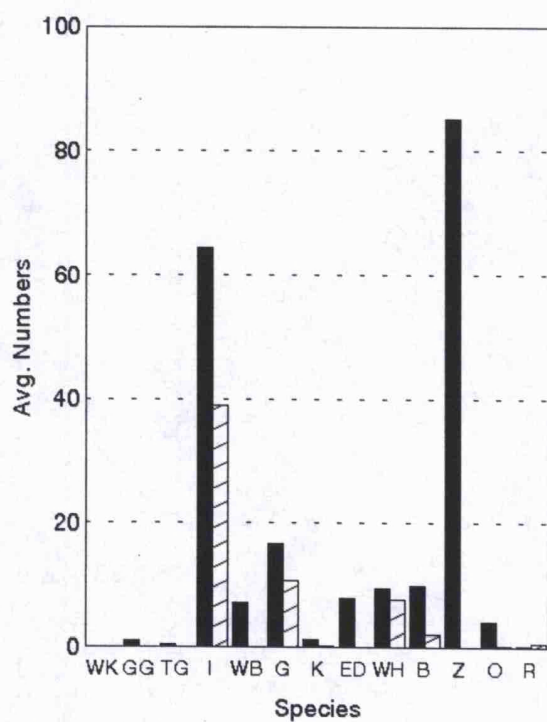
Block 8



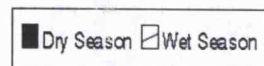
Block 9



Block 10a



Block 10b



Small-grazers showed large variation in their use of transects ($F=8.17$ $P<0.0001$ df 9,6). Transect 2, a burn plot in Sosian was used in preference to all the others, transect 6 at the swamps to the west of Hyena dam was also selected. Transect 2 had the shortest grasses sampled. Transect 6 which had 2 sections to it, 6.1 and 6.2 also had short grass. Of these 2 transects, 6.2 had very short vegetation e.g. (table 7.1) at certain times accounted for the high selection by small grazers. Transect 6.1 had taller grasses. This transect was also selected by medium grazers.

7.2.4 Wildlife distribution and use patterns using random measurements around the park

Analysis of the selection patterns using grass height as the selectivity index showed different species to select different areas. A cluster analysis using height grouped wildlife into 4 major clusters (Fig. 7.4).

Cluster 1 had only one species in it; Buffalo, found in the tallest vegetation

Cluster 2 had eland, Grant's gazelle, impala, kongoni, ostrich and warthog. These were found in the medium height range. Cluster 3 contained Thompson's gazelle which was found in the shortest vegetation while zebra and wildebeest were in a cluster 4, based on height and the total numbers of individuals counted. Cluster 4 fell in the same height range as cluster 2, but the numbers of individuals selecting this height was large.

7.2.5 Dung distribution patterns

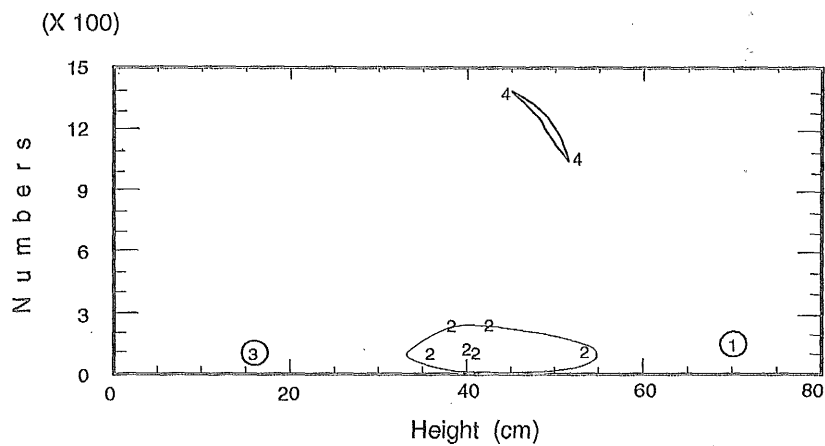
The first sample for this study taken in June 1993 was analysed to find out what transects were selected by the various herbivores. Medium sized grazers, small grazers and large grazers used the transects at variable intensities. Small grazers used transect 3 and 5 the most; medium sized grazers preferred transects 2 and 6.2 while large grazers used transects 4, 5 and 6.2 (table 7.5).

Comparisons between transects for 14 samples by date using an analysis of variance (table 7.6) showed that the variation in use of transects by the small grazers was significant for all samples except June 1994. Use by medium sized grazers varied significantly throughout the sampling period and that of large grazers did not vary in late July 1993, October 1993, January 1994 and March 1994 samples. But it is important to note that large grazers were few in the park (see chapter 5 for numbers) when compared with the more numerous medium sized grazers at the height of the dry season.

A two-way analysis of variance was used to determine the variation in dung density and therefore use within transects over time. Initial analysis included transect 8, sampled between February 1994 and June 1994. However, lack of data for this transect for part of the study (several months) made it difficult to run these analyses. Transect 8 was as

Fig. 7.4

Cluster of large herbivores based on grass height
and animal numbers in Nairobi National Park



Results of Clustering by Average Method

Observation	Cluster	Cluster	Frequency	Percentage
1. BUFFALO	1	1	1	10.0000
2. ELAND	2	2	6	60.0000
3. GRANTS	2	3	1	10.0000
4. IMPALA	2	4	2	20.0000
5. KONGONI	2			
6. OSTRICH	2			
7. THOMSONS	3			
8. WARTHOG	2			
9. WILDEBEEST	4			
10. ZEBRA	4			

a result removed from the main analysis. The results (table 7.7) showed that time and transect were significant sources of variation for all the species groups, but time was more significant for medium and large grazers (i.e that the changes in dung in the transect were temporal). Transect attributes were more significant in explaining small grazer distribution and time and transect together had significant impact on the distribution and use patterns of all the species groups.

In further analysis, transect 5 was also removed. The first point on this transect was too close to water attracting wildlife to this area, a fact that could have had significant impact on the distribution and use trends. The variation due to transect increased for small grazers and browsers (table 7.8c & d). The results were similar to those obtained when transect 8 was excluded alone (tables 7.8 a-d).

Table 7.5 Average densities for various sized herbivores by transect in June 1993.

Average Dung Density x 100 (Piles/m ²)				
Transect	Large grazers	Medium grazers	Small grazers	Browsers
1	0.073 ± 0.073	9.927 ± 1.046	-	0.073 ± 0.049
2	-	33.67 ± 1.677	0.109 ± 0.056	0.800 ± 0.171
3	-	19.018 ± 2.773	0.873 ± 0.256	0.873 ± 0.234
4	1.673 ± 0.263	0.982 ± 0.165	0.073 ± 0.073	0.655 ± 0.390
5	1.733 ± 0.434	14.20 ± 2.036	0.733 ± 0.300	0.267 ± 0.084
6.1	0.933 ± 0.321	15.06 ± 2.655	-	1.000 ± 0.354
6.2	1.400 ± 1.000	25.600 ± 2.000	-	3.000 ± 0.200
7	0	19.564 ± 1.755	0.145 ± 0.111	0.073 ± 0.049

Table 7.6 Analysis of variation in the dung distribution by species groups and between transects within a sampling period. The table shows that over much of the sampling period the use of transects by large herbivore groups varied significantly.

Sample	Small Grazers		Medium Grazers		Large Grazers		Browsers	
	F-ratio	P-value	F-ratio	P-value	F-ratio	P-value	F-ratio	P-value
6/1993	5.49	df 7,61 0.0001	29.99	df 7,61 0.0000	17.05	df 7,61 0.0000	5.87	df 7,61 0.0000
8/3/7/1993	2.71	df 7,61 0.0165	13.04	df 7,61 0.0000	—	—	2.83	df 7,61 0.0127
28/7/1993	23.54	0.0000	10.22	df 7,61 0.0000	1.43	0.21 NS df 7,61	5.02	0.002 df 7,61
8/1993	11.92	df 7,61 0.0000	11.17	df 7,61 0.0000	999.99	df 7,61 0.0000	7.33	0.0000
8/9/1993	7.83	df 7,61 0.0000	15.97	df 7,61 0.0000	999.99	df 7,61 0.0000	3.25	df 7,61 0.0054
29/9/1993	31.61	df 7,61 0.0000	44.76	df 7,61 0.0000	999.99	df 7,61 0.0000	2.23	df 7,61 0.0437
10/1993	16.28	df 7,61 0.0000	8.80	df 7,61 0.0000	1.48	0.191 NS	2.91	0.0109
11/1993	11.94	df 7,61 0.0000	17.74	df 7,61 0.0000	999.99	df 7,61 0.0000	2.36	0.0339
12/1993	2.95	df 7,61 0.0099	10.82	df 7,61 0.0000	2.27	df 7,61 0.040	0.32	df 7,61 0.94 NS
1/1994	8.26	df 7,61 0.0000	11.20	df 7,61 0.0000	2.31	df 7,61 0.371 NS	3.01	df 7,61 0.0087
2/1994	10.32	df 8,71 0.0000	8.25	df 8,71 0.0000	4.31	df 8,71 0.0003	5.60	df 8,71 0.0000
3/1994	3.56	df 8,71 0.0017	10.62	0.0000	1.92	0.071 NS	6.41	0.0000
5/1994	999.99	df 8,71 0.0000	—	—	2.55	0.017	999.99	0.0000
6/1994	0.64	df 8,71 0.739 NS	47.86	0.0000	—	—	—	—

- Data were not analysable because most dung density values were zero.

Table 7:7 Results of a two way analysis of the effects of time and transect on dung density distribution in Nairobi National Park (excluding transect 8).

a)

Large Grazers			
Sources of Variance	F-ratio	P-value	df
Time	34.11	<0.0001	13
Transect	22.96	<0.0001	7
Time x Transect	7.90	<0.0001	91

b)

Medium Grazers			
Sources of Variance	F-ratio	P-value	df
Time	63.2	<0.0001	13
Transect	34.3	<0.0001	7
Time x Transect	14.1	<0.0001	91

c)

Small Grazers			
Sources of Variance	F-ratio	P-value	df
Time	23.93	<0.0001	13
Transect	53.56	<0.0001	7
Time x Transect	8.65	<0.0001	91

Table 7.8 Results of 2-way analysis of variance on effects of time and transect on dung density distribution in Nairobi National Park(Excluding transects 5 and 8)

(a)

Large grazers			
Sources of variation	F-ratio	P-value	df
Time	36.7	<0.0001	13
Transect	26.7	<0.0001	6
Time X Transect	11.8	<0.0001	78

(b)

Medium-sized grazers			
Sources of variation	F-ratio	P-value	df
Time	56.1	<0.0001	13
Transect	39.5	<0.0001	6
Time X Transect	14.0	<0.0001	78

(c)

Small grazers			
Sources of variation	F-ratio	P-value	df
Time	21.3	<0.0001	13
Transect	66.8	<0.0001	6
Time X Transect	10.8	<0.0001	78

(d)

Browsers			
Sources of variation	F-ratio	P-value	df
Time	17.23	<0.0001	13
Transect	28.49	<0.0001	6
Time X Transect	3.84	<0.0001	78

7.2.6 Interaction between vegetation height and dung distribution

Dung data were combined for all species types in order to find out whether there were differences arising from the species groups. A selection of several samples covering high, medium and low vegetation biomass and height was made. Analysis showed that species type, transect and an interaction of these 2 variables all accounted for some variation in the dung density (table 7.9).

Height measures were ordered from the lowest to the tallest and corresponding dung densities were cumulated along the height gradient and plotted. This was done to determine the 50% and 75% cut-off point along the vegetation height gradient and also to determine whether height was an important factor in explaining wildlife distribution and

use patterns in NNP. Graphs of cumulative dung density against average height for systematically selected samples (Figs. 7.5 a to g) showed the following:

1. Large grazers (buffalo) used taller vegetation than the other species groups.
2. Smaller grazers preferred shorter vegetation.
3. There was a wide selection spectrum by the medium sized grazers (wildebeest, zebra, kongoni). This group ranged widely across the height band from short to tall grass.

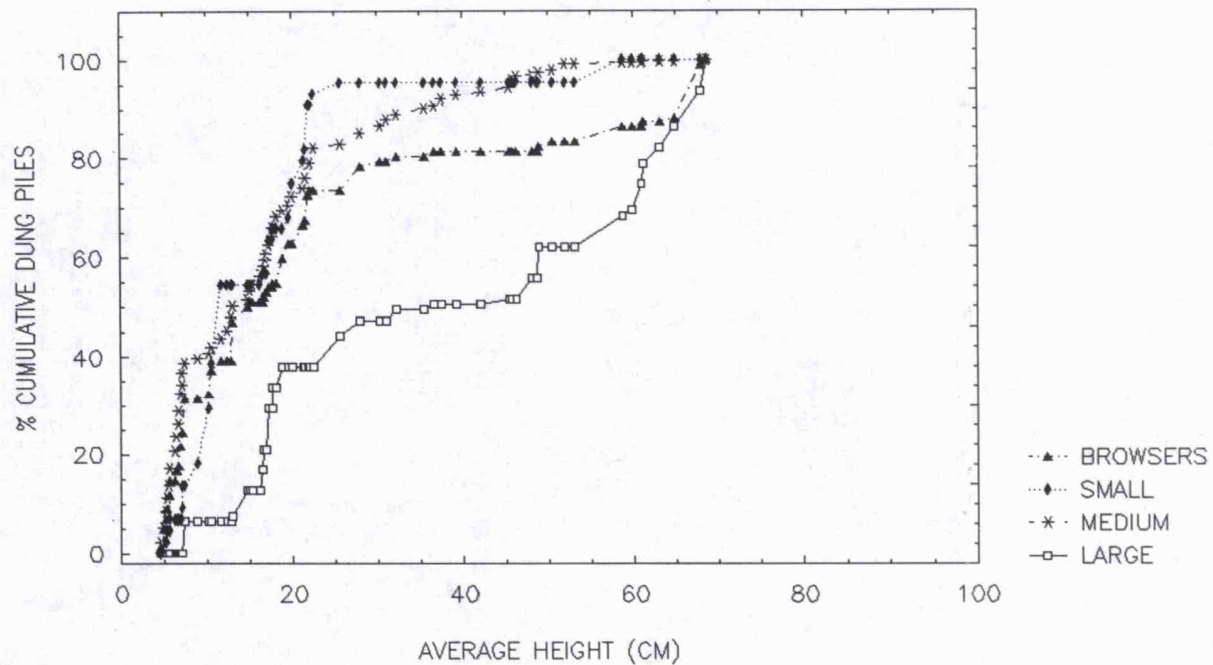
The June 1994 sample was different from other samples. Small grazers were not sampled in any of the transects and only very few medium sized grazers. During this month grasses were tall in all transects following the long rains. A close look at the trends in vegetation use showed that the animals used progressively shorter vegetation as the dry season progressed.

Table 7.9 Two-way analysis of variance on dung by transect and species for selected samples.

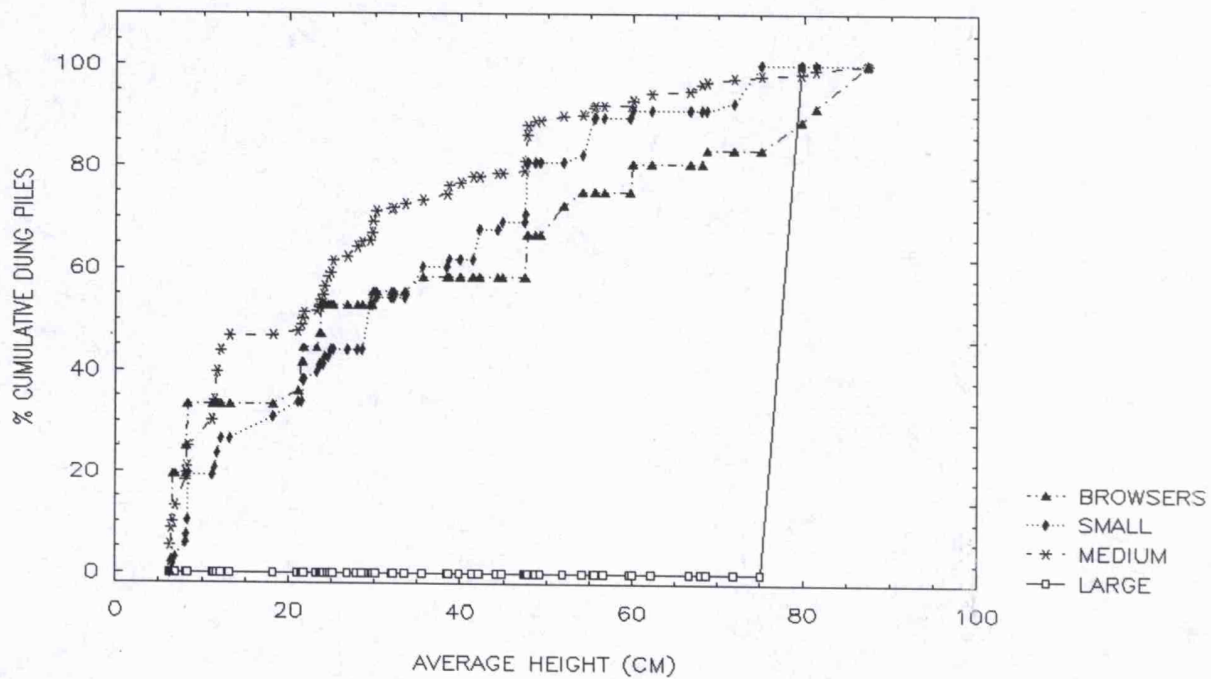
Month	TRANSECT			SPECIES			TRANSECT BY SPECIES		
	F-Ratio	P	df	F-Ratio	P	df	F-Ratio	P	df
June 93	27.95	0.000	10,7	538.24	0.000	10,3	29.84	0.000	10,21
Aug 93	20.40	0.000	10,7	97.62	0.000	10,3	7.95	0.000	10,21
Oct 93	7.37	0.000	10,7	56.36	0.000	10,3	9.54	0.000	10,21
Dec 93	11.59	0.000	10,7	70.92	0.000	10,3	10.16	0.000	10,21
Feb 94	11.34	0.000	11,8	81.64	0.000	11,3	8.65	0.000	11,24
June 94	47.93	0.000	11,8	66.14	0.000	11,3	47.72	0.000	11,24

Sources of variation - Main effects
Transect
Species
2-way variation Transect by Species

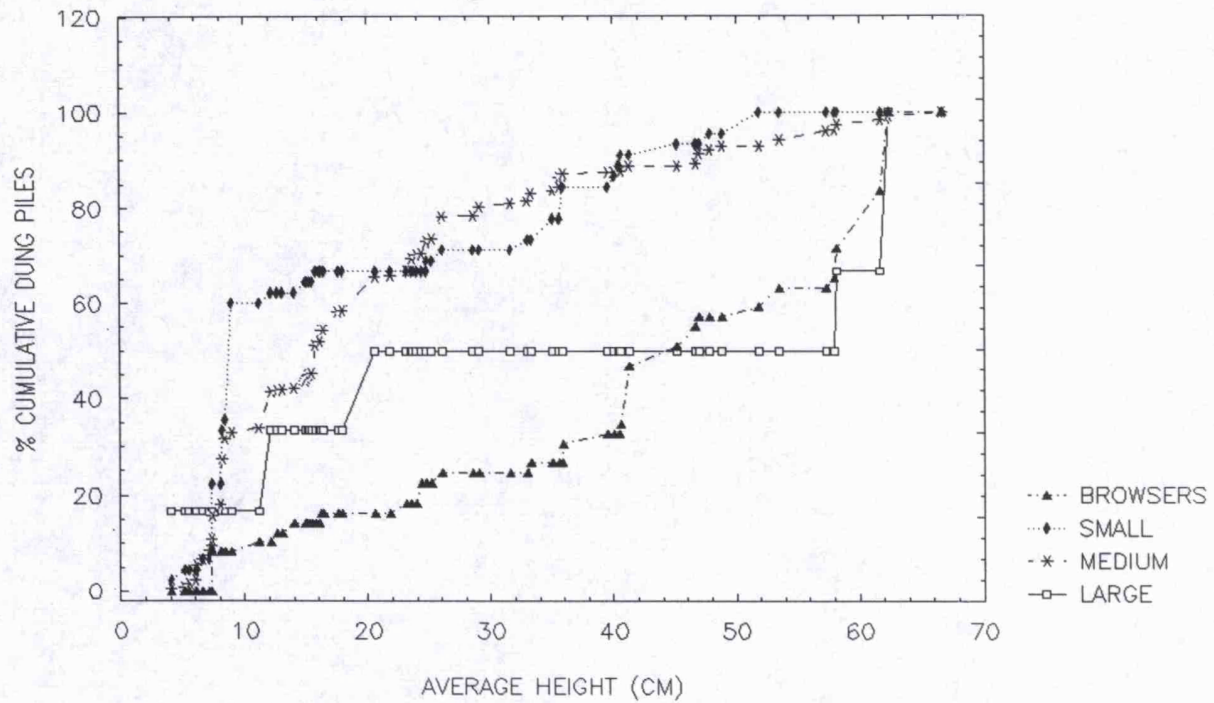
FIG 7.5
 CUMMULATIVE DUNG FOR DIFFERENT SIZED HERBIVORES
 AGAINST MEAN GRASS HEIGHT IN NAIROBI NATIONAL PARK
 a) JUNE 1993



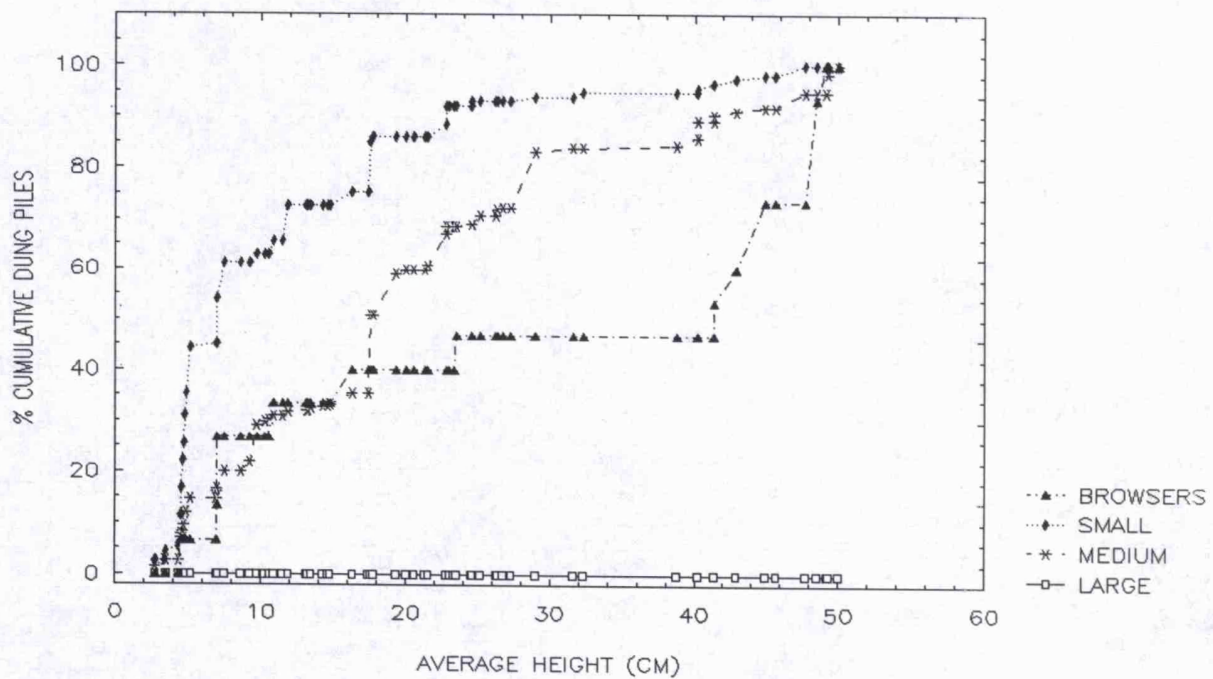
b) EARLY JULY 1993



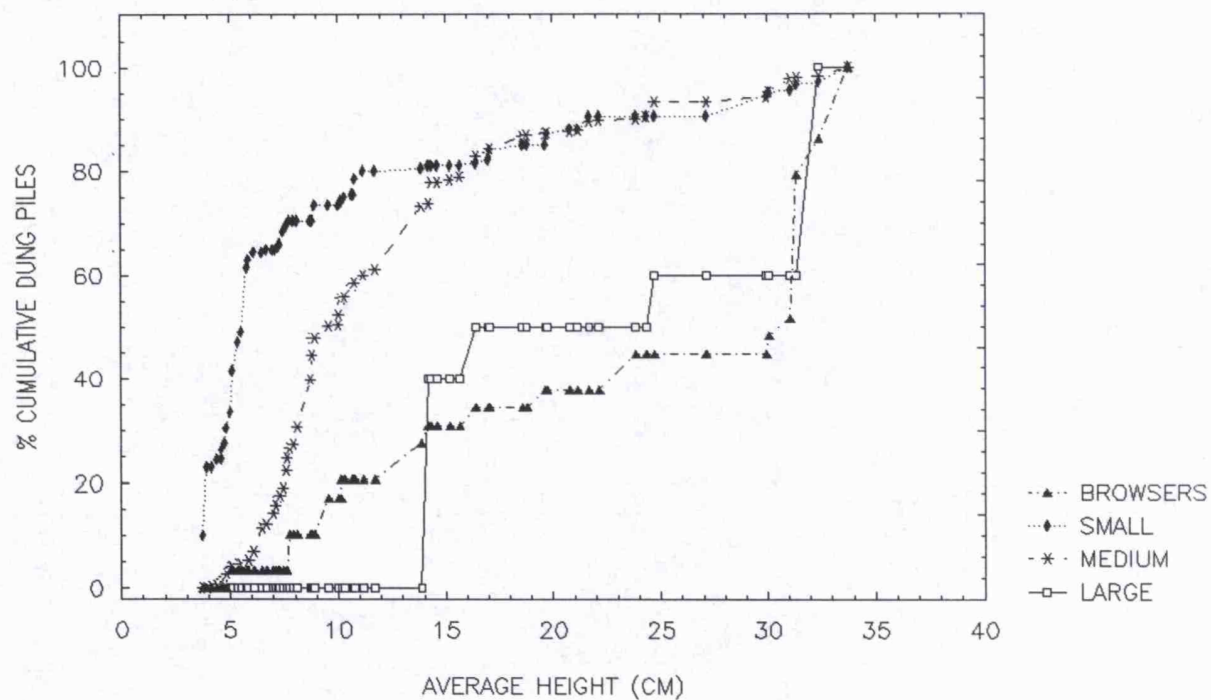
CUMULATIVE DUNG FOR DIFFERENT SIZED HERBIVORES
AGAINST MEAN GRASS HEIGHT IN NAIROBI NATIONAL PARK
C) LATE JULY 1993



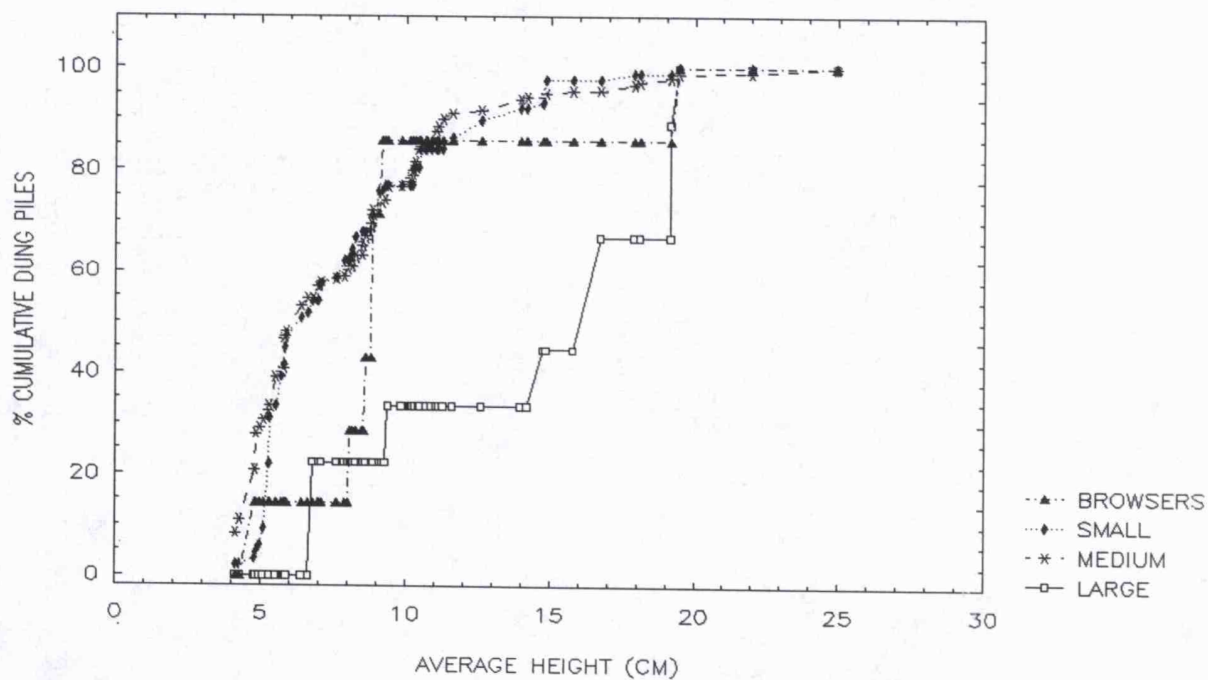
d) EARLY SEPTEMBER 1993



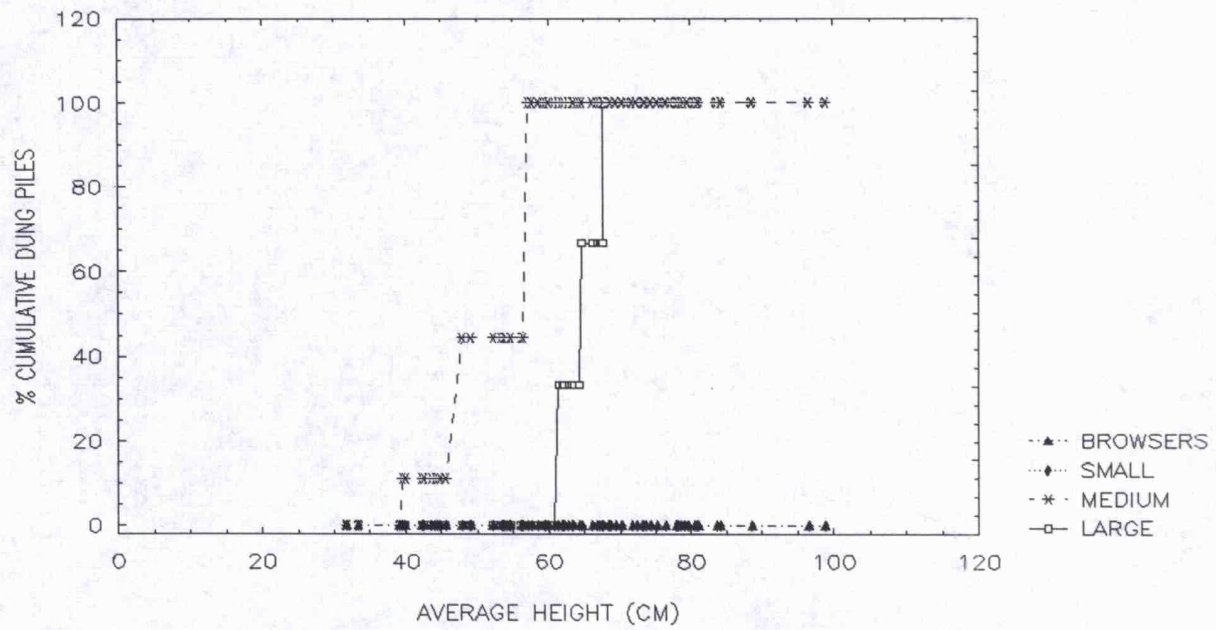
CUMULATIVE DUNG FOR DIFFERENT SIZED HERBIVORES
AGAINST MEAN GRASS HEIGHT IN NAIROBI NATIONAL PARK
e) OCTOBER 1993



f) DECEMBER 1993



CUMULATIVE DUNG FOR DIFFERENT SIZED HERBIVORES
 AGAINST MEAN HEIGHT IN NAIROBI NATIONAL PARK
 g) EARLY JUNE 1994



7.3 Vegetation utilization patterns around settlements

7.3.1 Vegetation distribution patterns around settlements

Vegetation biomass was averaged for the 10 transects for each sampling occasion during the study. The results showed different means (table 7.10) for the different occasions. Multiple comparisons using the Student-Newman's test showed differences in quantity of biomass based on the weather conditions at the time data were collected ($H=211.2$, $p<0.0001$, $df\ 7$). Using a pairwise comparison, similar samples were grouped initially into 3 seasons, wet, dry and extreme dry. But a further analysis on the wet season samples showed that the late July 1994 biomass was still significantly lower than the other samples grouped with it ($H=23.7$, $p<0.0001$, $df\ 3$). Exclusion of the late July 1994 sample from the wet season group removed these differences ($H=4.39$ $p=0.111$). In all, 4 seasons therefore emerged, wet season (May 1994, June 1994 and early July 1994), early dry (End of July 1994), dry (July 1993, August 1993 and August 1994) and extreme dry season or drought (October 1993).

These seasonal groups were analysed for differences between transects and along the distance gradient from settlement. An analysis of variance on vegetation biomass between transects showed that some transects had higher biomass than others even within the same season. The patterns of vegetation use from wet to dry season could be inferred by the progressive decline in both vegetation height and biomass along the transects. The largest variation between transects was in the wet season. The value of H was highest during this season and declined along the seasonality gradient from wet to extreme dry (table 7.11). Although the overall mean biomass was at its highest in the wet season ($91.92 \pm 2.462\text{g/m}^2$, $73.08 \pm 3.85\text{g/m}^2$, $65.50 \pm 1.938\text{g/m}^2$ and $33.70 \pm 2.231\text{g/m}^2$ from wet to extreme dry respectively), certain areas had higher biomass than others (table 7.12). Transect 1 in Olrimirui and transect 9 in the Kitengela area had the highest biomass while transect 10 in the Kitengela area had the least.

Vegetation was quickly consumed in the wet season in transects 1, 2, 3, 4, 5 and 6 in Olrimirui and Enkigirri. By the dry season, the northward movement of the migrants was obvious from the significant decline in the biomass. Analysis of vegetation biomass along the distance gradient away from settlement over the 4 seasons showed that vegetation biomass was higher near the settlement in the wet, early dry and dry seasons (table 7.13). Overall, the differences in the wet, early dry and dry seasons were significant (table 7.14). Under extremely dry conditions however, the differences along this gradient were not significant.

Most of the differences in distance were between the two points closest to the settlement

(0 to 50) and all other distances. The only exception was 0 and 50m in the early dry, 0 and 200m in the dry season and between 50m and all other distances away (table 7.15). These differences had been obscured perhaps as a result of the intense grazing and trampling around the settlement.

The largest differences as indicated by the means (table 7.15) were between the 0 distance and 250 m to 450 m in the wet season and 0 and 400 m in the early dry season. There was a significant interaction between distance and transect found in the dry season ($F=1.63$ $p<0.0001$ 9,90).

Table 7.10 Vegetation biomass in 10 transects around settlements averaged for each transect for each sampling occasion

T. N°	7/93	8/93	10/93	5/94	6/94	1/7/94	25/7/94	8/94
1	79.53 ± 10.60	74.81 ± 9.38	38.98 ± 7.59	135.44 ± 10.67	108.67 ± 9.92	89.37 ± 7.69	83.47 ± 6.91	66.54 ± 8.69
2	73.23 ± 9.57	72.84 ± 8.40	34.25 ± 6.72	84.65 ± 13.01	72.05 ± 6.16	57.09 ± 7.41	72.84 ± 6.81	50.79 ± 5.45
3	-	76.38 ± 10.88	32.29 ± 6.19	110.64 ± 15.87	105.52 ± 7.57	83.47 ± 8.26	60.63 ± 6.50	63.39 ± 8.22
4	-	90.56 ± 12.14	47.25 ± 7.89	108.67 ± 8.00	90.16 ± 7.85	81.89 ± 7.49	58.66 ± 8.01	51.18 ± 3.64
5	-	85.44 ± 9.63	45.28 ± 9.33	129.93 ± 14.58	95.28 ± 7.59	80.32 ± 6.54	66.15 ± 6.91	61.03 ± 5.11
6	-	103.15 ± 13.49	46.85 ± 7.59	111.82 ± 11.18	94.89 ± 15.15	80.71 ± 6.65	78.35 ± 7.37	66.15 ± 10.67
7	51.18 ± 6.12	60.63 ± 8.44	27.56 ± 5.10	56.30 ± 14.36	101.58 ± 12.25	91.34 ± 6.22	75.99 ± 6.87	59.45 ± 7.13
8	64.18 ± 9.94	49.21 ± 7.62	22.84 ± 5.81	56.70 ± 14.36	102.37 ± 11.83	105.91 ± 16.00	72.05 ± 8.10	64.18 ± 7.83
9	-	52.37 ± 4.69	20.87 ± 3.14	106.69 ± 20.89	126.38 ± 17.88	126.78 ± 21.71	114.57 ± 18.38	77.56 ± 16.16
10	-	42.52 ± 4.88	20.87 ± 4.95	49.61 ± 13.23	54.38 ± 10.58	59.06 ± 11.13	48.03 ± 11.52	43.31 ± 9.63

NB. T.N° = Transect Number.

Table 7.11 Results of an analysis of variance on vegetation biomass between transects in the 4 seasonal categories.

Season	F-Ratio	P-value
Wet	13.03	<0.0001
Early Dry	4.50	<0.0001
Dry	3.293	0.0009
Extreme Dry	2.71	0.0078

df = 9,10

Table 7.12 Changes in mean grass biomass by transect for each season.

TRANSECT	WET	EARLY DRY	DRY	EXTREME DRY
1	111.160 ± 6.278	83.471 ± 6.912	73.627 ± 5.443	38.90 ± 7.59
2	71.264 ± 5.591	72.840 ± 6.805	65.621 ± 4.839	34.26 ± 6.72
3	99.874 ± 6.607	60.634 ± 6.503	69.886 ± 6.805	32.29 ± 6.19
4	93.574 ± 4.779	58.666 ± 8.014	70.871 ± 7.531	47.25 ± 7.89
5	101.842 ± 6.788	66.146 ± 6.912	73.232 ± 5.949	45.28 ± 9.33
6	95.806 ± 7.056	78.351 ± 7.374	84.650 ± 9.315	46.85 ± 7.59
7	83.075 ± 5.982	75.989 ± 6.869	57.091 ± 4.144	27.56 ± 5.10
8	88.325 ± 8.854	72.051 ± 8.097	59.190 ± 4.928	22.84 ± 5.81
9	119.953 ± 11.428	114.573 ± 18.378	62.603 ± 6.055	20.87 ± 3.14
10	54.334 ± 6.578	48.035 ± 11.524	42.916 ± 5.269	20.87 ± 4.949

Table 7.13 Mean seasonal vegetation biomass along a distance gradient away from settlement

Distance away from settlement	Biomass			
	wet	early dry	dry	extreme dry
0	145.23 ± 19.28	109.57 ± 21.55	91.31 ± 14.78	25.55 ± 8.23
50	120.69 ± 12.00	92.25 ± 11.33	65.18 ± 6.98	32.05 ± 7.64
100	88.21 ± 7.23	68.00 ± 5.56	67.06 ± 6.19	29.45 ± 6.22
150	84.02 ± 8.15	73.19 ± 8.48	70.52 ± 7.40	44.18 ± 7.58
200	91.53 ± 7.34	80.12 ± 6.62	80.20 ± 8.15	55.87 ± 9.18
250	70.45 ± 5.35	61.93 ± 7.16	57.24 ± 5.10	30.75 ± 6.47
300	86.62 ± 11.73	73.19 ± 11.00	69.29 ± 8.69	32.48 ± 4.67
350	80.99 ± 9.00	68.43 ± 8.31	64.75 ± 6.84	26.42 ± 6.88
400	75.36 ± 9.01	49.81 ± 8.60	53.27 ± 5.75	29.86 ± 5.34
450	79.98 ± 7.91	62.37 ± 5.69	50.96 ± 4.23	30.75 ± 6.82
500	88.06 ± 8.78	64.96 ± 7.42	58.47 ± 5.34	33.35 ± 9.20

Table 7.14 Results of an analysis of variance on biomass and distance gradient away from settlement.

Season	F-Ratio	P-value
Wet	15.62	<0.0001
Early Dry	3.35	<0.0010
Dry	5.10	<0.0001
Extreme Dry	1.71	0.091 NS

Table 7.15 Student-Newman-Keuls-Method Pairwise multiple comparison of vegetation biomass along a distance gradient.

Season	distances (m)	diff of means	q
WET	0-50	24.54	4.43
	0-100	57.02	10.30
	0-150	61.21	11.06
	0-200	53.70	9.70
	0-250	74.78	13.51
	0-300	58.61	10.59
	0-350	64.24	11.61
	0-400	69.87	12.62
	0-450	65.25	11.79
	0-500	57.17	10.33
	50-100	32.48	5.87
	50-150	36.67	6.62
	50-200	29.16	5.27
	50-250	50.24	9.08
	50-300	34.07	6.15
	50-350	39.70	7.17
	50-400	45.33	8.19
	50-450	40.71	7.35
	50-500	32.63	5.90
EARLY DRY	0-50	17.32	1.95 NS
	0-100	41.58	4.68
	0-150	36.38	4.10
	0-200	29.45	3.32
	0-250	47.64	5.36
	0-300	36.38	4.10
	0-350	41.14	4.63
	0-400	59.77	6.73
	0-450	47.21	5.31
	0-500	44.61	5.02
DRY	0-50	17.13	3.69
	0-100	21.37	4.61
	0-150	15.53	3.35
	0-200	5.61	1.21 NS
	0-250	27.91	6.02
	0-300	18.90	4.07
	0-350	24.10	5.19
	0-400	34.37	7.41
	0-450	31.68	6.83
	0-500	26.22	5.65
	200-250	22.30	4.61
	200-400	28.76	6.20
	200-450	26.07	5.62
	200-500	20.61	4.44
EXTREME DRY	There were no significant differences along the distance gradient in this season.		

7.3.2 Large herbivore occupancy patterns around settlements.

Dung data were classified by the size of the grazing herbivore into small, medium and large; by feeding type into grazer or browser and into cattle and 'shoat' (sheep and goat). Cattle and 'shoats' were left in separate categories due to their importance around settlements.

Dung data were split by season to match the biomass data and allow for seasonal comparisons between dung and biomass trends. The highest occupancy by medium sized-grazers was found in transects 7 and 8 in the Kitengela followed by the dry season in plots 7, 8, 9 and 10 (Fig. 7.6a). For the small grazers (Fig. 7.6b), transect 10 in the Kitengela was preferentially used in dry conditions. Transect 7 had the highest occupancy in the extreme dry conditions.

Browsers used transect 2 and 10 more than the others (Fig. 7.6c). Transect 2 was a wooded plot with predominantly *Acacia drepanolobium*. They were absent in transect 4. Transect 2, 7 and 8 were used the least by shoats (Fig. 7.6d) and transect 7 by cattle (Fig. 7.6e).

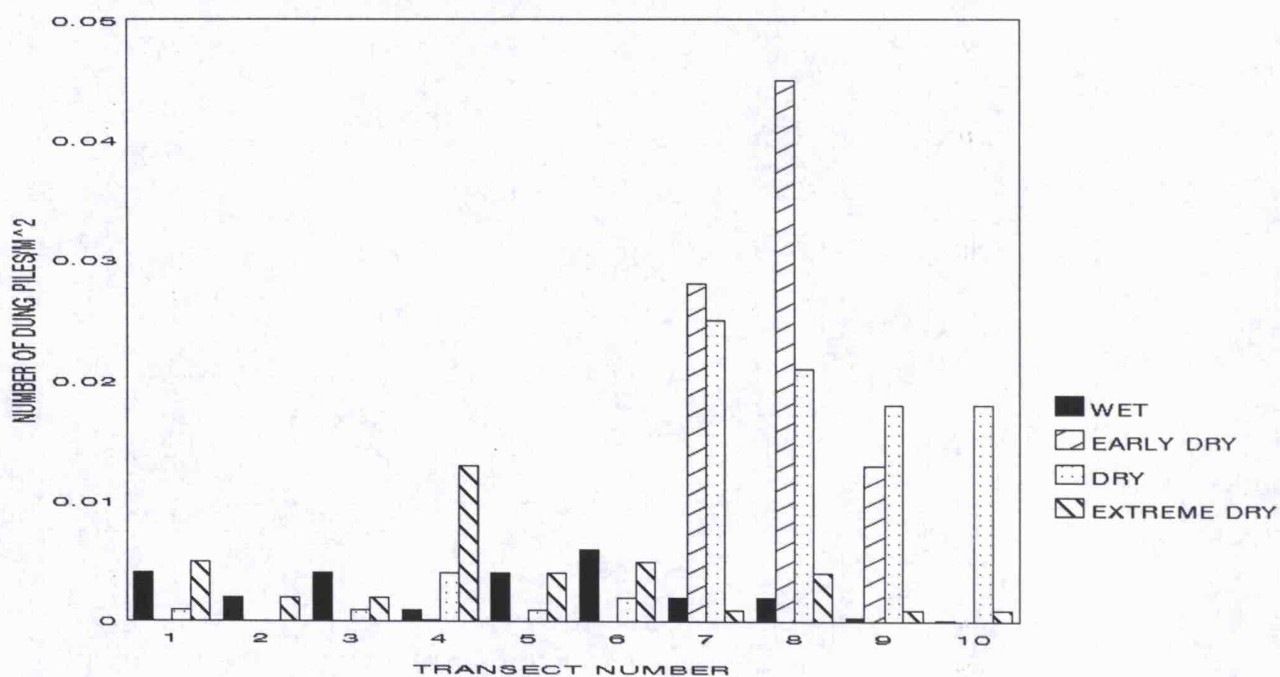
Analysis of use patterns between and along the transects was carried out for each season for each species group. Analysis of variance generally showed that occupancy around settlements was not the same for the different species groups between transects within a sampling season (table 7.16 a-e). However, there were several exceptions such as cattle in the early dry season, browsers in early dry and extreme dry conditions and small grazers in extreme dry season. These showed no difference in the way transects were used.

The largest differences between transects were found in the early dry season for medium sized grazers where a pairwise comparison showed that transect 7 and 8 differed significantly from all other transects ($p < 0.05$). In the dry season, there were distinct differences between the use of all transects in Oirimirui and those in Kitengela. Transects 7, 8, 9 and 10 in Kitengela were more intensively used by medium sized grazers than transects 1, 2, 3, 4, 5 and 6. Pairwise comparisons gave a $p < 0.05$. Comparisons within these 2 groups showed there was no significant difference. Wildebeest dung was the most numerous in this category of herbivores.

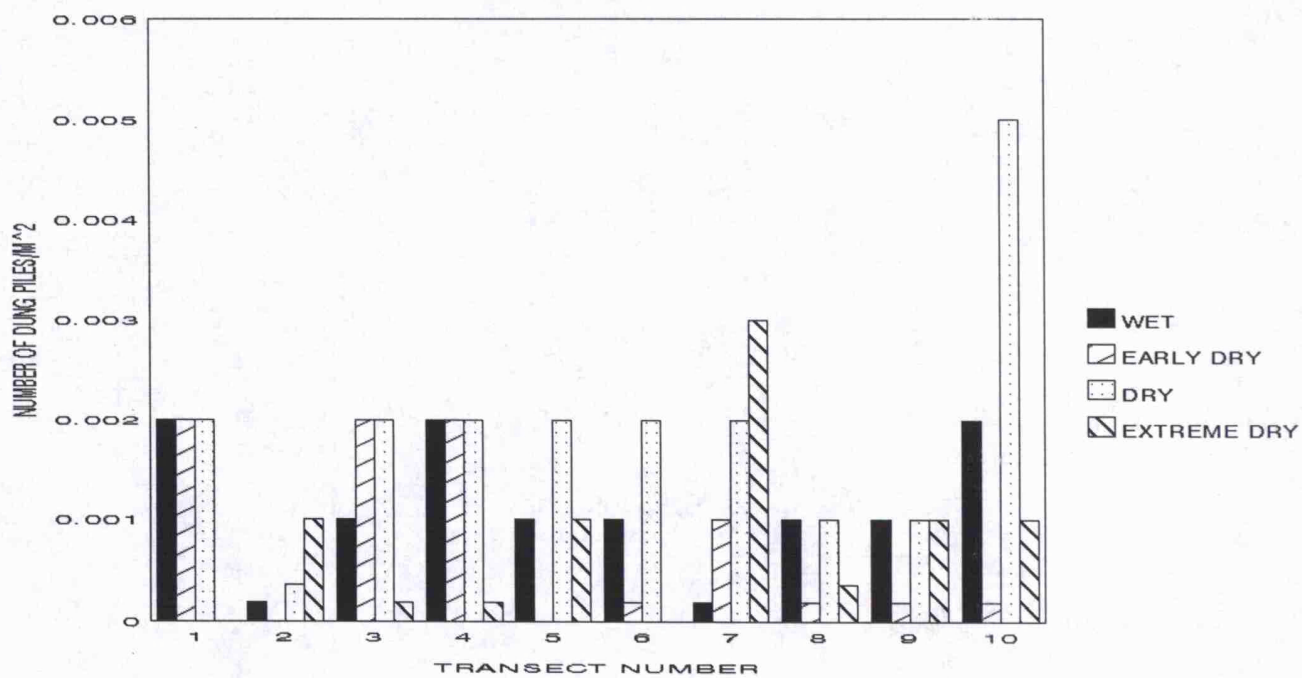
Unlike the medium-sized grazers the Kitengela/Oirimirui distinction was not present.

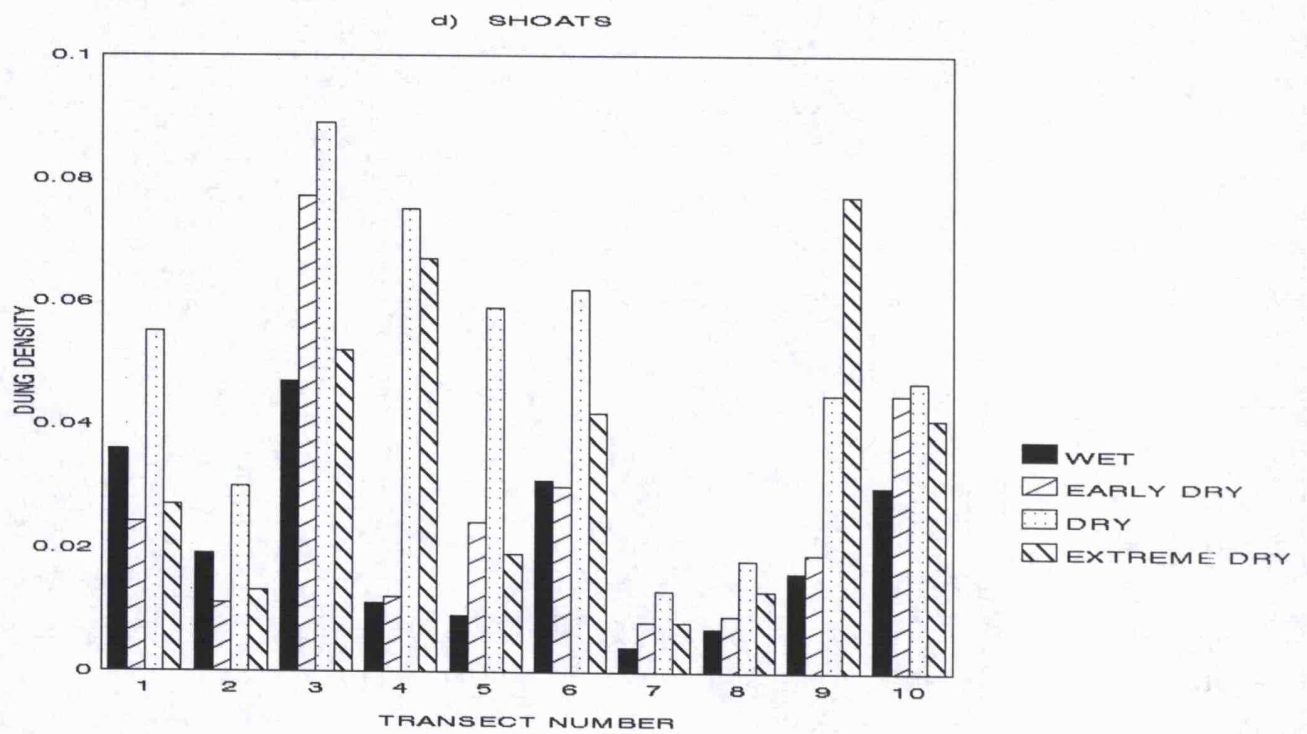
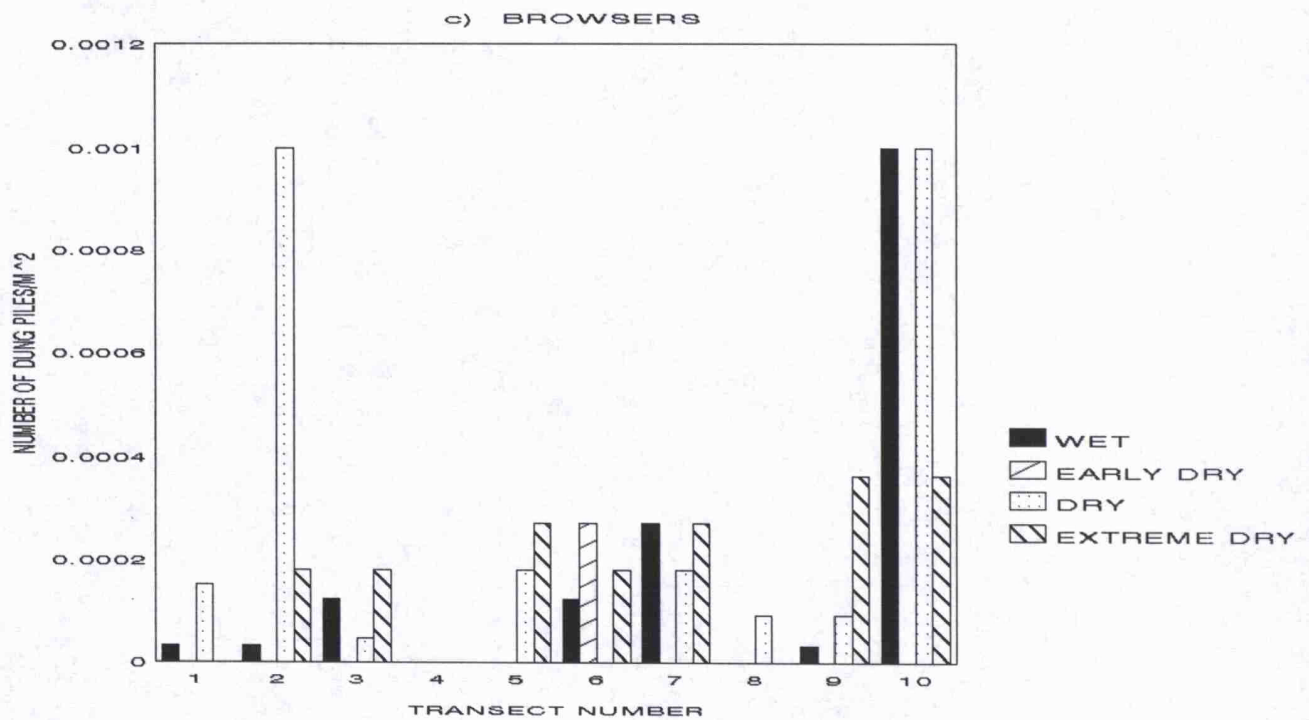
Analysis of dung patterns along the gradient away from settlements yielded different results. For most of the wildlife groups, the use patterns along the gradient were not significantly different i.e. use was no different close to or further away from the settlement. Among the wild herbivores significant differences were found in the distance gradient for the medium sized category and only under extreme dry conditions with the highest use at 350 m in the dry season and 400 m in the early dry season (Fig. 7.7 a). There were no significant differences for small grazers (Fig. 7.7b) and browsers (Fig. 7.7c) (though some distances had slightly more dung than others).

FIG 7.6
Seasonal changes in dung density for each transect in the settlement study
a) MEDIUM GRAZERS

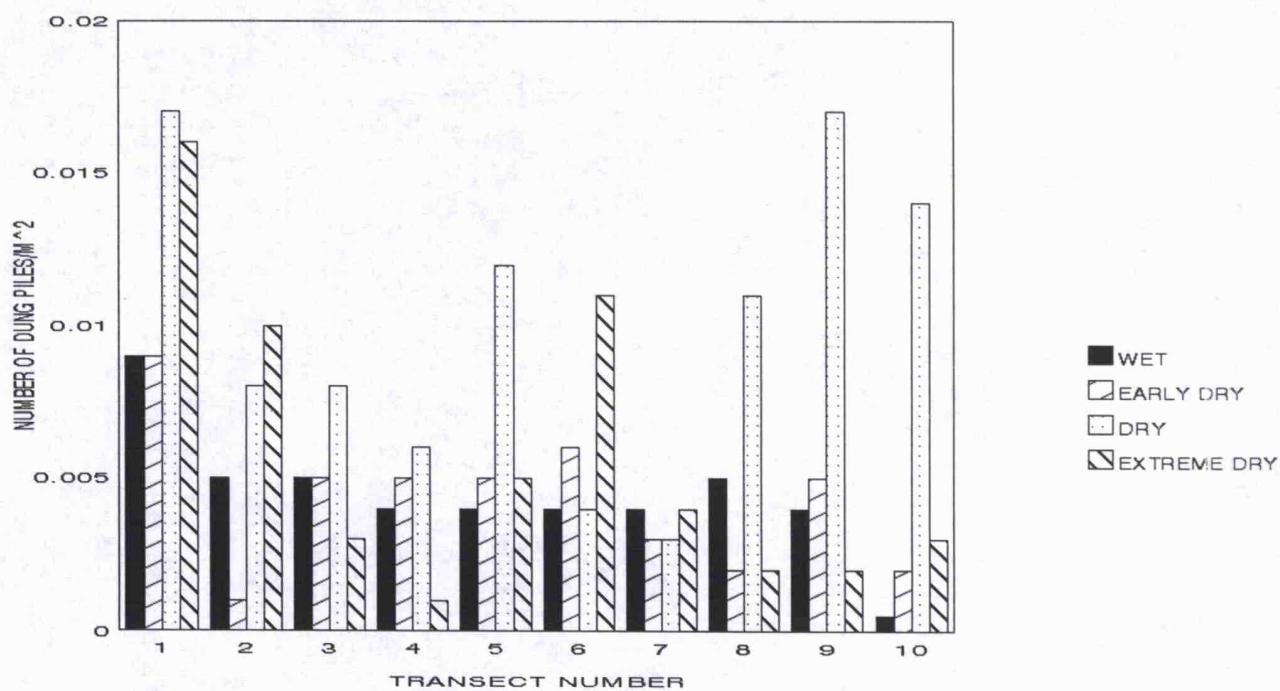


b) SMALL GRAZERS





e) CATTLE



Without exception differences were significant for livestock, with substantial use confined to the immediate surroundings of the settlement (Fig. 7.7 d & e) during the four seasons. This intense use did not spread too far out on the transects; beyond the 50 m there were no distinctive trends (table 7.17 a-e).

Anova for interactions between transect and distance against dung density showed significant interactions in cattle occupance only in the wet season ($F=1.87$, $p<0.0001$ df 9,10). For all the other transects, there were no interactions.

Comparisons of use patterns in the 10 transects between the various herbivore groupings by season using two-way analysis of variance showed the following:

Dry season use varied between species ($F=93.30$, $p<0.05$, df 4 and $F=1.97$). All species differed in their use patterns ($p<0.05$) with the exception of cattle and medium-sized grazers.

In the wet seasons, differences were significant for both species and transect ($F=47.40$, $p<0.05$ df 5 and $F=3.24$, $p<0.05$, df 9) respectively. But when pairwise comparisons were done, only shoat were found to differ from all the other species groupings. In the early dry season only shoat distribution and use of transects differed significantly with all the others, medium sized grazers from browsers and small sized grazers. Results from analysis of variance demonstrated the differences ($F=22.96$, $p<0.05$ df 4) for species. In the extreme dry season, only shoat distribution differed from the other species groups.

Table 7.16 Results of analysis of variance on herbivore use (dung density - piles/m²) by transects around settlements for each season.

(a). Small grazers

Season	F-Ratio	P-Value
Wet	2.68	0.006
Early Dry	2.45	0.015
Dry	2.31	0.018
Extreme Dry	1.72	0.100 NS

(b) Medium Grazers

Season	F-Ratio	P-Value
Wet	2.77	0.0044
Early Dry	35.27	<0.0001
Dry	12.55	<0.0001
Extreme Dry	15.78	<0.0001

(c) Cattle

Season	F-Ratio	P-Value
Wet	3.00	0.002
Early Dry	1.89	0.063 NS
Dry	2.80	0.004
Extreme Dry	2.24	0.026

* NS.

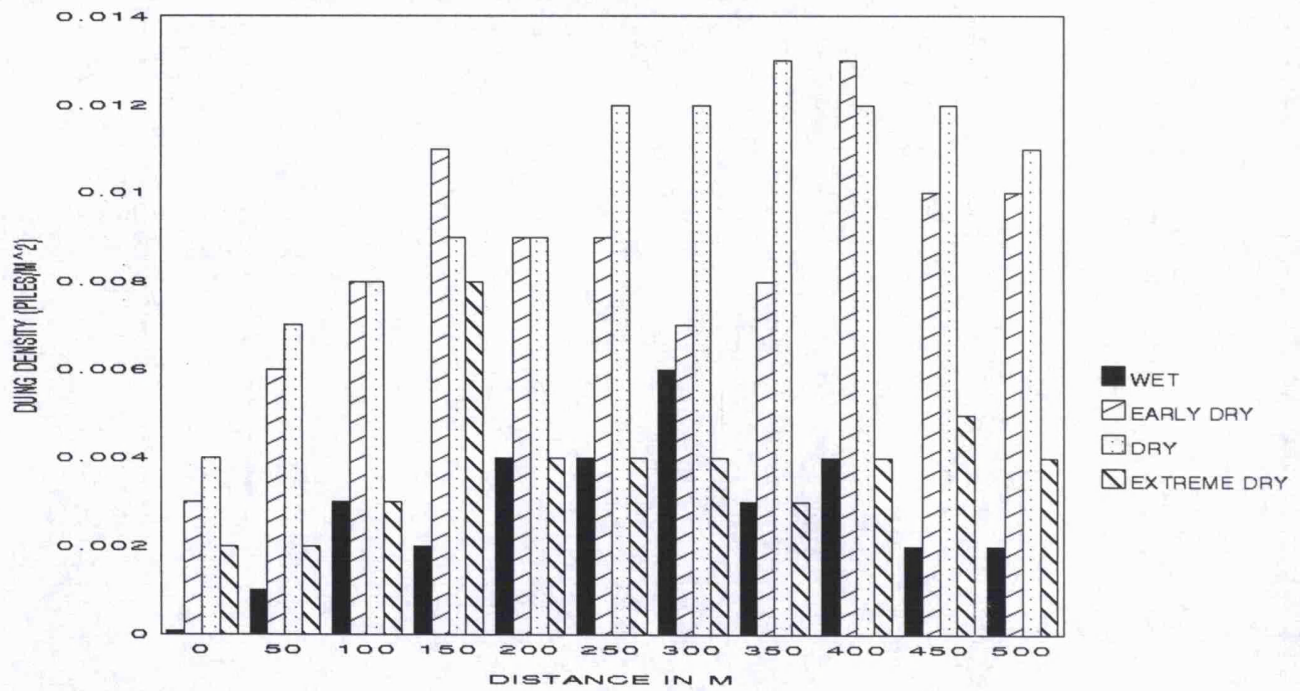
(d) Shoats

Season	F-Ratio	P-Value
Wet	4.90	<0.0001
Early Dry	2.92	<0.0044
Dry	4.23	<0.0001
Extreme Dry	6.01	<0.001

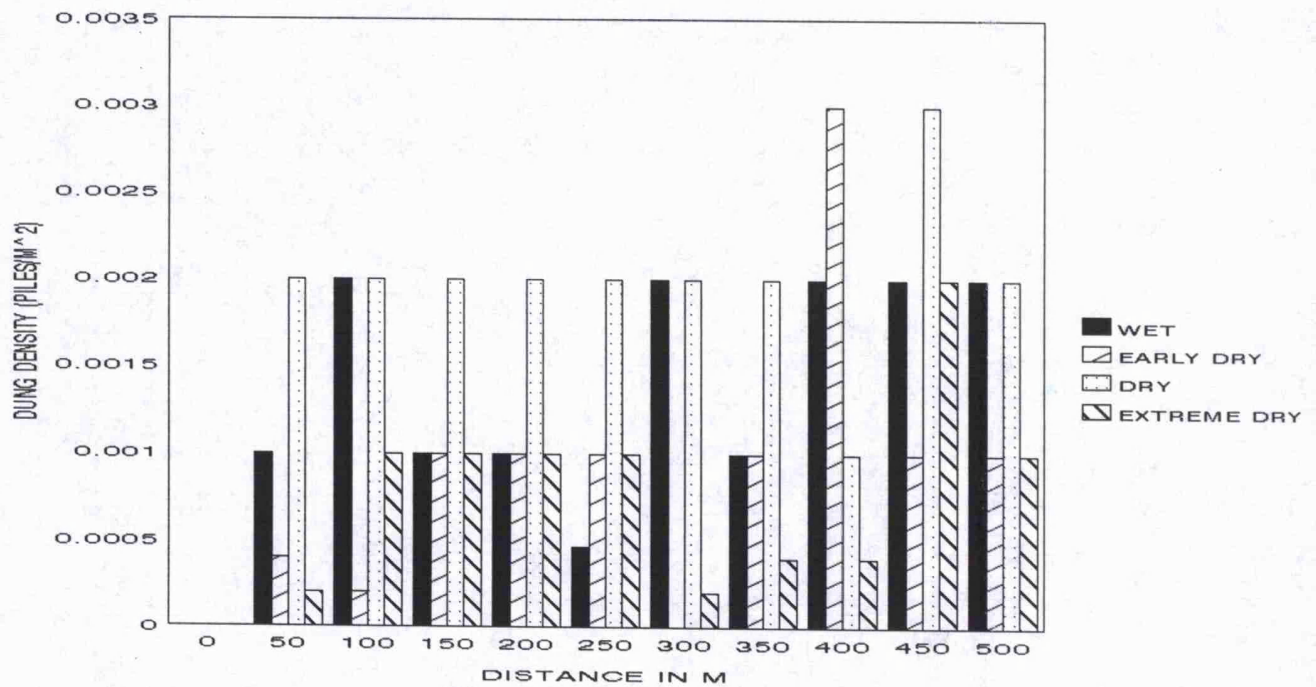
(e) Browsers

Season	F-Ratio	P-Value
Wet	3.31	0.0008
Early Dry	1.45	0.1786 NS
Dry	3.55	0.0005
Extreme Dry	0.46	0.69 NS

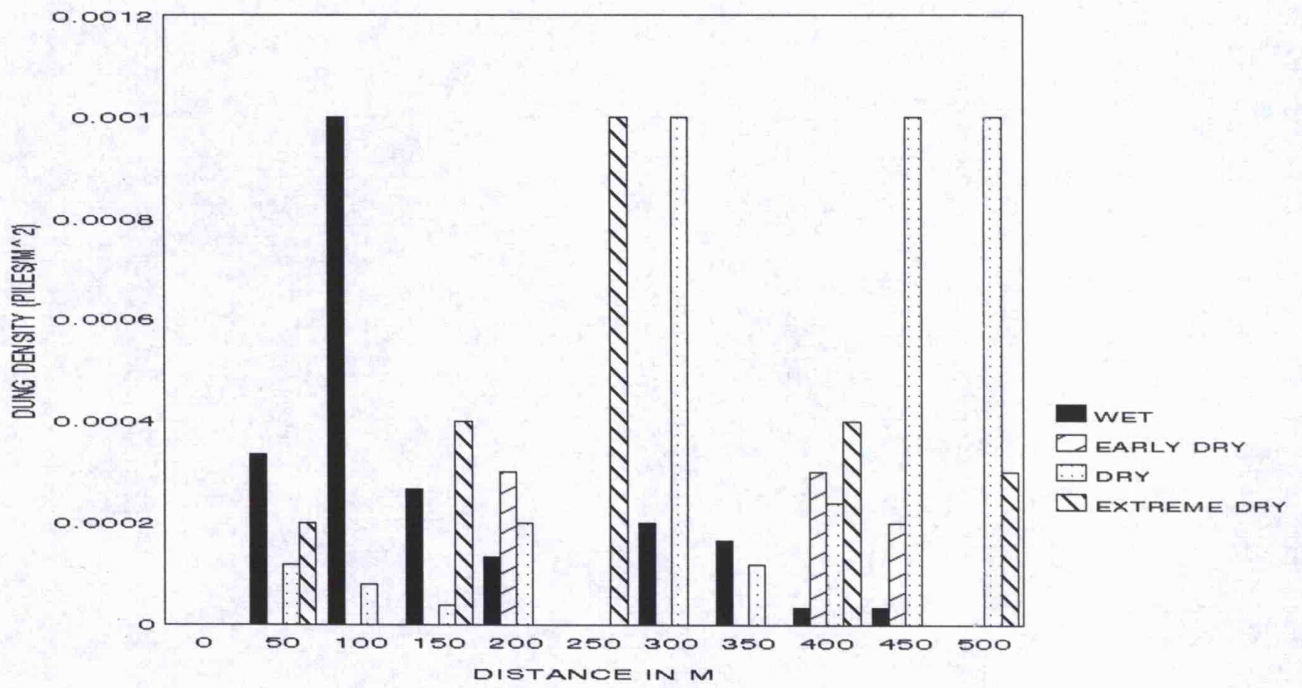
FIG 7.7
Seasonal changes in dung density along a distance gradient from settlement
a) MEDIUM GRAZERS



b) SMALL GRAZERS



c) BROWSERS



d) SHOATS



e) CATTLE

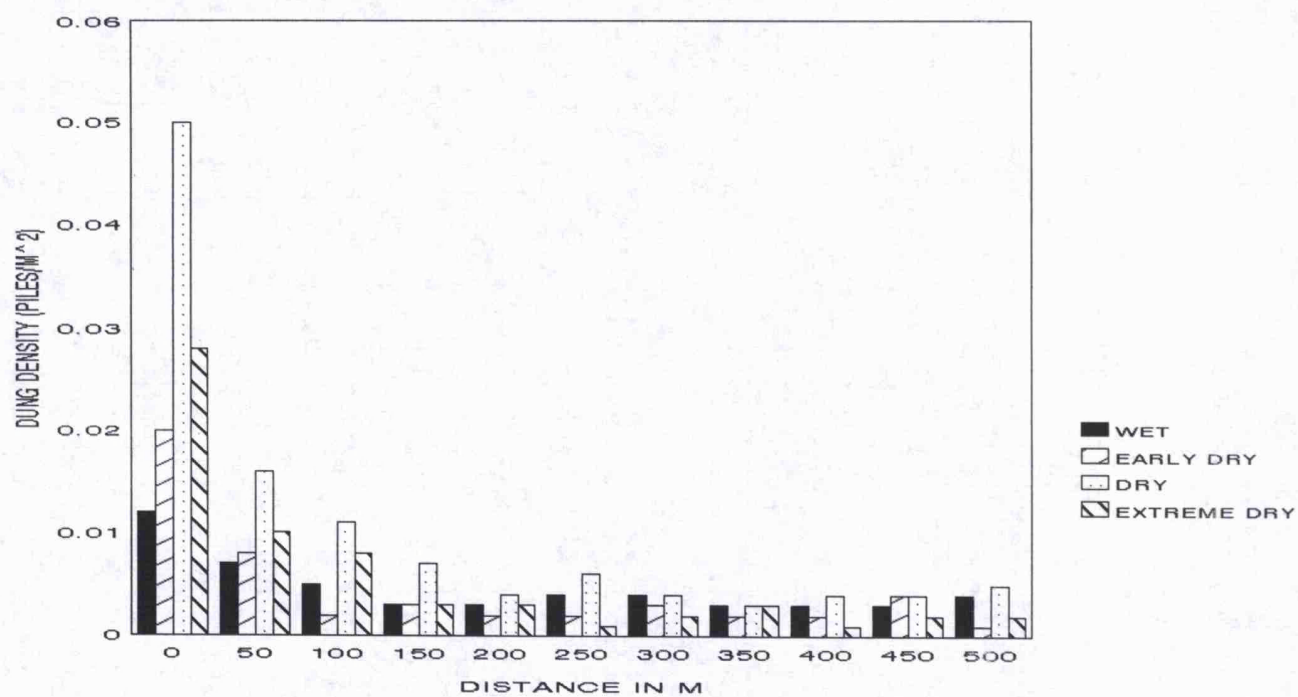


Table 7.17 Results of analysis of variance on herbivore use of areas around settlements on a distance gradient.

(a) Small-sized grazers

Season	F-Ratio	P-Value
Wet	1.61	0.105 NS
Early Dry	1.11	0.363 NS
Dry	0.90	0.535 NS
Extreme Dry	0.69	0.730 NS

(b) Medium-sized herbivores

Season	F-Ratio	P-Value
Wet	1.41	0.175 NS
Early Dry	0.97	0.477 NS
Dry	0.44	0.927 NS
Extreme Dry	2.84	0.004

(c) Cattle

Season	F-Ratio	P-Value
Wet	4.42	<0.0001
Early Dry	8.36	<0.0001
Dry	16.14	<0.0001
Extreme Dry	5.29	<0.0001

(d) Shoats

Season	F-Ratio	P-Value
Wet	17.61	<0.0001
Early Dry	5.88	<0.0001
Dry	11.67	<0.0001
Extreme Dry	8.09	<0.001

(e) Browsers

Season	F-Ratio	P-Value
Wet	1.27	0.25 NS
Early Dry	0.84	0.59 NS
Dry	1.96	0.41 NS
Extreme Dry	1.22	0.29 NS

7.3.3 Relationship between herbivore occupancy and vegetation around settlements.

Relationship between the vegetation condition and herbivore occupancy was not easy to discern. Graphs of vegetation height and dung density against distance away from settlement (Fig. 7.8 and appendix 4,5,6 & 7) showed the seasonal trends.

7.4 Human impacts

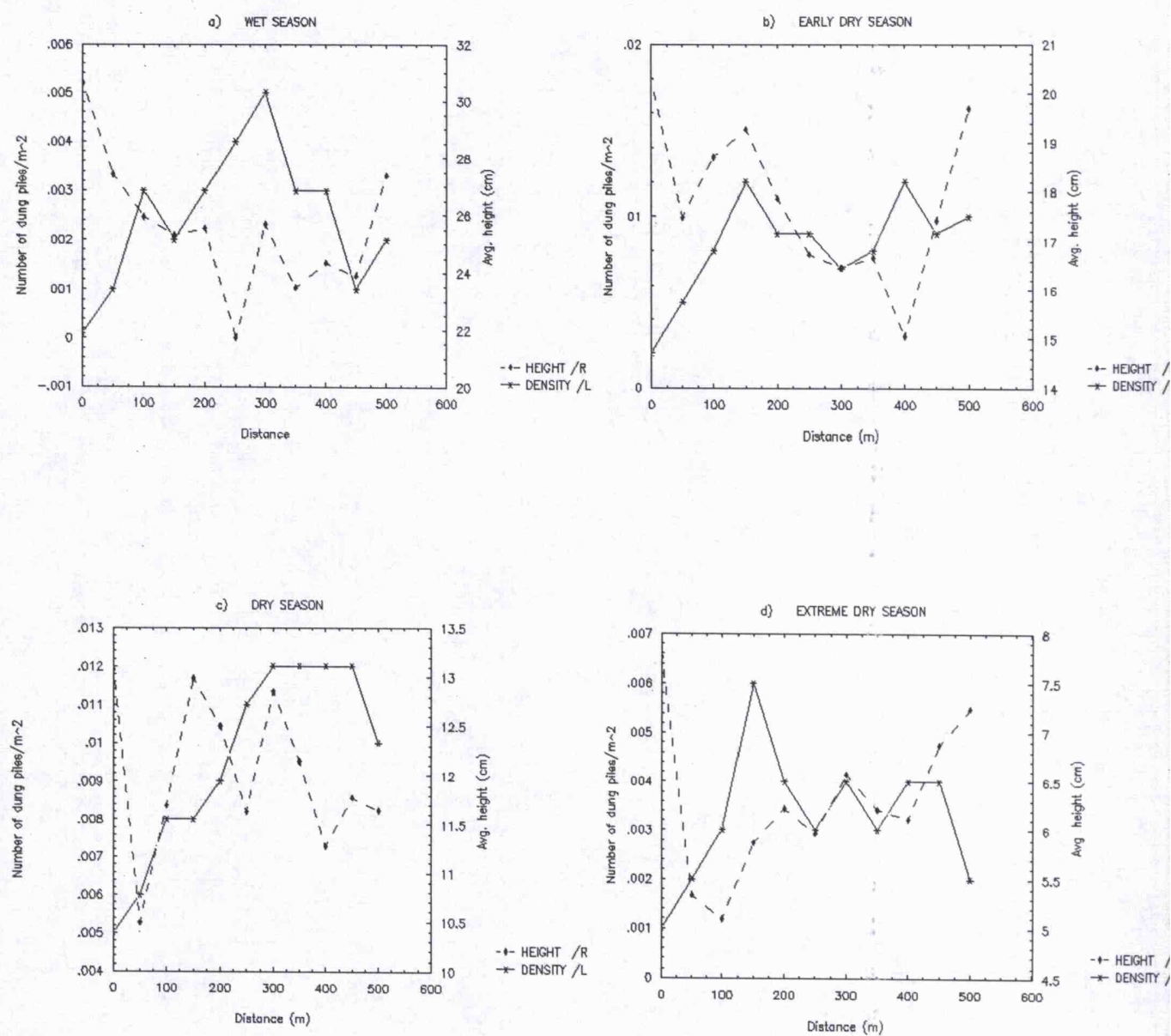
Fig. 7.9 shows human activities in the Kitengela, the area immediately south of NNP. There has been tremendous increase in human settlement driven by changes in lifestyle of the local Maasai, growing industrialization of the Athi-river town and Kitengela township and increased demand for land for settlement in both Ongata Rongai to the north west and Kitengela. The Export Processing Zone (a tax-free industrial zone producing goods for the export market) in the south east has created tremendous growth in the town, resulted in a huge influx of people looking for employment and business prospects. It has also created speculation on land, driving its value up several orders of magnitude.

In order to provide material for the building industry stone quarrying along dry river valleys in the Kitengela has become a lucrative business and land owners with suitable sites are either selling them or leasing them out. The construction of an all weather road northwest and marked **(A)** has facilitated this activity and opened up the area to further development.

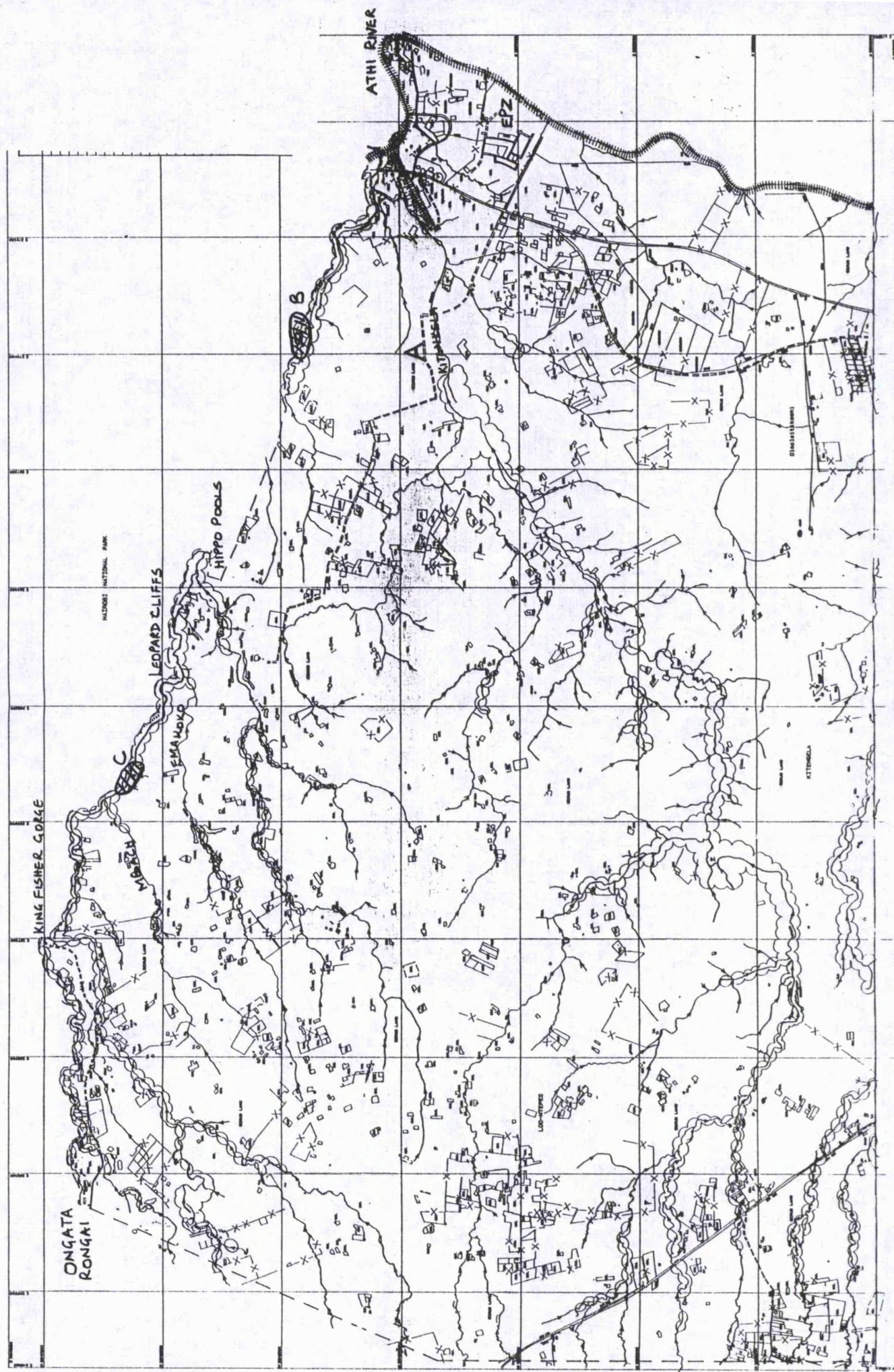
Ongata Rongai on the northwest has also continued to grow. This town has attracted a somewhat different group of people from Nairobi city, people looking for cheaper land for housing and some crop agriculture.

The net result of all the above activities is that the space available for wildlife use is quickly diminishing. The encroachment of human settlement along the Mbagathi river frontage, parts of which constitute the exit and entry points for the wildlife migrants (roughly **B** and **C** on the map) coupled with increased fencing and crop agriculture

Fig 7.8
Dung density and grass height along a distance gradient for medium-sized grazers

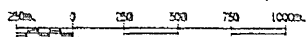


Map of the northern Kitengela showing distribution
of human settlements



LEGEND

SCALE 1 : 25,000



Park Boundary	-----
Tarmac Road	=====
Murray Road	=====
Motorable Track	-----
Footpath	-----
Railway Line	-----
Building, Hut	
Building under construction	
Fence	-----
Hedge	-----
Cultivation	
Tree, Bush	
Ditch	
Rivers	
Water Hole	
Water Tank	
Quarry	
Marsh, Swamp	
Principal Point	
Spot Height	
Contours (V.I. 10m. Index 50m.)	

threaten to totally disrupt the migrations and migratory routes. Some traditional routes have already been closed off by recent fences (personal observation) and this trend will continue unless measures are taken to prevent it.

7.5 Interpretation and discussion

7.5.1 Local Utilization in Nairobi National Park

Utilization of vegetation by herbivores seems to be size related. From these initial analyses it is clear that the large-sized grazers selected the taller vegetation which was also coarser (see chapter 4). Small grazers on the other hand used the lower end of the spectrum selecting areas of shorter grasses. Such grasses normally have higher quality. The medium sized grazers fell between this spectrum using taller vegetation than the small grazers and shorter than the large grazer extreme.

Other important factors that affected wildlife distribution in the park included water. Most herbivores water at mid-morning and areas close by water are therefore intensively used. Though this is an important aspect of structure, generally areas with water were avoided during sampling since use by animals may not at all be related to vegetation parameters as exemplified by transect 5. This transect had water close by and although there was no browse vegetation, browsing species were commonly sampled.

7.5.2 Settlements

Vegetation biomass and height declined from a peak in the wet season to the lowest level in the drought. The large changes could be directly linked to animal grazing and trampling particularly around settlements. Despite this, grass height and biomass was much higher near the settlement for most part of the seasonal cycle and in woody habitats in both the Kitengela and Olirimirui. Faster growth rates have been indicated due to the nutrient rich soils around settlements which provide suitable growth conditions. These should result in preferential use, which, though not directly demonstrated, could be inferred from the seasonal changes in grass biomass. Grass biomass declined progressively through the seasonal cycle and although the grass quantity and height were significantly higher near the settlement, no such differences were evident by the extreme dry conditions.

Temporal and spatial changes were also demonstrated. Temporal changes in each transect followed the seasonal patterns while spatial changes were also demonstrated by the differential use of transects, for example, in the dry season the

transects in Kitengela (7, 8, 9, 10) were more intensely used by medium sized grazers than those at Olrimirui (1-6). The use intensities related to the large scale migrations were also clear from the shifts in dung distribution from areas in Olrimirui normally used in the wet season, to Kitengela which is intensively used in the dry season. This differential use coincided with the northward migration of wildebeest and zebra to NNP, starting with Olrimirui in the wet season northwards to Kitengela as the dry season progressed.

In general, wildlife occupancy around settlements demonstrated utilization patterns at the ecosystem scale. The south eastern end was used in the wet season and the northern areas in the dry season. It also demonstrated the seasonal shifts in use patterns around settlement. Wildlife seemed to use all the areas equally so that any displacement by humans during the day was perhaps compensated for by night use. Animal counts around settlements during the day showed that many species maintained a safe distance away from the homesteads and from livestock which are normally accompanied by humans. Dogs were observed chasing wildlife around many times under the supervision of humans.

Large herbivores were absent in this study except for the one sampling event in Kitengela at the 500 m distance during the wet season. During this season, the buffalo sometimes venture out of the park but because of the danger they pose to humans, they are usually forced back into the park. The differences along the gradient were not progressive, therefore some factor confined close to the settlement may have been responsible for the very localized differences.

CHAPTER 8

GENERAL DISCUSSION

The study on the distribution, movement patterns as well as large herbivore utilization patterns in the Athi-Kapiti plains allows certain general and more specific statements to be made about the structure of this ecosystem. The basis of the structure seems to be rainfall quantity, its distribution as well as the nutritional status of vegetation within the ecosystem.

8.1 Vegetation differences along the north/south rainfall differences

Vegetation biomass and quality were broadly described using the rainfall gradient in the Athi-Kapiti plains. Exclusion of large herbivore defoliation resulted in less defined peaks in the wet season, normally a prominent feature of this and other grazing ecosystems.

Biomass accumulation in the exclosures reflected the differences in precipitation. The highest biomass measured in the exclosures during the study period was in the high rainfall regime (chapter 4). The two exclosures, one in NNP the other next to plot 1, attained these peaks more rapidly than those in lower rainfall areas. The biomass accumulation rates and the quantity range within the exclosures also seemed to reflect the grazing intensity prior to exclusion of large herbivores. The NNP exclosure which was in an area that generally experienced less grazing had the least percentage change in biomass at 39.17% (chapter 4). The other three exclosures experienced large changes, 84.90 %, 67.30% and 123.60% for exclosures 1, 10 and 11 respectively. Vegetation quality similarly followed this gradient but the differences were not as large and distinct (chapter 4). The highest quality was in exclosure 10 (low rainfall) at 6.24 % crude protein and the lowest in exclosure 16 (high rainfall) at 4.88 % crude protein.

Overall, diversity seemed to have declined in exclosures 1, 10, 16 by May 1994, more than two years after the areas were exclosed.

8.2 Vegetation and wildlife interactions

The results of this study demonstrated that vegetation biomass and quality patterns changed seasonally and with this the distribution and use by large herbivores. The cyclical changes in biomass to a large measure depended on rainfall quantity and distribution and the extent of vegetation removal by grazing herbivores. In general, and regardless of location and grazing intensity, biomass was at its highest during the wet months and lowest during the dry.

The Park falls within a higher rainfall zone and had taller, coarse and poorer quality grasses (Chapter 4). The highest grass biomass was recorded here. Intense grazing was confined to the dry season when plant growth had ceased and grazing had least impact. During the growing period in the wet season, grazing was at a minimum, and grasses were thus able to recover and maintain their vigour. The Parks' grasses were used by few resident grazers in the wet season but experienced heavy defoliation in the dry season when the migrants returned. Few species of grass dominated making the herb layer less diverse than on the plains. Tall grass forms such as those found in NNP have relatively more investment in above-ground production particularly in stem tissue and are thought to be adaptations to enhance grasses' competitiveness. This does however make them more vulnerable to grazing (Milchunas *et al.*, 1988; 1990).

The plains on the other hand received lower rainfall (chapter 4), grasses were shorter, heavily grazed in most areas, were of smaller growth form with more tillering. Intense grazing in the wet season seemed to encourage tillering and prostrate growth in grasses (personal observation). These short forms were common in the wet season feeding areas such as those represented by plots 1, 10 and 12. The major differences between NNP and plains and caused primarily by differential grazing intensity were in plant structure, height, quality, species composition and diversity (chapter 4). The species dominating the herb layer in the Park and plains were different. Where these sites were selected in the wet season the grasses would be freshly sprouting and comprise young leaf, flowers and very little stem. Herbivores therefore change the structure, biomass and species composition of vegetation in heavily grazed areas.

Differences in vegetation structure related to a rainfall gradient and grazing patterns have been observed and reported by McNaughton (1985) in the Serengeti and more recently in the Yellowstone in the USA (Frank and McNaughton, 1992). Isolation of these factors along a rainfall gradient alone have not been done.

Changes in population size distribution towards higher frequencies of smaller grasses due to heavy grazing have also been reported by Heady (1966); Milchunas *et al.*, (1990), Briske (1991) and Pfeiffer and Hartnett (1995). Grasses that dominate in the presence of grazers are dwarf low-growing forms with short internodes. They invest heavily in rapidly-growing leaf tissues (McNaughton *et al.*, 1988). Heady (1966) found the short-prostrate growing forms to be common in areas of heavy grazing in Maasai Mara and suggested that these were adaptations for avoidance of grazing.

Food availability to herbivores is therefore not a passive consequence of rainfall-driven primary productivity but a dynamic and interactive relationship between the animals and the vegetation. The animals interact with the vegetation to regulate its production

rates stimulating it in grasslands of the Serengeti (McNaughton, 1976; 1985) and South Africa, Timlinson (McNaughton *et al.*, 1988) so the vegetation and herbivores form a highly dynamic, interactive subsystem (McNaughton, 1985). Food sources in these areas are however less predictable, primary production and food availability are often highly stochastic in time and space due to prevailing rainfall patterns (McNaughton, 1979a; 1984; 1985).

8.3 Body-size differences and their effects on diet selectivity

The selection of food by large herbivores requires the solution of two problems, that of maximum quality and adequate quantity. Each animal has to look for the best combination of these two in order to meet its energy requirements.

Most wildlife selected the high quality plots (chapter 5 & 7) except buffalo which were confined to the Park. For small-sized ungulates the selection patterns were strongly correlated to high quality in the ecosystem. Areas of low quality vegetation such as the Park and plot 5 outside were avoided by this group. Regressions of small grazer occupance against quality showed that as quality decreased, so did their occupance. Large herbivores were negatively correlated to vegetation quality and used bulk vegetation in the Park. These two extremes of body size, small and large, demonstrated contrasting grass use patterns. In the middle were the medium-sized grazers which demonstrated quality-related patterns only in the wet season but with less specificity compared to the other groups. This confirmed selectivity patterns based on body size. Shoa and livestock did not follow any clear patterns and the relationship between them and quality was poor.

The correlation between height a good surrogate for estimating quality, (chapter 4) and herbivore selectivity was also high. Small grazers selected the shortest grasses in both the dry and wet seasons. Medium grazers selected from a wider spectrum in grass height but were more concentrated in shorter grass areas in the wet and in taller grasses in the dry season (Chapter 7). Large grazers preferred the tallest grasses. Again there was no correlation between shoa and cattle distribution with vegetation height. When resources were abundant, most grazers utilized the vegetation communities which contained the most digestible material. However, when growth ceased and biomass and sward height began to decrease (Chapter 4) shifts in habitat use patterns also began to occur. Wildebeest for example began their northward trek leaving behind small grazers in areas that seemed almost devoid of vegetation.

Quantity did not seem to be a major limitation for small ungulates and their persistence on the plains in the dry season, their continued selection of the marginally

higher quality patches in the dry season when there was so little biomass in these plots supports this contention. Quality is therefore the most important determinant of habitat choice by this group.

Many large- and small-scale movements have been shown to follow gradients that stabilize dietary requirements on an inter-seasonal basis. Resident grazers normally move along a catena, using the upper catenas (Bell, 1970) in the wet season and the lower catenas in the dry while migrants normally use the drier parts of the ecosystem. As the dry season progresses residents move topographically downward and migrants move up an increasing rainfall gradient (Maddock, 1979). Food quality and quantity declined as the dry season progressed (see Chapter 4), but these mobility patterns partially stabilize intake and dietary quality (McNaughton, 1985).

An explanation for shifts from short to tall grasses by larger grazers, leaving behind the small grazers has been suggested by Gordon (1989). He says that large mammals will be at a disadvantage where size of food items is small since small animals will be more able to satisfy their requirements on these and since each item provides a greater proportion of their metabolic requirements. This is also the point at which resource partitioning is likely to occur. Lamprey (1963), noted that it is usually the larger grazing species which leave the preferred areas first. Clutton-Brock and Harvey (1983) proposed that the underlying reason for this was the differential scaling of metabolic requirements and incisor arcade breadth with body weight. A model developed by Illius and Gordon (1987) showed that swards impose greater limitations on food intake of larger animals than smaller ones because of mouth and bite size. This suggests that the feeding mechanism may be important in the common phenomena of ecological separation in grazing species (Vesey-Fitzgerald, 1960; Bell, 1971).

Dung protein clearly illustrated the differences in quality of the diets selected by the browsers and grazers in the ecosystem. In every season browsers had the highest dung quality both in small and large species, an indication of high overall quality in their diet. Among the grazing herbivores the trends also confirmed size-determined selectivity patterns. The data revealed significant declines in dung protein with increasing body weight (chapter 7). Small grazers were on the top end of the quality scale, zebra and large grazers on the lower end. Zebra turned out to be the least selective of the grazers despite its much smaller size compared to buffalo for example. Its body weight was closest to that of a cow, yet its dung protein was lower than that of a buffalo which is approximately twice its weight. Even with the zebra included in the regression (chapter 7), the body size/quality trend was significant and confirmed selection patterns found using vegetation quality and height. When zebra (the only non-ruminant in the group)

was excluded from the analysis, the regression improved markedly in the wet season and only marginally in the dry. Zebra's exception to the general body weight trend in the wet season seems to suggest that the ruminant digestion confers advantages to the herbivores only when food is both of high quality and readily available, a time which normally coincides with the wet season. Based on the dung quality analysis the ruminant is a more selective forager than the caecal digester, but being a more efficient digester the ruminant requires a lower absolute quality of forage. Zebra would therefore be at a selective advantage in the dry season when quality rather than quantity is limiting. It has been generalized that where forage quantity is limiting, a ruminant digestive system is advantageous; whereas where quality is limiting, a caecal digestive system is an advantage (Bell, 1971; Janis, 1976; Jarman and Sinclair, 1979).

Cattle and shoat fitted within the body-size regression, despite falling out of the general patterns related to grass height and quality. This is harder to explain in a mixed group, but it seems that despite the inability of cattle to range as widely as wildlife on a daily basis, they are still able to select vegetation of high quality.

In summary several factors may be acting in concert to structure the ungulate communities of the Athi-Kapiti plains. These are food quality and quantity, mediated through rainfall and grazing and through two suggested morphological factors -body size and types of digestive systems (caecal or ruminant).

8.4 The influence of the rainfall gradient on the large herbivore structure

The results showed that wildlife movements followed the north/south rainfall gradient. Evidence of this can be derived from the migration of wildebeest from higher rainfall in NNP to the more arid Kapiti plains in the southeast with the onset of the rains, and back along an increasing rainfall gradient during the dry season, a higher proportion of small ungulates using the plains (low rainfall) than NNP (high rainfall) (chapter 4), preference of NNP by large bulk feeders. Wildebeest migrations are often used to characterise the Athi-Kapiti wildlife and most obviously illustrate the distinct use of the two rainfall extremes in the ecosystem. The largest proportion of them used the extreme south east of the plains during the wet months and the extreme north in the dry season. The high specificity of the seasonal feeding areas has become more pronounced over the last few years as human settlement and population in the area has increased. Wildebeest and zebra distribution maps from earlier work (Peterson and Casebeer 1972) show more widespread use of the area compared to dispersion patterns obtained from this study. The basic seasonal selection patterns of high and low rainfall areas have however not been altered.

Calving occurred in the wet season range and the Maasai moved their cattle herds to prevent them from grazing in calving spots and avoid contracting malignant catarrh fever. This has clearly been a point of contention with the wildlife authorities and many individuals who can fence out wildebeest are increasingly doing so.

Mineral nutrition (McNaughton, 1988; 1989; 1990; Kruegen, 1975) and dietary quality (chapter 4) together cannot account fully for the increasing site specificity since there were many areas with high quality grazing closer to the park, and other parts of the Kapiti plains which they used previously. Changing human settlement patterns, increasing harassment of animals in their wet season range and dwindling space may be confining wildebeest to a smaller wet season range. Because they are gregarious they need more space than animals that feed in small groups. Their social habits also put them into more direct conflict with people because of the large quantity of vegetation they use. These greater requirements for food and space may be a major constraint in this system.

Apart from the rainfall-mediated vegetation differences in the two ecosystem extremes, grazing regimes have played a significant role in increasing the seasonal selection trends of migrants. In addition to higher precipitation, NNP is distinct from the plains in another important respect, the absence of human activities, specifically livestock grazing. The impact of livestock which moves much less seasonally would have been to graze down the tall grasses and provide grazing lawns in the Park; demonstrated by the vegetation comparisons between exclosures and grazed areas and between Park and plains. These would attract grazers and perhaps hold back some migrants as also demonstrated by burning experiments (Gichohi, 1990). The exclusion of livestock grazing has created habitat changes in NNP and accentuated the differences between Park and plains. The presence of livestock in NNP in the 1960s might have accounted for large numbers of resident wildebeest, zebra and kongoni (unpublished records - Kenya National Parks). Their subsequent removal may in turn explain the commencement of the exodus of wildebeest and zebra from NNP in the wet season in the mid 1970s and the inability of the kongoni population to recover within the park after the drought of 1974 (Stanley-Price, 1974). Kongoni did not display any preference for tall grasses in this study though the exclusion of livestock was at the time seen as removal of a competitor. If this was correct, kongoni should have thrived under the circumstances.

The Maasai Mara provides a similar example where protection has created habitat changes of immense proportions and resulted in concentrations of large herbivores in group ranches surrounding the reserve, while frequently avoiding the inside (Rainey, Pers. comm.).

Perhaps more than anything, the results underline the very significant impacts that

livestock have in savanna systems. The enclosure-like conditions described for NNP also describe the significant vegetation differences created by the absence of this large grazing component.

Zebra migrations were less distinct in the plains but obvious in the park. Zebra differed from wildebeest in their choice of food (chapter 5), feeding areas and therefore in their overall distribution (chapter 7). They were able to persist on the plains in large numbers during the dry season.

8.5 Scale

One of the objectives of the study was to demonstrate that large herbivore structure was controlled by similar factors at different scales.

8.5.1 The Park

Many animals congregated in the park during the dry season when grazing and water conditions were less favourable on the plains. Large herbivore biomass increased in the park as migrants returned from the plains (chapter 5). During this season the animals grazed down the herb layer changing biomass and grass height significantly. An analysis of occupancy patterns along an increasing height gradient showed that small ungulates used the shorter vegetation, large ungulates the taller grasses and medium grazers over a larger grass height range between these two extremes as they did at the ecosystem level. These patterns were however much harder to discern as the high quality patches were fewer and less distinct than on the plains.

8.5.2 Settlements

The settlement studies did not reveal any size-related structure patterns nor the displacement of wildlife around the settlements. Although wildlife were driven out from the vicinity of the settlement during the day (personal observation) they seemed to compensate for this by using the areas at night. Of course this may have given the advantage for selecting the better food items to the livestock but results of the dung quality analysis did not show this. There were no distance related changes in herbivore use around settlements. The presence of settlement did however provide the animals with vegetation well into the dry season (chapter 6), biomass was significantly higher around settlements than further away because of the presence of higher levels of nutrients from livestock (Muchiru, 1994). My conclusion is that patterns if any become more difficult to discern as the scale gets smaller. Perhaps sampling should be conducted over a longer period in a locality with large numbers of wildlife to help to provide more conclusive data.

8.6 Relevance of this study to the conservation of wildlife populations of the Athi-Kapiti plains

Severe human impacts are confined to the area immediately south, southeast and southwest of NNP. The main threats include quarrying, fencing, settlements and spreading industrial development from the Athi-river and Kitengela townships. These activities have the potential to fragment the ecosystem, slowly block off the migrations and finally isolate NNP.

The study has demonstrated that many of the community structure patterns continue to operate in highly altered, human inhabited ecosystems as long as the basic dietary requirements are provided for and the space is available. The presence of livestock has been shown to be of real benefit to grazing large mammals and although their presence might increase competition for food, their grazing activities have profound but positive impacts on the food sources of the animals. It has also been demonstrated that livestock fit into the general body size scaling in this ecosystem, and despite being herded by man retain their ability to select and optimize their diets in the same way as the wild ungulates.

The major migrants have also been shown to have very specific requirements that continue to be met in this system despite the diminishing space and increased human population. Given the current activities and the lack of any tangible benefits to land owners for supporting wildlife and the thriving but competing economic activities around the fringes of the NNP, wildlife is unlikely to survive. This is compounded by many landowners' unwillingness to participate in conservation activities. Under these circumstances much of the Athi-Kapiti plains cannot be set aside for wildlife. So what are the alternatives?

The knowledge of the food requirements and the key areas selected in the system can be used to delimit potential sites in which to concentrate conservation activities. Corridors to these sites can be proposed using key migration routes (Fig. 8.1). For example a migration corridor through the Kitengela to the Kapiti plains would provide access between the wet season dispersal and the dry season concentration areas to allow the migrations to continue. The corridor could also be used by zebra to the Ololotikoshi area where they feed in the wet season (Fig. 8.1). The size of the migration corridor and its exact location would need to be more clearly defined by closely following the animals during the migrations. Their routes may have changed over the last few years due to loss of certain crossing points and certain parts of their range. The current costs of land also make land buying an expensive conservation option.

With some additional information it would be possible to find out which of these ecological requirements can be met within the Kitengela. This would lead to proposals of a less optimum but more practical option of conserving a contiguous area (with compatible land use activities). This may have the advantage of providing one large area rather than two distant islands that might eventually be severed (Fig. 8.2).

Both options call for some land buying, the first for corridor space, the second for major crossing points to NNP. These are both expensive options; current land prices for key parcels along the Mbagathi river are as high as Kenya shilling (Kshs.) 300,000 per acre (1 British pound is approximately 86 Kshs.). Despite this, buying of the migration crossings has already begun.

The more economical but probably difficult option is that of involving the communities in conservation of this land. This will require that community programs demonstrate the many values of wildlife to land owners. Current development in the Kenyan wildlife policy are towards providing an environment in which landowners who continue to tolerate wildlife can benefit from it directly. Although tourism is the main foreign exchange earner for the country, the returns from wildlife have mainly been to the nation and tour operators, little has found its way to the people on whose land the wildlife survives. The result is that many landowners have been quick to find alternative land uses that can provide them direct income. A change in policy towards individual economic gains may slow the pace of loss of wildlife habitat, and more specifically in the Kitengela provide an atmosphere in which conservation can be discussed from a position of potentially mutual benefit to both landowners and wildlife.

Proposed policy reforms in Kenya's Wildlife Act reemphasize that in order to conserve biodiversity of primary concern in ecosystems, the processes that create, maintain and threaten it must be identified. It also recognises that humanity is the main problem confronting wildlife. Therefore in order to conserve wildlife outside parks, the support of the landowners must be enlisted. They must also be supported in developing activities that enhance the conservation of wildlife while at the same time returning tangible economic and social benefits. Where economic returns from wildlife are not realisable then other incentive or subsidy systems must be devised by the government in order to compensate the opportunity costs from wildlife.

8.7 Recommendations for future research

1. Definition of the precise migration routes using well timed aerial and ground counts.
2. A more thorough look at the suitability of the Kitengela as a truncated ecosystem.
3. More exhaustive analysis of body size-vegetation-rainfall relationships using first principles.

Fig 8.1
Map showing possible conservation areas or areas for purchase

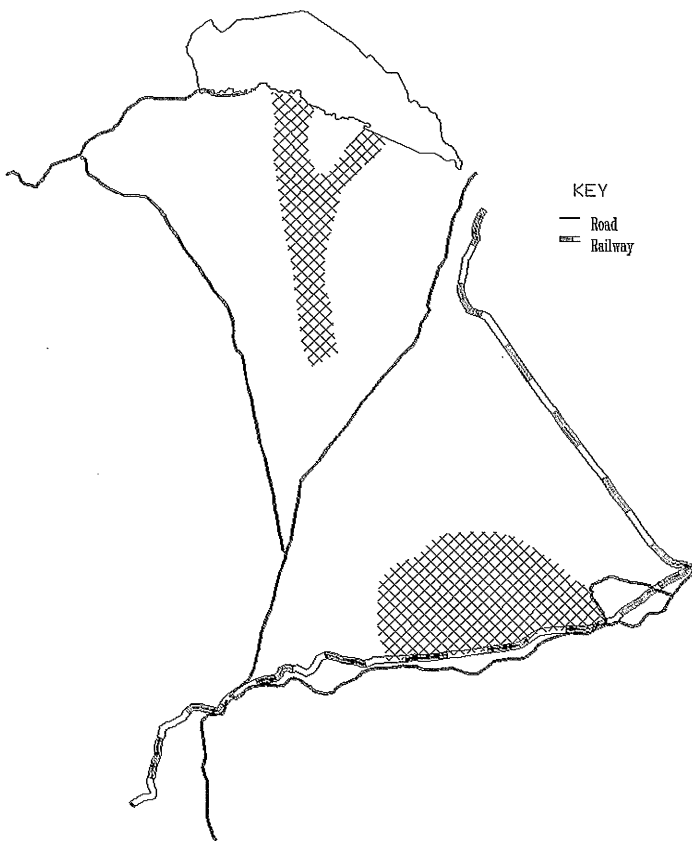
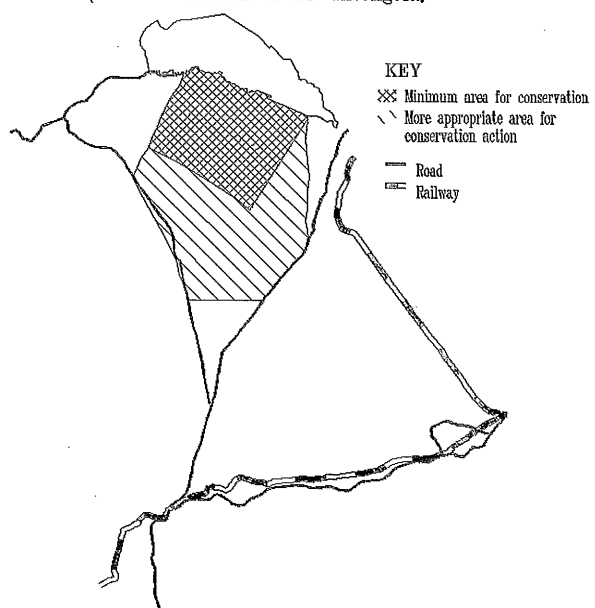


Fig 8.2

Map showing a further truncated ecosystem
(NNP and section of the Kitengela)



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APPENDIX 1: LIST OF ANIMAL WEIGHTS USED IN BODY WEIGHT ANALYSIS

SPECIES	WEIGHT (KG)
Coke's Hartebeest (Kongoni)	136
Zebra	238
Buffalo	500
Eland	363
Giraffe	772
Thomson's Gazelle	20
Grants Gazelle	50
Warthog	59
Impala	45
Wildebeest	166
Shoat	82
Cattle	364

**APPENDIX 2: LIST OF SOME OF THE HERBACEOUS SPECIES
FOUND IN THE ATHI-KAPITI PLAINS**

OLCHORO-ONYORI (1)

Abutilon hirtum	Indigofera schimperi
Abutilon mauritianum	Justicia uncinulata
Amaranthus graezians	Justicia exigua
Anagallis arvensis	Kalanchoe lanceolata
Anthericum sp.	Kyllinga comosipa
Asystasia schimperi	Leucas neuflyzeana
Athroisma psylloides	Mariscus macropus
Baleria eranthemoides	Microchloa kunthii
Becium obovatum	Monadenium rhizophorum
Bothriocloa insculpta	Monsonia angustifolia
Bracharia eruciformis	Ocimum gratissimum ssp gratissimum
Cassia mimosoides	Ocimum kenyense
Chloris virgata	Oxygonum sinuatum
Coccinia grandis	Panicum subalbidum
Commelina africana	Pavonia elegans
Commelina benghalensis	Pennisetum mezianum
Craterostigma hirsutum	Pennisetum stramineum
Crossandra subacaulis	Pentansia ouranogyne
Crotalaria spinosa	Phyllanthus maderaspantes
Crotalaria lotifolia	Plecanthus sp.
Crotalaria spinosa	Portulaca quadrifida
Cucumis aculeatus	Psilotrichum schimperi
Cyathula erinacea	Rhamphicarpa montana
Cynodon dactylon	Rhynchosia minima
Cyperus kilimandscharicum	Ruellia patula
Cyphostemma orondo	Senecio coronopifolius
Digitaria abyssinica	Setaria incrassata
Digitaria sp.	Sida masaiica
Digitaria macroblephara	Sida ovata
Digitaria milianjana	Solanum incanum
Dinebra retroflexa	Sporobolus marginatus
Dyschoriste radicans	Sporobolus pellucides
Echinochloa hapclodata	Tephrosia subtriflora
Eragrostis tenuifolia	Themeda triandra
Eragrostis cilianensis	Thesium schweinfurthiana
Erucastrum arabicum	Tripogon curvatus
Eustachys paspaloides	Vigna frutescens ssp frutescens var
Felicia muricata	fragrans
Gutenbergia fischeri	Zaleya pentandra
Gynura sp.	Aerva lanata
Harpachne schimperi	Priva curtisiae
Helichyrsom glumaceum	Digitaria abyssinica
Heliotropium steudneri	Commelina purpurea
Heliotropium longiflorum	Tetragonium acanthocarpa
Hibiscus flavifolius	Sporobolus discoporus
Hibiscus trionum	Chenopodium album
Hypoestes verticillaris	
Hypoxis obtusa	

KIPETO (2)

Pennisetum stramineum
Digitaria macroblephara
Bracharia eruciformis
Themeda triandra
Commeiina africana
Setaria incrassata
Ischaemum afrum
Eragrostis cilianensis
Digitaria abyssinica
Pennisetum mezianum
Indigofera volkensii
Bidens schimperi
Justicia exiqua

UPPER KISAJU (3)

Alyscarpus rugosus
Themeda triandra
Achyriopsis greenwayi
Bothriocloa insculpta
Digitaria macroblephara
Digitaria abyssinica
Pennisetum stramineum
Setaria incrassata
Indigofera schimperi
Indigofera nairobiensis
Ischaemum afrum
Aristida kenyense
Eragrostis tenuifolia
Eustachys paspaloides
Ruelia patula
Microchloa kunthii
Corchorus trilocularis
Bracharia eruciformis

LOIYANGALANI (4)

Abutilon mauritianum
Acacia hockii
Aeolanthus repens
Amaranthus hybridus
Anagallis arvensis
Anellema hockii
Anthericum cooperi (A. subpapillosum)
Aristida kenyense
Barleria eranthemoides
Bothriocloa insculpta
Bracharia sp.
Bracharia eruciformis
Centemopsis rubra

Chenopodium schraderianum
Commelina purpurea
Crotalaria lotiformis
Cucumis sp.
Cynium tubulosum ssp. montanum
 (Syn. *Rhamphicarpa montana*)
Cymbopogon caesius
Cynodon dactylon
Cyperus kilimandscharica
Cynium ajugifolia
Digitaria macroblephara
Digitaria abyssinica
Enneopogon elegans
Eragrostis racemosa
Eragrostis cilianensis
Eragrostis papposa
Ficus pretoriae
Gnaphalium declinatum
Gomphocarpus interger
Harpachne schimperi
Heliotropium steudneri
Heteropogon contortus
Hibiscus trionum
Hirpicium diffusum
Hyparrhenia papillipes
Hypoestes verticillaris
Indigofera arrecta
Ipomea jaegeri
Ipomea mombassana
Ipomea ionenthera
Ischaemum afrum
Justicia uncinulata
Kalanchoe latifolia
Kohautia aspera
Kyllinga nervosa
Kyllinga comosipes
Leucas neuffizeana
Leucas mollis
Lippia javanica
Lysimachia volkensii
Microchloa kunthii
Medicago lacinata
Monadenium rhizophorum
Monsonia longipes
Nesaea lythroides
Oxygonium sinuatum
Panicum poaoides
Pennisetum stramineum
Pollichia campestris
Portulaca kermensina
Scilla kirkii

Senecio coronopifolius
Setaria incrassata
Setaria sphacelata
Silene burchellii
Sporobolus pellucides
Sporobolus marginatus
Stachys hildebrandtii
Tephrosia sp.
Themeda triandra
Thunbergia gregorii
Tragus berteronianus
Eustachys paspaloides
Felicia muricata
Gutenbergia fischeri
Gutenbergia cordifolia (Erlangea cordifolia)
Gynura sp.
Heliotropium longiflorum
Hermanii uhligii
Hibiscus flavifolius
Hypoxis obtusa
Indigofera volkensii
Indigofera schimperi
Ipomea hildebrandtii
Ipomea sp. (palmate leaves)
Kalanchoe lanceolata
Kalanchoe glaucescens
Leucas venulosa
Lintonia mutans
Monsonia angustifolia
Ocimum kenyanse
Ormocarpum trachycarpum
Orthosiphon parvifolius
Panicum subalbidum
Panicum poaoides
Pavonia elegans (there could be a change of name)
Pennisetum mezianum
Pentanisia ouranogyne
Perlagium quinquelobatum
Phyllanthus rotundifolius
Phyllanthus maderaspatensis
Polygala sphenoptera
Portulaca oleracea
Portulaca quadrifida
Priva curtisiae
Rhynchosia minima
Schkuria pinnata
Sida massaica
Sida ovata
Solanum coagulans
Solanum incanum
Tephrosia subtriflora
Tephrosia pumila

Tribulus terrestris
Trichomeria macrocarpa
Vigna frutescens ssp *frutescens* var *fragrans*
Vulutaria lipii
Zaleya pentandra

ELUAI (5)

Themeda triandra
Digitaria macroblephara
Eustachys paspaloides
Lintonia mutans
Pennisetum mezianum
Microchloa kunthii
Orthosiphon parvifolius
Harpachne schimperi
Indigofera volkensii
Bracharia eruciformis
Indigofera schimperi
Pennisetum stramineum
Cynodon dactylon
Monsonia angustifolia

OLOONTEPPES (6)

Setaria incrassata
Digitaria milanjiana
Themeda triandra
Aspilia mossambicensis
Orthosiphon parvifolius
Ischaemum afrum
Bothriocloa insculpta
Eustachys paspaloides
Cyperus rigidifolius
Setaria pumila

ERETETI (7)

Bracharia eruciformis
Commelina africana
Setaria incrassata
Digitaria milanjiana
Themeda triandra
Commicarpus pedunculatus
Digitaria macroblephara
Ischaemum afrum
Lintonia mutans
Commelina benghalensis
Rhynchosia minima
Bracharia eruciformis
Cyperus rigidifolius
Corchorus trilocularis

LOWER KISAJU (8)

Aspilia mossambicensis
Themeda triandra
Microchloa kunthii
Digitaria macroblephara
Tripogon curvatus
Harpachne schimperi
Senecio coronopifolius
Bothriocloa inculpta
Eustachys paspaloides
Pennisetum mezianum
Bracharia eruciformis
Anthericum sp.
Digitaria abyssinica
Rhynchosia minima
Ischaemum afrum
Hibiscus flavifolius
Orthosiphon parvifolius
Crotalaria latiformis
Barleria eranthemoides
Sporobolus discoloratus

OLRIMIRUI (9)

Abutilon mauritianum
Aellanthus repens
Amaranthus graecizans
Anthericum brehmerianum
Anthericum saltii
Alyscarpus rugosus
Aspilia mossambicensis
Asystasia schimperi
Baleria eranthemoides
Bidens schimperi
Bothriocloa inculpta
Bracharia eruciformis
Chloris virgata
Commelina erecta
Commelina purpurea
Conyza aegyptica
Corchorus trilocularis
Craterostigma hirsutum
Crinum kirkii
Crotalaria pychnostachya
Crotalaria latifolia
Cyperus sp.
Cyphostemma macrophyllum
Cyphostemma orondo
Digitaria abyssinica
Digitaria macroblephara
Dolichos formosus
Eragrostis tenuifolia
Erlangea cordifolia

Erucastrum arabicum
Felicia muricata
Gnaphalium declinatum
Gutenbergia fischeri
Gutenbergia calvicina
Heliotropium steudneri
Hermannia uhligeri
Hibiscus flavifolius
Hypoxis obtusa
Indigofera nairobiensis
Ipomea oenonthera
Justicia uncinata
Kalanchoe lanceolata
Kohautia coccinea
Kohautia aspera
Lintonia mutans
Medicago laciniatum
Melhania velutina
Monsonia angustifolia
Neotonia wightii
Notonia hildebrandtii
Orthosiphon parvifolius
Oxygonum sinuatum
Panicum subalbidum
Panicum poaeoides
Pavonia elegans
Pennisetum mezianum
Pentstemon ouranogynae
Peucedanum harnisianum
Phyllanthus maderaspatensis
Polygala sphenoptera
Portulaca kermansiana
Rhynchosia minima
Senecio coronopifolius
Setaria incrassata
Sida masalca
Solanum coagulans
Sporobolus pellucides
Sporobolus marginatus
Tagetes minuta
Tephrosia subtriflora
Themeda triandra
Vigna frutescens ssp. *frutescens* var. *fragrans*

OLRIMIRUI (10)

Achyranthus aspera
 Aeolanthus repens
 Alternanthera pungens
 Amaranthus graecizans
 Aneilema hockii
 Anthericum cooperi
 Asparagus buchananii
 Athroisma psylloides
 Becium obavatum
 Bidens pilosa
 Blepharis fruticosum
 Bothriocloa insculpta
 Bracharia eruciformis
 Cassia mimosoides
 Chlorophytum bakeri
 Cleome monophylla
 Commelina purpurea
 Commelina erecta
 Commiphora flaviflora
 Conyza stricta
 Commelina sp.
 Corchorus trilocularis
 Crassula granvikii
 Crassula pentandra
 Craterostigma hirsutum
 Cyathula erinacea
 Cynodon dactylon
 Cyperus stuhlmannii
 Digitaria macroblephara
 Digitaria abyssinica
 Digitaria sp.
 Dinebra retroflexa
 Dyschoriste radicans
 Echinochloa colona
 Emilia discifolia
 Eragrostis tenuifolia
 Eragrostis cilianensis
 Eriochloa nubica
 Erythrina burtii
 Eustachys paspaloides
 Felicia muricata
 Gutenbergia fischeri
 Gutenbergia cordifolia
 Helichyrsom glumeceum
 Heliotropium steudneri
 Hermania uhligii
 Harpachne schimperii
 Hirpium diffusa
 Hypoxis obtusa
 Indigofera volkensii
 Ipomea jaegeri
 Justicia uncinulata

Kalanchoe lanceolata
 Kohautia aspera
 Kyllinga comosipes
 Kyllinga nervosa
 Leucas neuflyzeana
 Lintonia mutans
 Microchloa kunthii
 Monsonia angustifolium
 Murdannia clarkeana
 Ocimum kenyense
 Orthosiphon parvifolius
 Panicum poaoides
 Pennisetum stramineum
 Pennisetum mezianum
 Phyllanthus rotundifolius
 Polygala Sphenoptera
 Priva curtisiae
 Rhamphicarpa montana
 Schukuhria pinnata
 Setaria incrasata
 Solanum incanum
 Sphaeranthus gomphrenoides
 Sida ovata
 Aspilina mossambicensis
 Sporobolus pellucides
 Sporobolus marginatus
 Sporobolus discoporus
 Tephrosia hiciida
 Tephrosia subtriflora
 Themeda triandra
 Trachyandra saltii
 Tripogon curvatus
 Volutaria lipii

SHEEP & GOAT (11)

Digitaria macroblephara
 Pennisetum mezianum
 Themeda triandra
 Bothriocloa insculpta
 Eustachys paspaloides
 Pennisetum stramineum
 Setaria incrassata
 Hermania uhligii
 Microchloa kunthii
 Aristida kenyense
 Bracharia eruciformis
 Orthosiphon parvifolius
 Rhynchosia minima
 Oxygenium sinuatum
 Eragrostis racemosa
 Anagallis arvensis
 Tephrosia subtriflora
 Sporobolus pellucides

LUKENYA (12)

Abutilon hirtum
Abutilon mauritianum
Achryopsis greenwayi
Aerva lanata
Alternanthera pungens
Alysicarpus rugosus
Amaranthus graecizans
Anellema hockii
Anthericum gregorianum
Aristida keniensis
Aristida adoensis
Asparagus bunchanani
Aspilia mossambicensis
Cucumis aculeatus
Balanites aegyptica
Baleria eranthemoides
Becium obovatum
Blepharis fruticosum
Bothriocloa insculpta
Cassia mimosoides
Cassia usambarensis
Chlorophytum sp.
Chlorophytum macrophyllum
Commelina purpurea
Commelina erecta
Commelina benghalensis
Commicarpus pedunculatus
Corchorus trilocularis
Crabia subcanlis
Crassula pentandra
Craterostigma hirsutum
Crotalaria spinosa
Crotalaria latiformis
Crotalaria pycnostachya
Cucumis prophetarum
Cyathula erinacea
Cynodon dactylon
Cyperus stuhlmannii
Cyperus kilimandscharica
Digitaria macroblephara
Dinebra retroflexa
Dolichos formosus
Dyschoriste radicans
Eragrostis racemosa
Eragrostis tenuifolia
Erlangea cordifolia
Erlangea calycina
Erucastrum arabicum
Eustachys paspaloides
Feilicia muricata
Gnaphalium declinatum

Gutenbergia fischeri
Gutenbergia cordifolia (Erlangea cordifolia)
Gynura sp.
Harpachne schimperii
Heliotropium longiflorum
Heliotropium stendneri
Hermania uhligii
Hibiscus fiavifolius
Hypoxis obtusa
Indigofera volkensii
Indigofera schimperii
Ipomea hildebrandtii
Ipomea sp. (palmate leaves)
Ipomea mombassana
Ipomea jaegeri
Justicia uncinulata
Kalanchoe glaucescens
Kalanchoe lanceolata
Kohautia aspera (Oldenladi)
Kyllinga nervosum
Kyllinga comosipes
Leucas neulizeana
Lintonia nutans
Michrochloa kunthii
Monsonia longipes
Monsonia angustifolia
Ocimum kenyense
Ormocarpum trachycarpum
Orthosiphon parvifolius
Oxygonum sinuatum
Panicum subalbidum
Panicum poaeides
Pavonia elegans
Pennisetum mezianum
Pentanisia ouranogyne
Perlagonium quinquelobatum
Phyllanthus rotundifolius
Phyllanthus mderaspantensis
Polygala sphenoptera
Portulaca quadrifida
Portulaca kermesiana
Portulaca oleracea
Priva curtisiae
Rhamphicarpa montana
Rhynchosia minima
Schkuhria pinnata
Senecio coronopifolius
Sida masaica
Sida ovata
Solanum incanum
Sporobulus marginatus
Sporobulus discoporus
Sporobulus pellucides

Sporobolus stapfianus
 Tephrosia subtriflora
 Tephrosia pumila
 Themeda triandra
 Tragus berteronianus
 Tribulus terrestris
 Trichomeria macrocarpa
 Vigna frutescens ssp frutescens var
 fragrans
 Vulutaria lipii
 Zaieya pentandra

STONY ATHI (13)

Themeda triandra
 Panicum poaides
 Pennisetum mezianum
 Digitaria macroblephara
 Eustachys paspaloides
 Digitaria abyssinica
 Microchloa kunthii
 Tripogon curvatus
 Kyllinga nervosa
 Bothriocloa insculpta
 Cynodon dactylon
 Pennisetum stramineum
 Indigofera volkensii
 Harpachne schimperi
 Sporobolus pellucides
 Justicia exiqua
 Tragus berteronianus
 Cyphostemma orondo
 Tephrosia subtriflora
 Cyperus stuhlmanii
 Anthericum sp.
 Anthericum gregorium
 Sida ovata
 Indigofera volkensii
 Commelina sp.
 Medicago laciniatum

NAISERIAN (14)

Themeda triandra
 Eustachys paspaloides
 indigofera volkensii
 Pennisetum mezianum
 Pennisetum stramineum
 Digitaria macroblephara
 Kyllinga comosipes
 Aristida kenyanse
 Cyperus stuhlmanii
 Tripogon curvatus

Commelina africana
 Kyllinga nervosa
 Psilochloa elliotii
 Cassia mimmosoides
 Cynodon dactylon
 Bracharia eruciformis
 Indigofera nairobiensis
 Ipomea mombassana
 Lintonia mutans
 Cyperus rigidifolius
 Panicum subalbidum
 Aspelia mossambicensis

OLOPOSAT (15)

Themeda triandra
 Cynodon dactylon
 Digitaria abyssinica
 Harpachne schimperi
 Microchloa kunthii
 Bothriocloa insculpta
 Aristida kenyanse
 Pennisetum mezianum
 Bracharia eruciformis
 Hypoxis obtusa
 Kyllinga nervosa
 Sporobolus pellucides
 Sporobolus discolorous
 Conyza pedunculosa
 Tripogon curvatus
 Eustachys paspaloides
 Panicum poaides
 Kyllinga comosipes
 Pentanisia ouranogyne
 Rhynchosia minima

NAIROBI PARK - ACACIA WOODLANDS (16)

Setaria incrassata
 Themeda triandra
 Digitaria millanjiana
 Panicum poaides
 Ischaemum afrum
 Aristida adoensis
 Orthosiphon parvifolius
 Digitaria macroblephara
 Aspilula mossambicensis
 Commelina africana
 Bothriocloa insculpta
 Eustachys paspaloides
 Eragrostis tenuifolia
 Polygala anboniensis
 Eragrostis heteromera

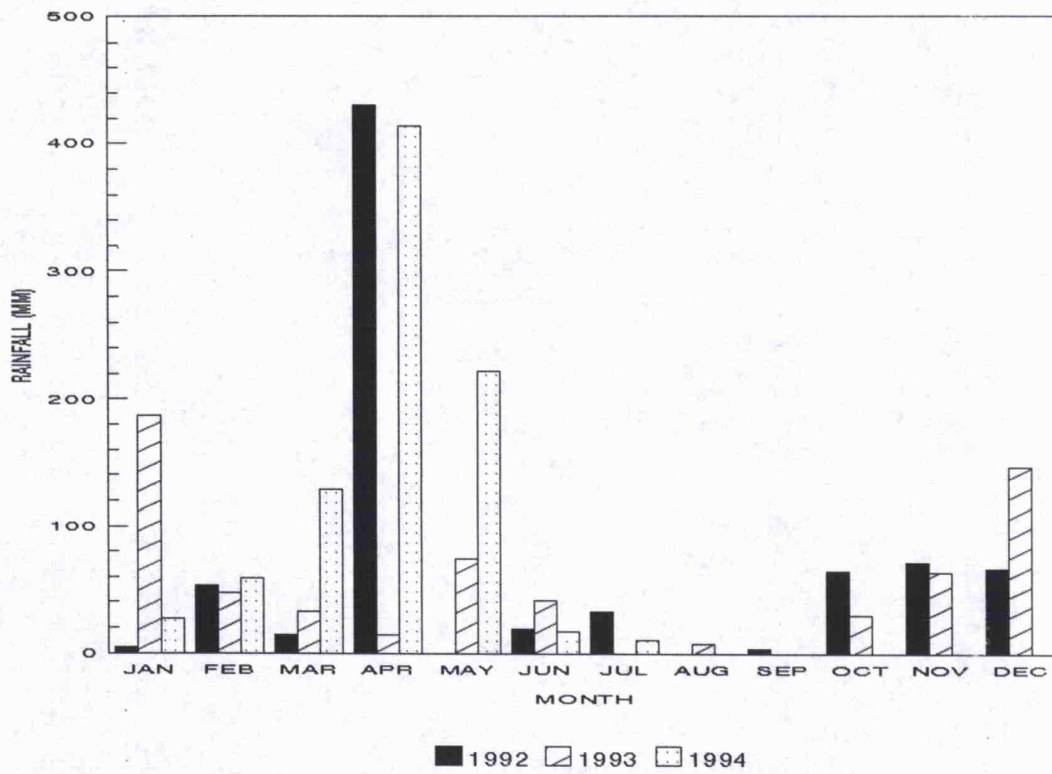
Indigofera nairobiensis
Pennisetum mezianum
Hermanii uhligii
Monsonia longipes
Indigofera schimperii
Cyperus rigidifolius

NAIROBI PARK - MBAGATHI (17)

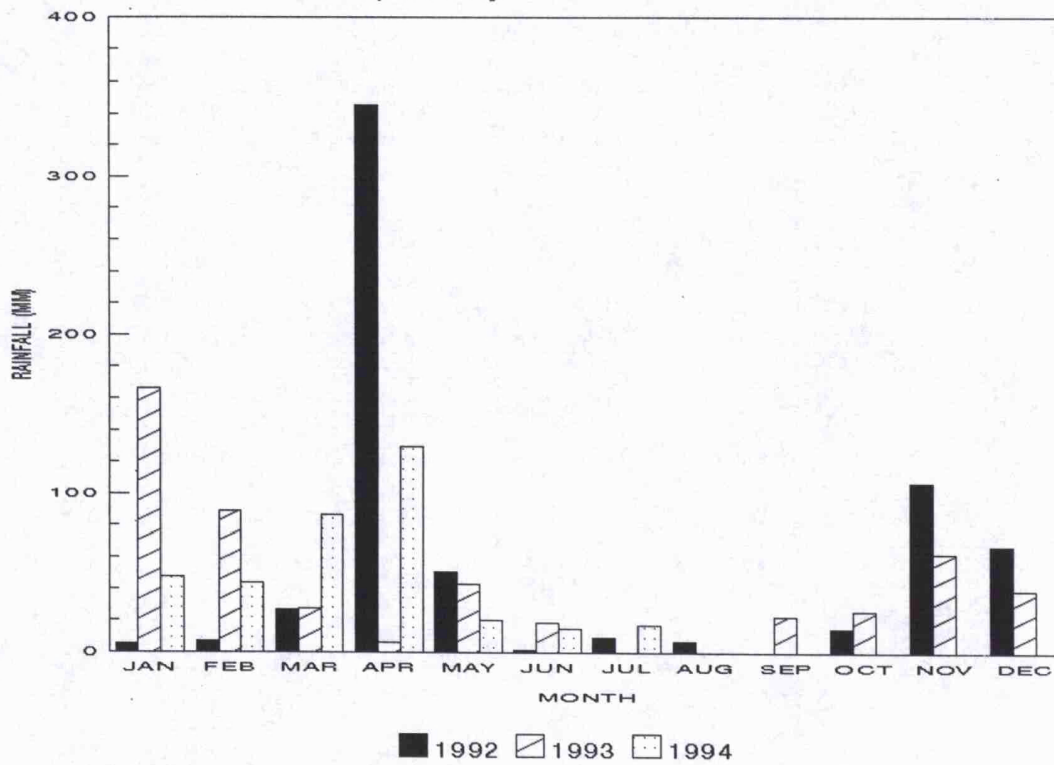
Themeda triandra
Ruelia patula
Plecanthus candida
Sonchus sp.
Cassia hildebrandtii
Aristida adoensis
Panicum poaeides
Digitaria abyssinica
Kyllinga nervosa
Ruelia patula
Pennisetum mezianum
Setaria incrassata
Commelina benghalensis
Bothriocloa insculpta
Lippia javanica
Solanum incanum

Justicia exiqua
Andropogon schimperii
Indigofera volkensii
Cyperus rigidifolius
Cynodon dactylon
Alyscarpus glumeceum
Cyperus stuhlmanii
Eragrostis tenuifolia
Commelina africana
Eragrostis heteromera
Bracharia eruciformis
Sporobolus stapfianus
Andropogon schimperii
Indigofera volkensii
Lippia javanica
Eragrostis exasperata

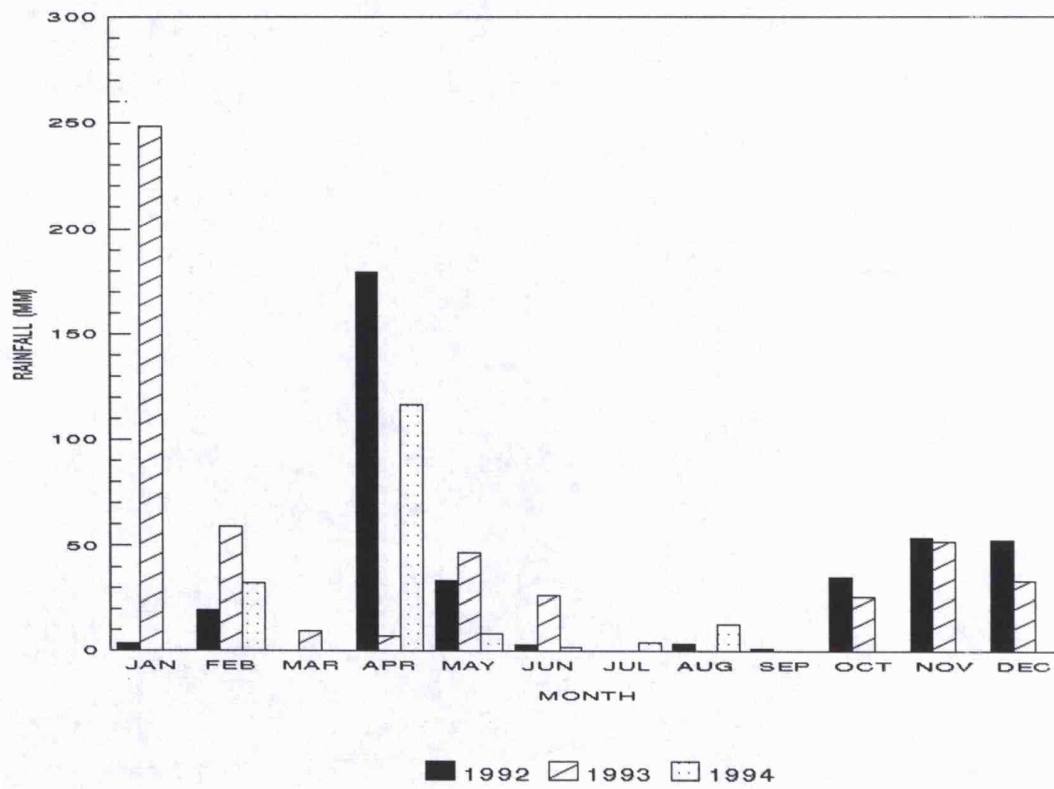
Appendix 3
a) Monthly rainfall at Ngong



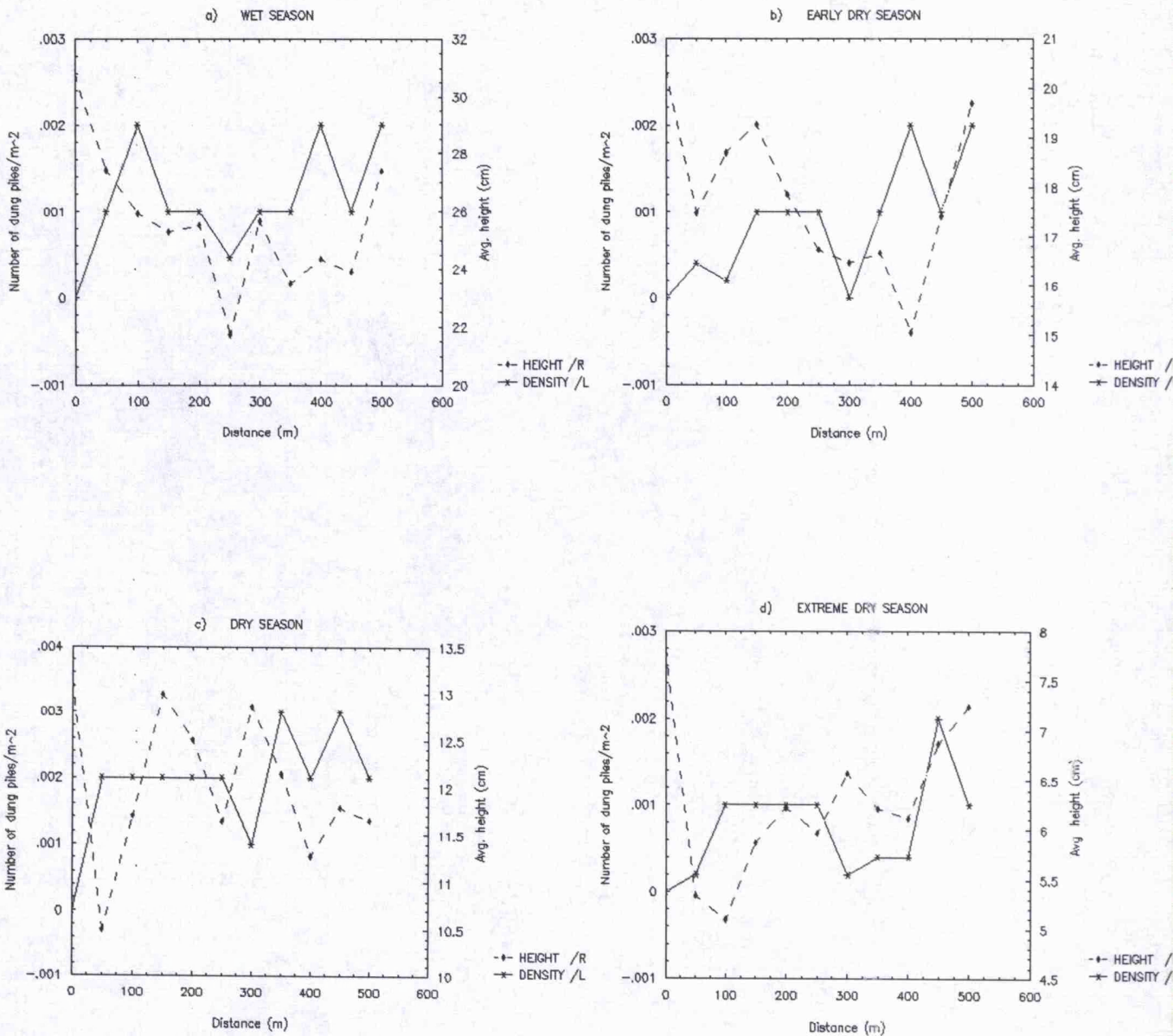
b) Monthly rainfall at Ereteti



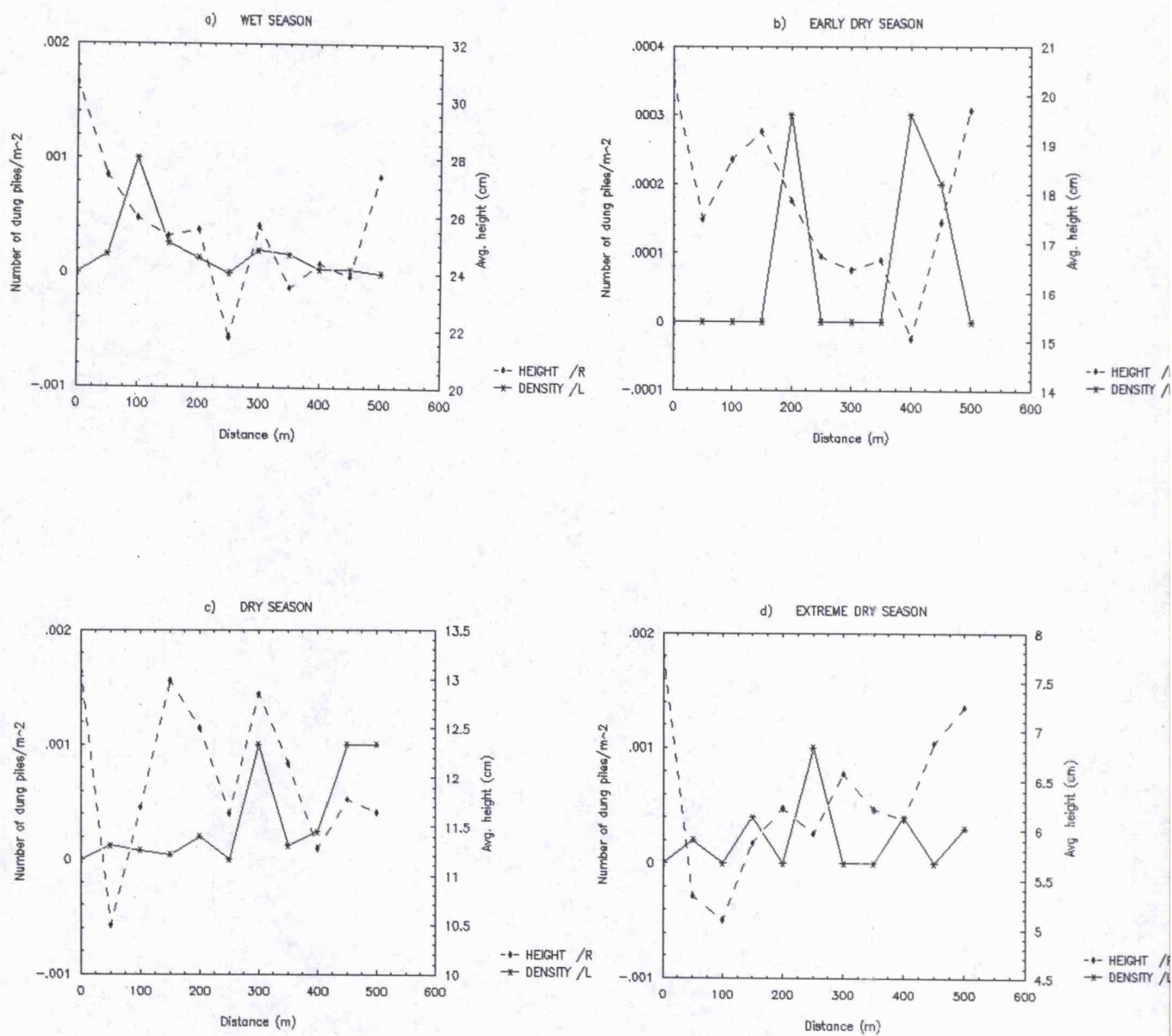
c) Monthly rainfall at Cheetah Gate



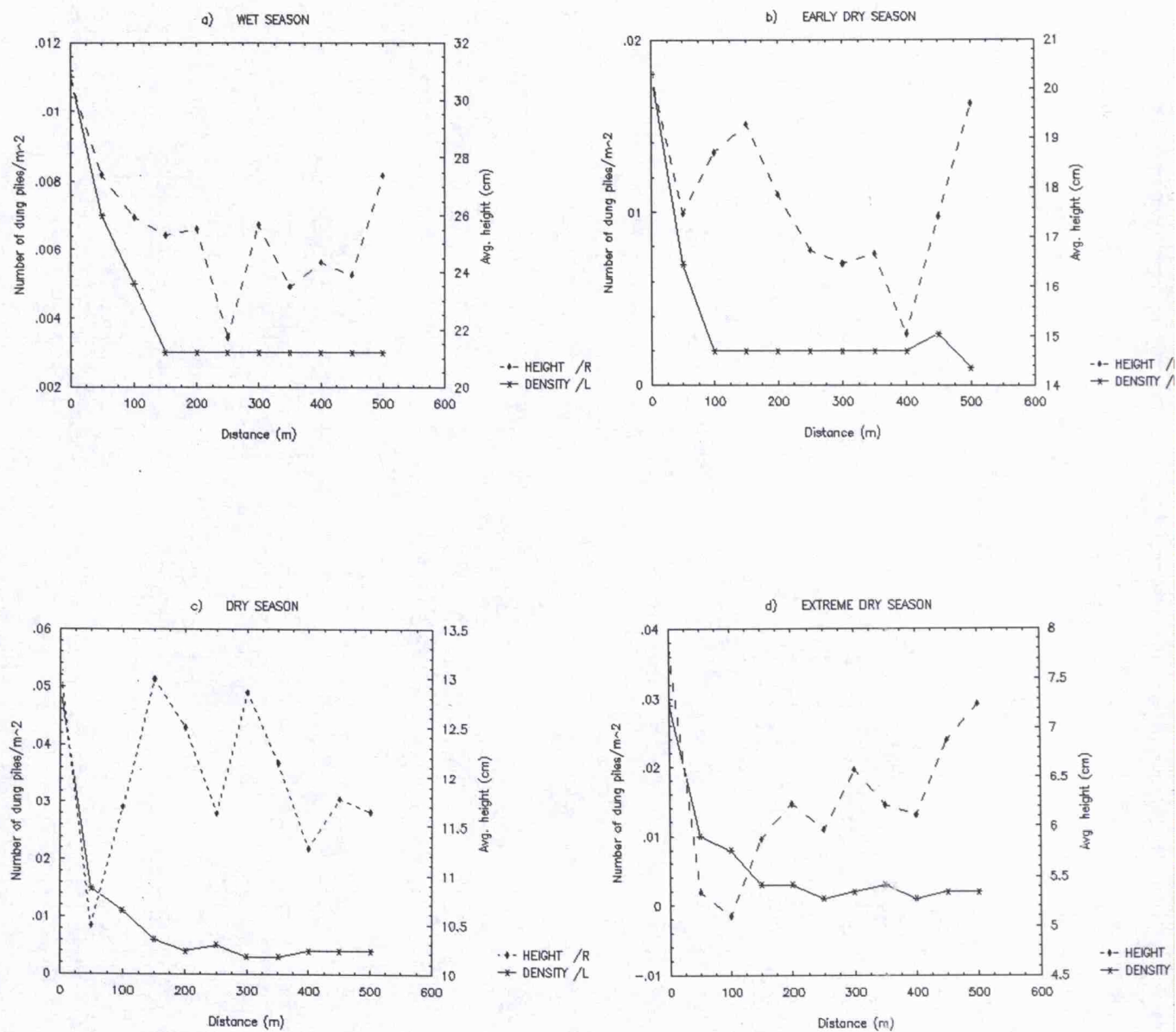
Appendix 4: Dung density and grass height along a distance gradient for small-sized grazers



Appendix 5: Dung density and grass height along a distance gradient for browsers



Appendix 6: Dung density and grass height along a distance gradient for cattle



Appendix 7: Dung density and grass height along a distance gradient for 'shoat'

