THE IMPACT OF HUMAN LAND USE ACTIVITIES AND SEASONAL CHANGES ON THE DUNG BEETLE DIVERSITY OF KAKAMEGA FOREST ECOSYSTEM

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Declaration

I, **Vincent Mahiva Shitakule**, hereby declare that this thesis is my original work and the work described herein has not been presented to any other University.

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Dedication

I dedicate this work to my father the late Menn Mahiva Ambehi and my mother Catherine Mahiva. This is due to their total support both morally and materially, without which I would not have reached this level of education.

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Abstract

Based on quantitative comparative data collected in Kakamega forest and the surrounding farmlands, analyses were done to ascertain to which extent different modes of land use and seasonal changes affect guild structure, abundance and species diversity of dung beetle assemblages. The human influences studied included extensive cattle farming and deforestation.

These studies were performed between October 2002 and August 2003 during the short rainy, dry, start of long rainy and end of the long rainy seasons in the primary forest, secondary forest, grazed, and ungrazed grasslands in Kakamega forest and the Surrounding farmlands. The experiments were done by depositing 10 standard samples of 1kg fresh cow dung on standard areas in the habitats in each season at night and during the day and the beetles were recovered using floating method. A total of 80 samples yielded a total of 21,604 dung beetles in all the habitats and seasons studied representing the families Scarabaeidae, Hydrophilidae, Staphylinidae and Histeridae. The tunnelers, dwellers, and rollers were the guilds represented in the family Scarabaeidae. For the effect of seasons on the dung beetles structure individuals and guilds were compared from different seasons

The studies indicate that the extensive cattle grazing and forest degradation influence both the guild structure and abundance of dung beetles. There was high abundance in the grazed grassland, followed by the ungrazed grassland. All the studied habitats had a significant conditional effect on the families and the guild structure of the dung beetles and that different guild of dung beetles have strong association with different habitats. During the day the dwellers were strongly associated with the primary forest, tunnelers with the secondary forest while rollers, Staphylinidae and Hydrophilidae were associated with the ungrazed grassland.

It is also shown that the dung beetle assemblages were significantly affected by seasonal changes and that the impact of the seasons on the dung beetle guilds is significantly influenced by human activities. The dung beetles were more abundant during the rainy seasons (start of long rainy and short rainy seasons) and fewer specimens were collected during the dry season. The tunnelers were strongly associated with the start of the long rainy and short rainy seasons at night while the rollers were strongly associated with the dry season during the day. At night, however, the tunnelers and the dwellers were strongly associated with the grazed grassland.

In the forest areas a total of 55 species of Scarab beetles were collected. As shown by various diversity indices, and rarefaction plot, primary forest had higher species diversity than the secondary forest. However dung beetles were more abundant in the secondary forest.

These studies have shown that differences in the beetle guild structure, abundance, and species diversity in Kakamega forest and the surrounding farmlands could be due to human land use modes and seasonal changes. The changes in the dung beetle assembleges were therefore significant predictors of susceptibility to habitat degradation.

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List of Abbreviations

BIOTA	Biodiversity Transect Monitoring Analysis in Africa
ICIPE	International Centre of Insect Physiology and Ecology
DRIP	Dissertation Research Internship Program
NHM	Natural History Museum
KWS	Kenya Wildlife Services
UoN	University of Nairobi
KIFCON	Kenya Indigenous Forest Conservation Programme
RDA	Redundancy Analysis
PCA	Principle Component Analysis
SSS	Statistics for Social Scientists

Chapter 1

1.0 GENERAL INTRODUCTION AND LITERATURE REVIEW

1.1 GENERAL INTRODUCTION

Biodiversity losses due to habitat alterations due to different land use needs by humans are acknowledged to be great, but their quantification is less satisfactory. Lack of adequate data, taxonomic competence and appropriate survey or sampling techniques are recognized as prime deterrents in obtaining adequate estimates of biodiversity losses. Since time immemorial land use by man has entailed habitat alteration and fragmentation, the process of modifying and sub-dividing a continuous habitat into smaller patches. Biodiversity loss could also occurs through natural systems for example, fire (Wright 1974, Pickett and Thompson 1978), wind fall (Foster 1980), floods and volcanicity (Eldredge 1998). However, the most important and large-scale cause of habitat modification is expansion and intensification of human land use to provide adequate means of livelihoods (Burgess and Sharpe 1981, Adren 1994).

Kakamega forest is the eastern-most end of the once vast rain forest stretching all the way from West Africa through Central Africa to East Africa (Kokwaro 1988, Tsingalia 1988, Clausnitzer 1999). It is a fertile tropical rain forest and human activities have converted it into a patchwork of indigenous forest patches, glades, secondary woodland and patches of exotics (Clausnitzer 1999, Kokwaro 1988, Tsingalia 1988). Such human activities that have caused this degradation include pastoral activities (livestock grazing), clearing both for commercial and domestic wood, and hunting and all these have had a negative impact on the biological diversity of the forest (Kokwaro 1988, Tsingalia 1988).

Dung beetles are known to be sensitive to changes in the environment and belong to the insect order Coleoptera, with families Scarabaeidae, Geotrupidae, Staphylinidae, Hydrophilidae and Histeridae. They have a worldwide distribution, except for the Polar Regions. Dung beetle assemblages also known as coprocenoses are dominated by species of suborder Scarabaeoidea, which have their highest diversity and abundance in the Afrotropics (Hanski and Cambefort 1991). This distribution has been attributed to the specific species-rich mammal fauna of Africa that provide dung pads, the main resource for nutrition and breeding for the beetles (Hanski and Cambefort 1991).

Dung beetles have received much attention because of the role they play in the improvement of the environment. Such roles include recycling of dung there by fertilising the soil, control of some parasites of vertebrate and pest flies, cleaning of the pasture environment and seed dispersal (Waterhouse 1974, Bornemissza 1976, Fincher 1981, Klein 1989, Hanski and Cambefort 1991, Andresen 2002)

Despite the fact that dung beetles play these significant roles in the environment and that they are very diverse and abundant in the afro-tropics, there has been relatively little work done on the effect of human activities on this group of insect in the tropical rain forests of Africa. From the forest systems in South America and south-east Asia is it known that degradation and fragmentation of primary forests leads to the impoverishment of the coprophagous fauna (Howden and Nealis 1975, Halffter *et al.* 1992, Davis 1993, Klein 1989, Kirk 1992, Didham *et al* 1998, Davis 2000).

Studies on the seasonal effects on the distribution of the dung beetle assemblages are important in understanding the role of dung beetles in the environment. Such studies are especially important before any species of dung beetles are considered for introduction in new areas. Such studies have been carried out in various part of the world (Janzen 1983, Fincher *et al.* 1986, Hunters *et al.* 1991, Cambefort and Walter 1991, Montes de Oca and Halffter 1995, Andresen 2002). However, this have mostly concentrated in the temperate regions and the in the tropical rain forest in South America and have shown that the dung beetle assemblage distribution is heavily influenced by seasonal changes. Few studies have been done on the seasonal effects on the dung beetle assemblages in the savanna grasslands (Coe and Kingston 1988) and no work has been done on the seasonal effect on the dung beetle assemblages in the tropical rain forest in Africa.

The studies were conducted between September 2002 and August 2003 and examined the influence of human land use modes and seasonal changes on the species diversity, guild structure, and the population density of the dung beetles in different habitats in Kakamega forest and the surrounding farmlands. The primary forest, the secondary forest, ungrazed grassland at the border of the forest, and the grazed pasture grasslands around the Kakamega forest were the habitats as well as all the major seasons were compared.

1.1.1 JUSTIFICATION OF THE STUDY

This study which intends to appraise the variety and abundance of the dung beetles, will increase our knowledge about the diversity of dung beetles in Kakamega forest and the surrounding areas biota and the effects of human activities on biodiversity. Nothing is known about the effect of the seasonal changes on dung beetle fauna of Kakamega and this is the first inventory of the dung beetle fauna of the easternmost relic of the Guineo-Congolian rainforest. The inventory will facilitate comparisons with similar future studies to detect biodiversity loses or gains that would enable policy makers to plan long-term protection and conservation strategies for the Kakamega forest.

1.1.2 OBJECTIVES

1.1.2.1 General Objective

To study the effects of land use modes and seasonal changes on the abundance, guild structure and species diversity of coprophagous beetles in the Kakamega forest and the surrounding farmlands.

1.1.2.2 Specific Objectives

1. To survey and compare dung beetle abundance and guild structure between the primary forest, secondary forest, ungrazed grassland at the border of the forest, and the grazed grassland pastures around the forest in order to determine the effect of human activity on the guild structure of dung beetles.

2. To correlate differences in the structure of the dung beetle assemblages with the seasonal changes in Kakamega forest and the surrounding farmlands in order to determine the effects of seasonal changes on the guild structure of dung beetles.
3. To evaluate the influence of forest degradation on the species diversity of dung beetles in order to determine the effect of human activities on the species diversity of dung beetles.

1.1.3 HYPOTHESES

1. Human land use modes have an influence on the abundance, species diversity and guild structure of the dung beetles.
2. Seasonal changes have an effect on the guild structure of dung beetles.

1.2 GENERAL LITERATURE REVIEW

1.2.1 Population Biology of Dung Beetles

According to the classification of Hanski and Cambefort (1991), dung beetles belong to the families of Scarabaeidae, Geotrupidae (not afrotropical) and Aphodiidae, the adult and larvae of which feed mostly on faeces. The coprophagous Scarab beetles use their substrates in different ways by which they are classified into guilds (fig.1) (Cambefort and Hanski 1991). The species of the roller (telecoprids) guild (plate 2) rapidly form balls of faeces, roll them away from food source to ensure the exclusive use of this part of the resource and deposit them in or on the soil. The tunnelers (paracoprids) (plate 1) burrow tunnels to make nests directly under the food source and bring dung into the nest where they form dung balls, while members of the dwellers (endocoprids) feed and reproduce directly in the dung pat (Hanski and Cambefort 1991). A fourth category is called kleptoparasites that invade and occupy nests built by the telecoprids and paracoprids groups.

According to Hanski and Cambefort (1991) other Coleopteran families that utilise the dung resource, include Hydrophilidae, Staphylinidae, and Histeridae. Their members dung resource in search of food predating on egg, larvae, and adults of other insects that are found in the dung pad.

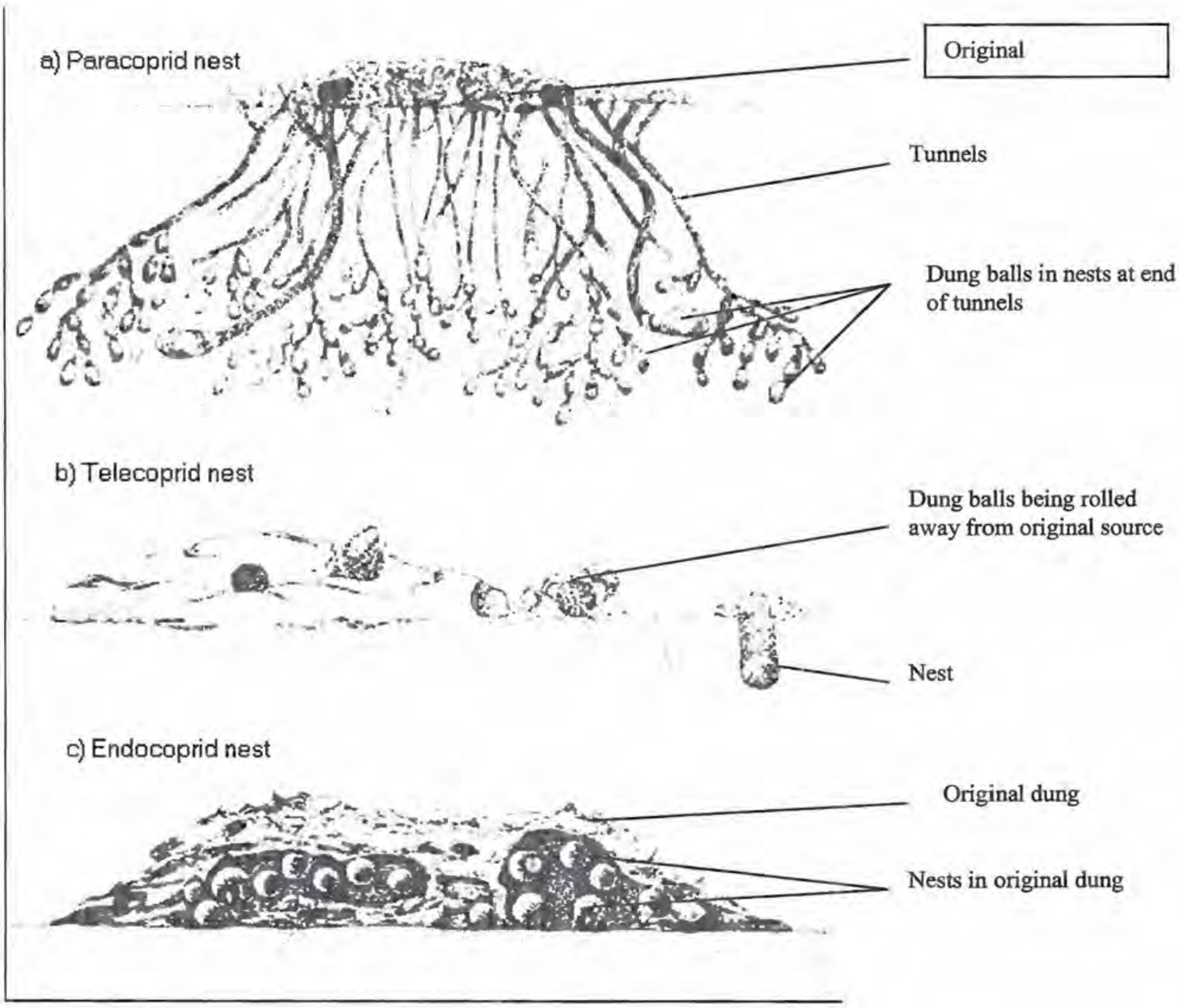


Fig.1. Schematic diagrams showing the paracoprid, telecoprid and endocoprid Guilds nests of Dung beetles (From Hanski and Cambefort 1991)

Plate 1. *Heliocopris mutabilis*. (belongs to tunneler guild)

Plate 2. A telecoprid (*Scarabaeus sp.*) rolling away ball of dung.

1.2.2 Importance of Dung Beetles

Many authors have reported the economic importance of dung beetles from various parts of the world. They include recycling dung and hence fertilising the soil, cleaning environment after the pasture has been contaminated by dung, and dispersing seeds (Marsh and Campling 1970, Waterhouse 1974, Bornemissza 1976, Klein 1989, Hanski and Cambefort 1991). Fincher (1981) estimated the benefits of nitrogen recycling by dung beetles at US$ 208,164,384 in the grazing areas of the United States of America. He also estimated the potential benefits as a result of reduced parasitism and pest flies caused by rapid burial of livestock faeces by dung beetles in the United States of America to be US$ 741,999,190 and US$ 515,000,000 respectively annually. On the role of dung beetles in cleaning of the pasture environment, he stated that there was a potential benefit of US$ 603,196,580 per annum as a result of increased grazing by beef cattle after the fouled pastures have been cleaned by the dung beetles in the United States of America.

Andresen (2002) worked on the importance of dung beetles as secondary seed dispersers in the Amazon rain forest and showed that dung beetles increase the survival rate of the seeds by storing them away from seed predators once buried in the ground and through the more humid environment, which stimulates germination.

Sakai and Inoue (1999) reported that dung beetles play a role in the pollination of some plants. He found that some members of the dung beetle genus *Onthophagus* pollinate the plant *Orchidantha inouei* in the family Lowiaceae. In this kind of pollination he reported that the flower does not offer any reward like nectar or pollen grains to the pollinators (dung beetles). The dung beetles are only attracted to the plant because of a particular dung scent emitted by its flowers.

1.2.3 Effect of Habitat Change on Dung Beetles

Generally, ecological studies on terrestrial organisms have shown that habitat characteristics are important in regulating diversity of species and population size. MacArthur and MacArthur (1961), Pianka (1967), Rosenzweig and Winakur (1960), Ajayi (1974) have shown that plants and animals tend to be sensitive to the quality of their habitats.

According to Hanski and Cambefort (1991) and Jankielsohn *et al.* (2001), habitat selection by the dung beetles is determined at two spatial scales that include the dung pad and the immediate surroundings (microhabitat), and the larger area with the parameters soil type, vegetation type, and the type of mammals present (macrohabitat). They showed that any change in the macrohabitat, such as a change in vegetation in an area, influences the different factors in the microhabitat and hence the composition of the dung beetles assemblages.

From the forest systems of South America it has been shown that deforestation and fragmentation of primary forests leads to the impoverishment of coprophagous fauna (Howden and Nealis 1975, Klein 1989, Kirk (1992), Halffter *et al.* 1992, Power 1996, and Didham *et al.* 1998). Howden and Nealis (1975) showed that the clearing of the rain forest in the Amazonas region of Colombia drastically reduced both the number of species and individuals of dung beetles in this area.

Working in the Mexican tropical rain forest, Halffter *et al.* (1992) also showed that by cutting down trees in the short term affects mostly the species that live within the forest, while the species that live at the edge have a greater probability of adaptation in the cleared areas. They found that although, the mosaic vegetation recovers slightly, the guild assemblage differs markedly from that of the original one.

Klein (1989), Power (1996), and Didham *et al.* (1998) have also shown that the fragmentation and degradation of primary rain forest in South America had a negative influence on the dung beetle assemblages. In Malaysia and Uganda it was also found that degradation of primary forest leads to reduced species diversity of dung beetles (Nummelin and Hanski 1989, Holloway *et al.* 1992, and Davis 2000).

Working in the forest-savanna mosaic of Côte d'Ivoire in West Africa, Krell *et al.* (2003) found clear patterns at guild level of dung beetles that were determined by habitat types and time of day. In the savanna parkland during the day, telecoprids and their kleptoparasites were dominant while in the river valley during the day and in the gallery forest all day and night the abundance of the dung beetles were very low.

Outside the tropics it has also been shown that different land use modes have an effect on the dung beetle assemblages. Comparing the dung beetle assemblages in a nature reserve and the neighbouring farmlands in South Africa, Jankielsohn *et a*l (2001) found that there are definite habitat preferences among the guilds of dung beetles. Also comparing the grazed and the ungrazed sand hill prairie in western Nebraska, Jameson (1989) found that the grazed site had slightly higher dung beetle diversity than in ungrazed sites.

1.2.4 Seasonal and Diurnal Separation of Dung Beetles

Cambefort and Walter (1991), Andresen (2002) demonstrated that the members of the dung beetles show great seasonal variation in both species richness and total abundance and biomass. They showed that there are more individuals and species during the rainy season as opposed to the driest part of the year. In the temperate climates, Hunter *et al.* (1991) also found a seasonal distribution and a diel flight activity pattern of Staphylinidae in open and wooded pasture in east central Texas. They found that most species were active during the spring, summer and the fall. The same trend was also reported by Fincher *et al.* (1986) among the dung feeding Scarabs.

Janzen (1983) and Montes de Oca and Halffter (1995) observed seasonal changes in the abundance of dung beetles of the Central American tropical rain forest and grasslands.

Many authors have worked on the diel activity of dung beetles in the tropics. Krell *et al.* (2003) and Krell-Westerwalbesloh *et al.* (2004) have shown that the guild structure of dung beetles differs between the day and night in the west African forest Savannah mosaics. Andresen (2002) on the other hand has shown that the species composition, abundance and mean body size of dung beetles captured during the day in the tropical rain forest show some differences from those captured during the nighttime.

1.2.5 Human Land use Activities in Kakamega Forest and the surrounding areas

Kakamega forest acts as a major water catchment area in western Kenya (Tsingalia 1988) and this is one of the indirect values of forests and Kakamega forest is by no means an exception. Other indirect benefit of Kakamega forest is carbon sequestration from the atmosphere. It has been reported that forests sequester about 90% of the world's terrestrial carbon, and store about 20 to 100 times more carbon than agricultural lands (Mungatana 1999). Carbon dioxide is a green house gas and its increased release into the atmosphere will have an effect of global warming.

According to Tsingalia (1988), the local communities living around the forest have used it for hunting wild animals, and gathering plants for food and medicine since time immemorial. Although proscribed from the perimeters of the forest reserve these activities are still practiced by some local residents in a non sustainable way hence impacting negatively on the its conservation (Kokwaro 1988).

According to Kokwaro (1988) and Tsingalia (1988) the major demand for the fuel and timber from Kakamega forest started in early 1900 when it was needed for the railway operation. This led to a major destruction of forest resources in western Kenya. Nowadays most wood from the forest is harvested illegally mostly for domestic use (Mungatana 1999).

The land around Kakamega forest is currently mostly used for agricultural production as the zone contains the most productive agricultural land in Kenya (Mungatana 1988). It is mostly food crops that are grown although a minority of farmers grow cash crops. The sizes of the farms are very small and range from 0.1 to 16 ha per household (Mungatana 1999). According to Kokwaro (1988) and Tsingalia (1988) the forestry department allows for the shamba system farming. In this system the families living around the forest are allowed cultivate food crops in cleared plantation areas of the forest and at the same time plant tree seedlings and take care of them until they form a canopy and then are required to stop cultivation in that area. Other people farm within the forest boundary illegally.

According to Kokwaro (1988) and Mungatana (1999) the local people around the forest also keep livestock. The cattle are either illegally driven into the forest reserve for grazing or tethered in the compound (Kokwaro 1988, Tsingalia 1988, and Mungatana 1999).

Kakamega Forest National Reserve is one of the tourist destinations in Kenya (KIFCON 1994, Mungatana 1999). Major tourist attractions in the forest are birds, butterflies, primates and trees.

Chapter 2

2.0 THE INFLUENCE OF LAND USE MODES ON THE GUILD STRUCTURE OF DUNG BEETLES IN KAKAMEGA FOREST, KENYA

2.1 Introduction

Anthropomorphic land practices in Kakamega forest and its environs, which would affect dung beetles and other related animals dwelling there include deforestation for fuel wood and timber, livestock grazing and undergrowth clearing for crop farming. In South America such kind of deforestation reduced both the beetle abundance as well as species variety and guild variability (Howden and Nealis 1975). Jameson (1989) worked in Nebraska, USA, and compared beetle populations in grazed and ungrazed grasslands. He concluded that the species diversity of dung beetles was statistically higher in the former grasslands than the latter. Similarly studies conducted in the Malaysian and Ugandan forests where deforestation was carried out to create fragmented portions of crop farmlands within the forest revealed that this activity greatly affected dung beetle species diversity as well as their guild structures (Holloway et al 1992, Nummelin and Hanski 1989).

This study was initiated to determine the influence of similar human activities of deforestation, livestock grazing, and crop farming (shamba system) in Kakamega forest on the Scarabaeid beetles inhibiting the forests and their adjacent farmlands. Such knowledge would be useful to ascertaining the importance the beetles play in this fragile forest ecosystem that has recently attracted much attention by the tourist industry in Kenya.

2.2 Material and methods

2.2.1 Study Area

This study was conducted in the Kakamega forest and the neighbouring farmlands. The forest is situated in Western Kenya (0°8'-0°24'N: 34°20'-34°33'E), and it covers an area of 240 km^2 and lies at altitudes 1500-1700 metres above sea level. The temperature varies between a mean maximum of 27°C and mean minimum of 15°C. The annual mean rainfall is more than 2000 mm with the major wet season stretching from March to July and short rains season from September to November. The dry season is between December and March.

The forest is situated 150 km west of the Great Rift Valley, from which it is separated by highlands stretching from the Cheranganis in the north to the Mau Escarpment in the south. The 2200-meter high Nandi Escarpment forms the eastern border. To the South-West, Lake Victoria forms another natural border into which all rivers crossing Kakamega forest from the escarpment flow.

Kakamega forest is the remnant of what used to be once a vast rain forest in the Pleistocene 1.8-0.5 million years ago (Kokwaro 1988, Tsingalia 1988, Clausnitzer 1999). The lowland forests of east and central Africa were connected to the highland rain forests of Uganda, expanding into Kenya. At about 10,000 years ago these forests began to shrink because of the increasing aridity to the present condition that has been reached probably 200-300 years ago (Clausnitzer 1999).

As human population increased, parts of those remaining forests were cleared or burnt and slowly replaced by bush or savanna, leaving relatively small islands of the Guineo-Congolian rainforest scattered across Uganda, Democratic Republic of Congo (former Zaire) and Kenya (the Kakamega forest and its outliers). Between 1965 and 1991 the area covered by the indigenous rainforest in Kakamega forest decreased by 50% (KIFCON 1994, Kokwaro 1988).

Kakamega forest shows the highest biodiversity of any forest in Kenya. Many plant and animal species occur nowhere else in Kenya, and show the former connection to Central Africa (Lockwood 1995, KIFCON 1994). However, there is a notable absence of large mammals such as elephants and buffaloes that are believed to have been wiped out at the turn of the 20th century, the last animals probably killed off by rinderpest disease (KIFCON 1994).

The main crops grown around Kakamega forest include maize, beans, sweet potatoes, and millet, which are mainly for subsistence. Tea and sugarcane are the main cash crops grown by the farmers around this forest. They also keep livestock, mainly cattle and sheep (Kokwaro, 1988) and extensively use the dung resource particularly for making the houses and making farmyard manure (personal communication with local people).

Fig.2. A map showing Kakamega Forest and the surrounding areas. Inset: The location of Kakamega forest on the Kenyan map.

2.2.2 Study sites

In this study, four sites were chosen within the Kakamega forest and the surrounding farmlands. They include: 1) Primary forest (0°21'31"N, 34°51'38"E). 2) Secondary forest (0°21'08"N, 34°51'55"E). 3) Ungrazed grassland (0°21'13"N, 34°51'49"E) at the border of the forest, 4) Grazed grassland pastures around the forest (0° 09'52'' N, 34°48'04''E). The primary forest comprises an area of the forest that is dominated by the climax vegetation that has been established over a long period of time, while the secondary forest included an area of the forest that is dominated by derived vegetation as a result of human induced disturbance of the primary forest in the recent times (Richards 1996). This area was used as a farm to grow millet, maize and beans about 15 years ago (personal communication from local residents).

The first three sites, namely primary forest, secondary forest and the ungrazed grassland, are found at Buyangu within the Kakamega Forest Nature Reserve (plates 3-5). The fourth site, the grazed grassland is situated at Shiveye village (0°09'52''N, 34°48'04''E) outside the Kakamega Forest Nature Reserve and about 25km from Buyangu and was part of the dense Kakamega forest about 100 years ago (Tsingalia 1988) (fig. 2).

2.2.3 Experiment

The collection of the dung beetles was done using the floating method with the sampling done in October 2002, January to February 2003, April 2003 and July 2003. These timings coincided with the beginning of the short rainy, dry, beginning of the long rainy (this time the long rains were late and started in April), and the end of the long rainy seasons respectively in the study area. The long rainy season was arbitrary divided into start and end of the long rainy season as it has been reported that the dung beetle assemblages during the start of the long rainy and end of the long rainy season are markedly different (Cambefort and Hanski 1991). During each of these seasons 20 portions of 1 kg fresh cow dung (plate 6) were randomly deposited on the soil on the ground in each of the four habitats (primary forest, secondary forest, ungrazed grassland at the border of the forest, and grazed grassland pastures around the forest). 10 of these portions were deposited during the day (6:00 h to 16:00 h), and 10 others during the night (18:00 to 6:00h), because the flight activity of dung beetles differs strongly between night and day at guild level (Krell-Westerwalbesloh *et al.* 2004). A maximum of two portions were exposed simultaneously per site and always the same number of samples in the first three sites (primary forest, secondary forest, and the ungrazed grassland), while the exposure in the grazed grassland was done independently but was distributed equally over a given sampling period. Each dung-pat portion was considered as a sampling unit. A summary of all treatments used is contained in Table 1.

Season	Habitat							
	Primary forest		Secondary forest		Grazed grassland		Ungrazed grassland	
	Day	Night	day	Night	Day	Night	Day	Night
Short rains	10	10	10	10	10	10	10	10
Dry season	10	10	10	10	10	10	10	10
Start long rains	10	10	10	10	10	10	10	10
End long rains	10	10	10	10	10	10	10	10

Table 1. Number of sampling units per habitat per season

Plate 3. Primary forest site in Kakamega forest (characterized by huge Trees of mostly*Teclea nobilis* (Rutaceae) and *Heinsenia dirvilleoides* (Rubiaceae) and less undergrowth).

Plate 4. Secondary forest site in Kakamega forest (Characterized by small tree and much undergrowth with *Acacia sp.* as the main tree type).

Plate 5. Ungrazed grassland site in Kakamega forest. Grass domimated by *Loudetia karensis* (Graminae).

Plate 6. 1kg portion of cow dung placed on the ground.

Plate 7. Mount of soil on top surface of dung brought up by tunneler beetles.

2.2.4 Sampling

Dung beetles were sampled using fresh cow dung as bait, which was collected, in a bucket from cattle shade nearby the study site. Before it was used, all adult dung beetles removed by picking them out using a pair of forceps to ensure that the beetles recovered later in the samples were only those that had occupied the dung during the exposure period and from the site under study.

The exposure period was from 6.00hrs (just after dawn) to 16.00hrs for the day samples and 18.00hrs (just before dusk) to 6.00hrs (before sunrise) for the night samples. One kilogram of dung per sampling unit was placed directly on the soil using a potty to ensure that the pad was in one piece and nearly round. The pad was then left in the field during the exposure period. If there was any rain during the exposure period of the dung, these pats were excluded, because many dung beetles leave the dung or would not fly during strong rains and most of the dung is washed away.

After the exposure period the dung-pad and the soil beneath it that was populated by dung beetles was collected into a bucket. A spade was used to dig out the dung and the soil beneath as a single cube (at least 10cm deep). The digging was extended in the direction of any soil hills (plate 7) and dung beetle tunnels to get the nests with the tunneling dung beetles.

The samples were processed as soon as possible after collection. The buckets containing the collected samples were filled with water and stirred vigorously to make the beetles to float (floatation method). They were then collected with a sieve of 0.5mm gauze size from which they were picked with a pair of forceps and placed in collecting bottles containing a tissue soaked with ethyl acetate to kill the beetles.

The dead beetles were then transferred to vials for preservation using 75% ethanol. The vials were labeled accordingly.

2.2.5 Family and Guild classification

With a permit from the National Museum of Kenya (NMK) the dung beetle samples were shipped to the Department of Entomology of the Natural History Museum (NHM) where classification was done under the supervision of Dr. Frank-Krell who is a Coleopteran taxonomist. The beetles collected from the dung sample were first identified to family. The members of the dung beetle family Scarabaeidae (the Aphodiinae was considered as a subfamily of Scarabaeidae) were further classified into guilds based on morphological features into telecoprids (rollers), paracoprids (tunnelers), endocoprids (dwellers) and obligatory kleptoparasites.

The other families considered were the Staphylinidae, Histeridae, and Hydrophilidae. All other insects collected were grouped as `others'.

2.2.6 Statistical Analysis

Diurnal and nocturnal samples were analysed separately as it is known that both daytime and night exert a significant influence on the guild structure of dung beetles (Krell-

Westerwalbesloh *et al.* 2004) and combing them will greatly influence the observed correlation in the ordination diagrams. Computer software Canoco for Windows 4.5 (Centre for Biometry Wageningen, The Netherlands) (Ter Braak and Smilauer, 1998), and Statistics for Social Scientists (SsS) I.Ia (Rubisoft Software) were used for the statistical analysis.

Using SsS 1.1a program, the statistical significance of differences in abundance of dung beetle guilds and families from different sites was tested using Kruskal-Wallis test when all sites were compared together, then followed by Dunn test for the significance of abundance between any two given sites

Correlation between the abundance of guilds is shown with a Principle Components Analysis (PCA) (Canoco) using log transformed guild abundance data. A standardised redundancy analysis (RDA) (Canoco) (Jongman *et al.* 1995, Leps and Smilauer 2003) using log transformed guild data shows the relationship between the site parameters and guild abundance. In both the PCA and RDA using Canoco for windows 4.5 the correlation between guilds and environmental variables (in this case different sites) gives ordination diagrams in which proximity of a particular guild to a particular site shows it is positive correlated to that site. However, if a particular guild is in an opposite direction to a particular site, then they are negatively correlated. In the diagram when the angle of guild and the site axis forms a right angle then there is no correlation at all.

The significance of environmental variables (in this case the sites) in explaining distribution of the guilds in different habitats was tested by constrained Redundancy Analysis (RDA) followed by Monte Carlo permutation Test (Canoco; 999 permutations). This analysis using Canoco for windows 4.5, gives both marginal effects and conditional effects measured in Lambda values, and the significance of simple regression model that describes the significance (P value) of dependence of the dung beetle guilds on different habitats (Sites). A marginal effect is the contribution of particular environmental variable e.g. different habitats in explaining the distribution of the dependent (guilds and families) variable when all the other variables are not considered. On the other hand conditional effect is the contribution of a particular environment variable in explaining the distribution of the dependent variable e.g. guilds and families when all other environmental variable are considered

2.3 Results

The telecoprids, paracoprids and endocoprids are the guilds that were represented in the samples among the family Scarabaeidae. Other families represented included the Hydrophilidae, the Staphylinidae and the Histeridae. The telecoprids included all members of the tribe Sisyphini, while Paracoprids included all Coprini, all Onitini, most Oniticellini, most Onthophagini and *Aphodius (Neocolobopterus)*. The endocoprids included all members of Aphodiinae (except *Neocolobopterus*) and *Oniticellus formosus* Chevrolat. Kleptoparasites were not represented in the collected samples.

2.3.1 Effect of different sites on the abundance of dung beetle families

The result in tables 2 and 3 shows the abundance of dung beetle families in different sites sampled. The abundance of Scarabaeidae, the Hydrophilidae and Staphylinidae are significantly different in all the sites both during daytime and night time (Kruskal-Wallis test P.05) (Table 4). When any two sites were compared, the abundance of Scarabaeidae was significantly different in most of them apart from between the primary forest and the ungrazed grassland during daytime. At night time they were not significantly different between the secondary forest and the primary forest, and between the secondary forest and the ungrazed grassland (Dunn test, $P<0.005$) (Table 4).

The abundance of the family Hydrophilidae when compared between any two sites is significantly different apart from between the secondary forest and the primary forest during the daytime. Also it is not significant between the grazed grassland and the ungrazed grassland, and the secondary forest and the primary forest during the night (Dunn test $P<0.05$). The abundance in the family Staphylinidae on the other hand are shown to be significantly different between any two sites apart from between grazed grassland and ungrazed grassland, and the secondary forest and ungrazed grassland during daytime. During the night the difference in abundance is not significant between the secondary forest and the primary forest, secondary forest and ungrazed grassland, and ungrazed grassland and the primary forest (Dunn test) (Table 4).

Land use	Grazed grassland		Ungrazed grassland		Secondary forest		Primary forest	
Guilds	Individuals	%	Individuals	%	Individuals	%	Individuals	%
Scarabaeidae	3310	62.40	614	32.9	1452	89.2	431	57
Hydrophilidae	1520	28.7	965	51.7	35	2.2	55	7.2
Histeridae	10	0.2	50	2.7	45	2.8	14	1.9
Staphylinidae	453	8.6	236	12.6	72	4.4	242	32.0
Others	4	0.1	1	0.1	23	1.4	14	1.9
Totals	5297	55.5	1866	19.5	1627	17	756	8.0
(n=9546								

Table 2. Abundance of families in dung beetle assemblages of different habitats collected in the daytime samples. n = the overall number of dung beetles collected.

Land use	Grazed grassland		Ungrazed grassland		Secondary forest		Primary forest	
Guilds	Individuals	%	Individuals	%	Individuals	%	Individuals	%
Scarabaeidae	6151	78.5	1376	35.6	625	80.1	471	61.6
Hydrophilidae	644	8.2	2374	61.4	61	7.8	112	14.7
Histeridae	0	0	10	0.2	2	0.3	1	0.1
Staphylinidae	1040	13.2	105	2.7	85	10.9	170	22.2
Others	4	0.1	4	0.1	7	0.9	11	1.4
Totals	7839	59.1	3869	29.2	780	5.9	765	5.8
(n=13253								

Table 3. Abundance of families in dung beetle assemblages of different habitats collected in the night samples. n = the overall number of dung beetles collected.

	Sampling	Test	Pair wise test (Dunn test)					
Family	time	Kruskal Wallis	GG/PF	GG/UG	GG/SF	SF/PF	SF/UG	UG/PF
Scarabaeidae	Day	0.000000	*	*	*	*	*	N.S
	Night	0.000000 0.0	*	*	*	N.S	N.S	*
Hydrophilidae	Day	0.000000	*	*	*	N.S	*	*
	Night	0.000000	*	N.S	*	N.S	*	*
Staphylinidae	Day	0.000000	*	N.S	*	*	N.S	*
	Night	0.000000	*	*	*	N.S	N.S	N.S

Table 4. Showing conversion of actual beetle family counts from various habitats into abundance values using Kruskal- Wallis and Dunn test indicating statistical differences between habitats in day and night collection. (GG= grazed grassland, PF= primary forest, SF= secondary forest, UG= ungrazed grassland, N.S= not significant, and *=significant (p<0.05).

2.3.2 Effect of different sites on the abundance of dung beetle guilds

Tables 5 and 6 show the abundance guilds in different habitats. The abundance of the guilds is significantly different between all sites studied (P< 0.005, Kruskal-Wallis test) (Table 7). The abundance of the tunnelers was significantly different between most sites (P < 0.05, Dunn test) (Table 7) apart from between the grazed grassland and secondary forest, and the ungrazed grassland and the primary forest during daytime. At night they were not significant different between the grazed grasslands and the primary forest, between the grazed grassland and secondary forest, and between the ungrazed grassland and the primary forest (P<0.05, Dunn test) (Table 7).

The abundance of the dwellers too was significantly different between any two given sites apart from between the secondary forest and the primary forest, between the secondary forest and the ungrazed grassland, and the ungrazed grassland and the secondary forest during daytime. During the night they were not significantly different between the secondary forest and the primary forest ($P < 0.05$, Dunn test) (Table 7).

The telecoprids are very rare in the study area (Tables 4, 5). They were not collected in the samples in the secondary forest. The kleptoparasites are completely absent from all samples.

Land use	Grazed grassland		Ungrazed grassland		Secondary forest		Primary forest	
Guilds	Individuals	%	Individuals	%	Individuals	%	Individuals	%
Paracoprids	3303	99.8	565	92	1374	94.6	307	71.2
Endocoprids	4	0.1	44	7.2	78	5.4	122	28.3
Telecoprids	3	0.1	5	0.8	0	0	2	0.5
Kleptoparasites	0	0	0	0	0	0	0	0
Totals (n=5807	3310	57	614	10.6	1452	25	431	7.4

Table 5. Abundance of Scarabid guilds in different habitats collected in the daytime samples. n = the overall number of dung beetles collected.

Land use	Grazed grassland		Ungrazed grassland		Secondary forest		Primary forest	
Guilds	Individuals	%	Individuals	%	Individuals	%	Individuals	%
Tunnelers	616	10	284	20.6	449	71.8	304	64.5
Dwellers	5535	90	1092	79.2	176	28.2	167	35.5
Telecoprids	0	0	2	0.2	0	0	0	0
Kleptoparasites	0	0	0	0	0	0	0	0
Totals (n=8625	6151	71.3	1378	16.0	625	7.2	471	5.5

Table 6. Abundance of Scarabid guilds in different habitats collected in the night samples. n = the overall number of dung beetles collected.

Guilds	Sampling	Test	Pair wise test (Dunn test)					
	time	Kruskal Wallis	GG/PF	GG/UG	GG/SF	SF/PF	SF/UG	UG/PF
tunnelers	Day	0.0000000	*	*	N.S	*	*	N.S
	Night	0.000842	N.S	*	N.S	N.S	*	N.S
Dwellers	Day	0.000000	*	*	*	N.S	N.S	N.S
	Night	0.000000	*	*	*	N.S	*	*

Table 7. Showing conversion of actual beetle guilds from various habitats into abundance values using Kruskal- Wallis and Dunn test indicating statistical differences between habitats in day and night collection. (GG= grazed grassland, PF= primary forest, SF= secondary forest, UG= ungrazed grassland, N.S= not significant, and *=significant ($p<0.05$).

2.3.3 Correlation of guilds and families with sites

The Principal Component Analysis (PCA) ordination diagram (Fig. 3) shows graphically the correlation of guilds and families of dung beetles. The rollers and the tunnelers are positively correlated since the angle of their vectors is less than 90 degrees and they are close together. The angle of the vectors of the rollers and the Staphylinids, however are perpendicular hence they are not correlated at all. There is negative correlation between the dwellers on one hand, and the rollers and the tunnelers on the other as their vector face in opposite direction.

The RDA in fig 4 shows the correlation of guilds and environmental parameters during daytime. During daytime the dung beetle assemblages in grazed and ungrazed grasslands are similar represented by the Staphylinidae and the Hydrophilidae, as well as those of the primary forest and the secondary forest represented by Histeridae. The abundance of the dwellers is negatively correlated to both the numbers of tunnelers and rollers while the numbers of rollers and the tunnelers are positively correlated. The dwellers show a strong preference for to the primary forest while most of the rollers were found in the ungrazed grassland. The tunnelers do not show any association with any of the sites while the staphylinids and hydrophylids prefer the ungrazed grassland and are negatively correlated to the histerids, which prefers the forest areas.

During daytime all the sites have their lambda values in the RDA more than 0.2, and most of them have highly significant conditional effect ($p<0.05$) in the interplay of all variables (conditional effect) (Table 8).

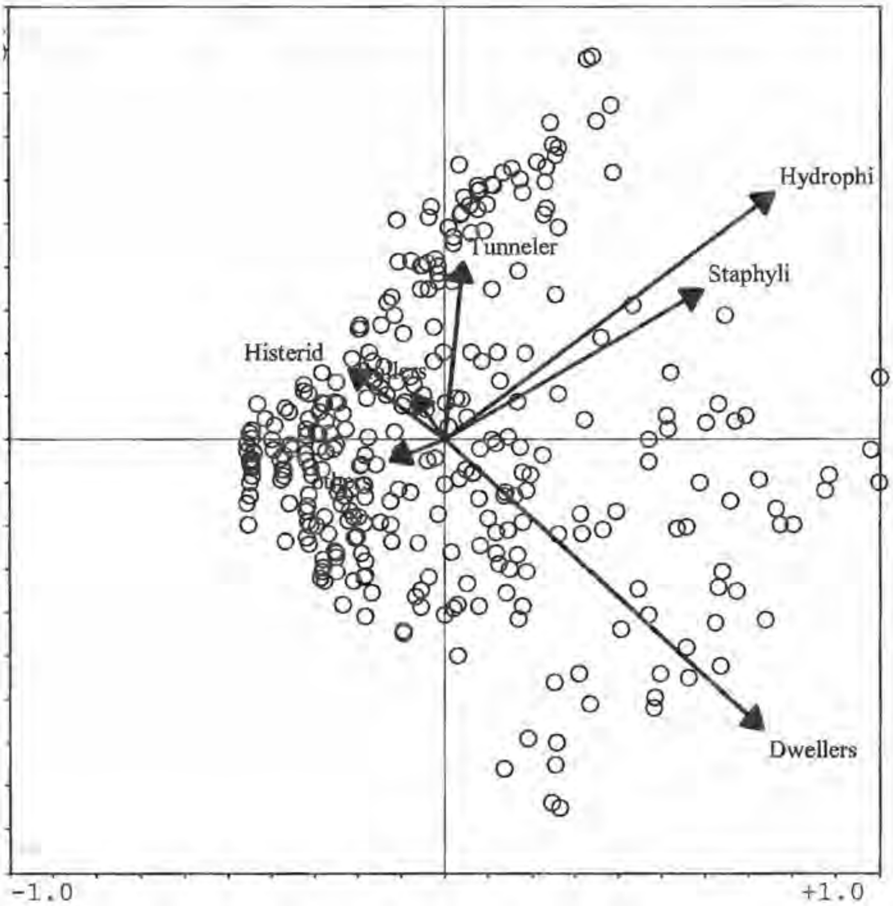


Fig 3. Principle component Analysis (PCA) biplot of log transformed absolute numbers of individuals in each guild showing graphically the correlation of guilds and families. The axes represent the gradient of guilds and families.

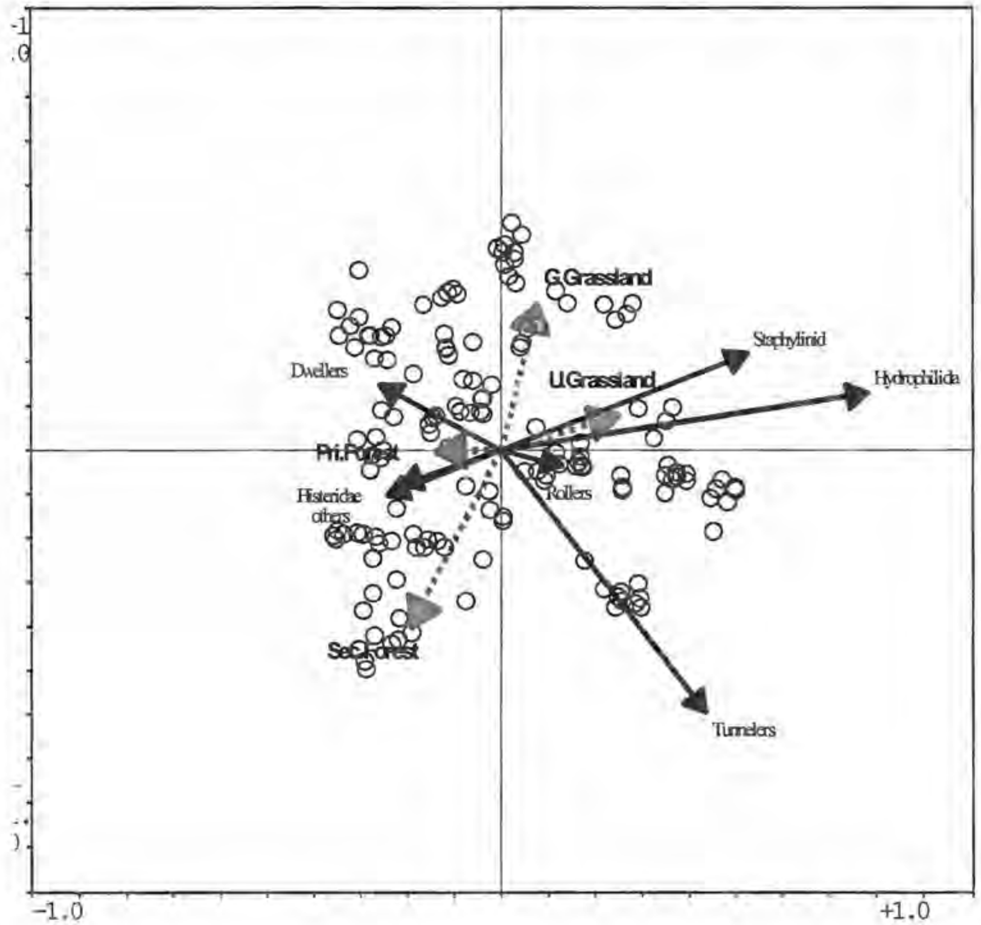


Fig. 5.

Fig 4. Redundancy Analysis (RDA) ordination biplot showing correlation between guilds and environmental variables (sites) based on log transformed absolute numbers of individuals within each guild during the day. The axes represent environmental (habitats) gradient G= grazed, u= ungrazed, pri= primary, sec.= secondary.

Marginal effects		Conditional effect		
Variable	Lambda	Variable	Lambda	P
Ungrazed grassland	0.03	Ungrazed grassland	0.03	0.001
Sec. forest	0.03	Sec. forest	0.03	0.001
Grazed grassland	0.02	Primary Forest	0.01	0.003
Primary Forest	0.01			

Table 8. Lambda values and associated statistical significance (p values) of environmental variables (sies) in the RDA during the day showing marginal and conditional effects. The significance of variables are tested by a Monte Carlo permutation Test (Canoco; 999 permutations).

During the night, RDA (fig 5) shows no correlation between the assemblages of secondary forest and primary forest. The grazed grassland is dissimilar to the grazed grassland. The dwellers are associated with the grazed grassland and not associated with the ungrazed grassland and the secondary forest. The tunnelers are associated with both the secondary forest and the grazed grassland while not associated with both the ungrazed grassland and the primary forest.

Most of the sites have their lambda values are <0.1, and they have a significant conditional effect ($p<0.05$) on the guild structure of the dung beetles (Table 8).

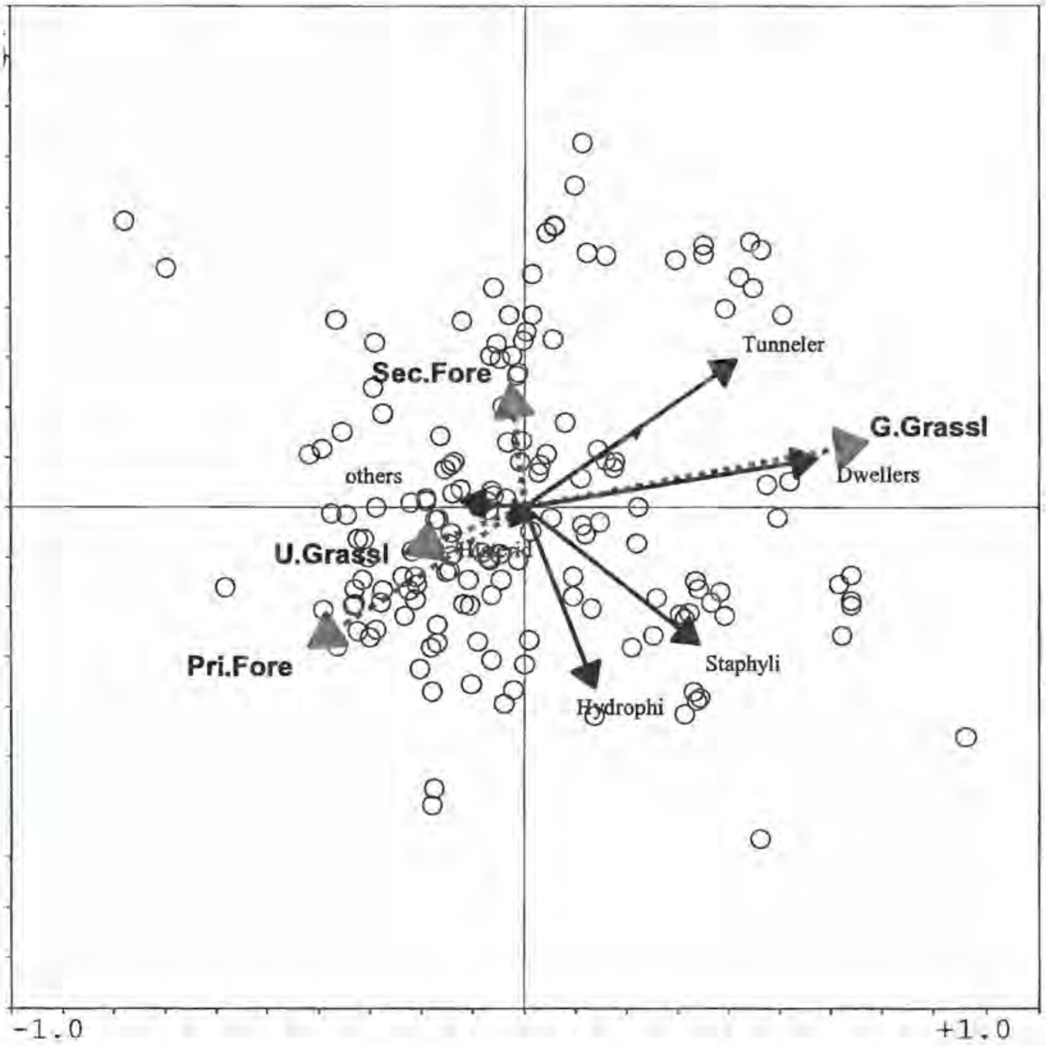


Fig 5. A Redundancy Analysis (RDA) ordination biplot showing the correlation between guilds and environmental variables (sites) based on log transformed absolute numbers of individuals within each guild during the night The axes represent environmental (habitats) gradient. (G= grazed, u= ungrazed, pri.= primary, sec.= secondary).

Marginal effects		Conditional effects		
Variable	Lambda	Variable	Lambda	P
Grazed grassland	0.08	Grazed grassland	0.08	0.001
Primary forest	0.03	Secondary forest	0.01	0.029
Ungrazed grassland	0.02	Primary forest	0.02	0.039
Secondary forest	0.01			

Table 9. Lambda values and associated statistical significance (p values) of environmental variables in the RDA during the night showing marginal and conditional effects. The significance of variables is tested by a Monte Carlo permutation Test (Canoco; 999 permutations).

2.3 Discussion

Many factors are known to influence the population dynamics of many groups of insects that include both the density depended and density independent. One of the most important factors is the influence of the surroundings, which in most cases the changes in the surroundings is influenced by man's activities. Findings from these studies have collaborates with the findings from other places of the world (Howden and Nealis 1975, Klein 1989, Kirk (1989), Halffter *et al.* 1992, Power 1996, and Didham *et al.* 1998) that the dung beetle assemblages in Kakamega forest too are influenced by human activities.

It is estimated that in the West African savanna dung beetles are responsible for the recycling of over one metric ton of dung per hectare per year (Cambefort and Hanski 1991). This is due to high abundance of dung beetles in these savannas. The abundance of dung beetles is affected by changes in the habitats. Dung beetles play an important role in the decomposition of the dung thereby recycling nutrients. Any changes in the abundance of the dung beetles as shown among different families and guilds of the dung beetles in these studies will have a ramification on the state of soil fertility in the study area.

Changes in habitat composition as a result of human activity have also altered the dung beetle family balance between different sites studied. The members of the family Staphylinidae and Histeridae play a very important role in the ecosystem in that they are predators of other insects in the dung (Cambefort and Hanski 1991). Any change in the population of these families as a result of the changes in the habitat will destabilise the community structure of the other insect community in the dung especially the pest flies.

The differences between the number of beetles in these sites could be due to the differences in the microclimate especially during daytime. During this time the secondary forest as a result of reduced canopy could be heating up faster compared to the primary forest. The higher dung temperature here creates a microclimate more suitable for the dung beetles and enhances the activity of the tunnelers (Krell *et al.* 2003, Davis 1993) hence the high number of beetles collected. This could also explain the disparity in the abundances of beetles between the grazed and ungrazed grasslands, as grass in the latter is taller and it takes longer to heat compared to the former.

At the guild level the dwellers that are normally a nocturnal guild display their highest relative abundances in the primary forest during daytime. It is known that primary tropical rain forests have very closed canopy. This makes it hard for the light to penetrate to the ground and hence they are dark as compared to the secondary forests and other open habitats. This condition mimics night situation and therefore favours the dwellers during the day. The availability of the dung resource may have also played a crucial part in the distribution of the dung beetles. During both daytime and nighttime it is observed from the RDA that the tunnelers are associated with the grazed grassland which has the highest dung availability.

Andersen 2002 demonstrated that, dung beetle guild of rollers play a very important role in seed dispersal. They do this due to the fact that they transfer dung that might be containing seeds of some vegetation from places where they could be more prone to predatory attack into places that favours their germination. From this study we have seen that the rollers despite fewer in numbers are strongly associated with the ungrazed grassland. In other places like the secondary forest and the grazed grassland they are totally lacking. The strong association with the ungrazed grassland as opposed to the ungrazed grassland is not clear. It is expected that they should be strong associated with the grazed grassland where we have less grass height as this will make rolling away dung easier as opposed to ungrazed grassland where the grass is taller. The lack of the rollers in some habitats will have the implication of reduced dispersal of seeds that could be found in the dung in these areas and hence vegetation regeneration.

It can therefore be concluded that the differences between the abundance and the guild structure of dung beetles in the different habitats in Kakamega forest and the surrounding farm lands is due to changes that have resulted by human activities. The logging of the forests, the extinction of the native large mammals and the exclusion of livestock from the forest have all influenced the dung beetle abundance and community composition at guild level.

Chapter 3

3.0 THE INFLUENCE OF SEASONS ON THE FAMILIES AND GUILD STRUCTURE OF DUNG BEETLES IN KAKAMEGA FOREST AND ADJACENT GRASSLANDS

3.1 Introduction

The influence of seasons on insect communities has been well documented (Wolda 1978, Janzen 1983, Fincher *et al* 1986, Hunter *et al.* 1991, Montes *et al.* 1995, Allsopps and Logan 1999). Seasonal fluctuation in food availability is one of the major causes in the fluctuation in the numbers of most insects. For the dung beetles, particularly where food resource is quite constant over changing seasons, seasonal fluctuations in abundance and community structure must be due to factors other than food availability. For example, changes in soil hardness (particularly pertinent for tunneling species) or seasonal fluctuations in the temperature regime (which are particularly pronounced in temperate countries with extreme summers and winters) (Cambefort and Hanski 1991). Seasonality in dung beetles assemblages has, however, also been reported in tropical grasslands (Coe and Kingston 1988) where dung beetle are more abundant in the rainy seasons compared to the dry seasons.

In the tropics, particularly in the tropical rain forest, seasonal fluctuations of temperature regime are low (Kokwaro 1988), the dry seasons are greatly reduced and the rainy seasons are prolonged. The objective study is therefore to examine the seasonal influence on the abundance and guild structure of dung beetles in Kakamega forest and the surrounding grasslands.

3.2 Material and methods

3.2.1 Study Area

These studies were conducted in Kakamega forest and the surrounding farmlands and this has been comprehensively described in chapter 2.

3.2.2 Experiment

The collection of the dung beetles was done using the floating method with the sampling done in October 2002, January to February 2003, April 2003 and July 2003. These timings coincided with the beginning of the short rainy, dry, beginning of the long rainy (this time the long rains were late and started in April), and the end of the long rainy seasons respectively in the study area. The long rainy season was arbitrarily divided into start and end of the long rainy seasons as it has been reported that the dung beetle assemblages during the start and end of the long rainy season are markedly different (Cambefort and Hanski 1991). During each of these seasons 20 portions of 1 kg fresh cow dung (plate 6) were randomly deposited on the soil on the ground in each of the four chosen habitats (primary forest, secondary forest, ungrazed grassland at the border of the forest, and grazed grassland pastures around the forest). 10 of these portions were deposited during the day (6:00 h to 16:00 h), and 10 others during the night (18:00 to 6:00h), because the flight activity of dung beetles differs strongly between nighttime and daytime at guild level. Therefore, dung beetle assemblages (coprocenoses) of freshly exposed substrate differ according to exposure time (Krell-Westerwalbesloh *et al.* 2004). Each dung-pat portion was considered as a sampling unit.

After the exposure period the processing of the samples was done using floating method as described in chapter 2.

3.2.3 Family and Guild classification

The classification of guilds and families is as described in chapter 2.

3.2.4 Statistical Analysis

Statistical analyses were done using Canoco for Windows 4.5 (Centre for Biometry Wageningen, The Netherlands), and Statistics for Social Scientists (SsS) I.Ia (Rubisoft Software) computer programs. Canoco for windows 4.5 was used to carry out the Redundancy analysis while SsS was used to carry both the Kruskal- Wallis and Dunn tests. Kruskal-Wallis ANOVA test was used to test for the significance of seasons on the abundance of families and the guilds of the dung beetles and then did a pair-wise Dunn test to determine the significance of differences in abundance between any two seasons.

A standardised Redundancy Analysis (RDA) (Canoco) (Jongman *et al.*1995, Leps and Smilauer 2003) using log transformed guild data would reveal relationship between the seasonal parameters – short rains, dry season, start of long rains and end of long rains - and families or guild abundance. Diurnal and nocturnal samples were analysed separately.

The significance of environmental variables (in this case the seasons) in explaining distribution of the guilds and families in different seasons was tested by constrained Redundancy Analysis (RDA) followed by a Monte Carlo permutation Test (Canoco; 999 permutations) using Canoco for windows 4.5 program. Monte Carlo permutation test shows the significance of simple regression model that describes the dependence of the dung beetle guilds and families on different seasons.

3.3 Results

The telecoprids, paracoprids and endocoprids are the guilds that were represented in the samples among the family Scarabaeidae. Other families represented included the Hydrophilidae, the Staphylinidae and the Histeridae. The telecoprids included all members of the tribe Sisyphini, while Paracoprids included all Coprini, all Onitini, most Oniticellini, most Onthophagini and *Aphodius (Neocolobopterus)*. The endocoprids included all members of Aphodiinae (except *Neocolobopterus*) and *Oniticellus formosus* Chevrolat. Kleptoparasites were not represented in the collected samples.

3.3.1 Effects of Seasons on Abundance of Dung Beetle Families in Different Habitats

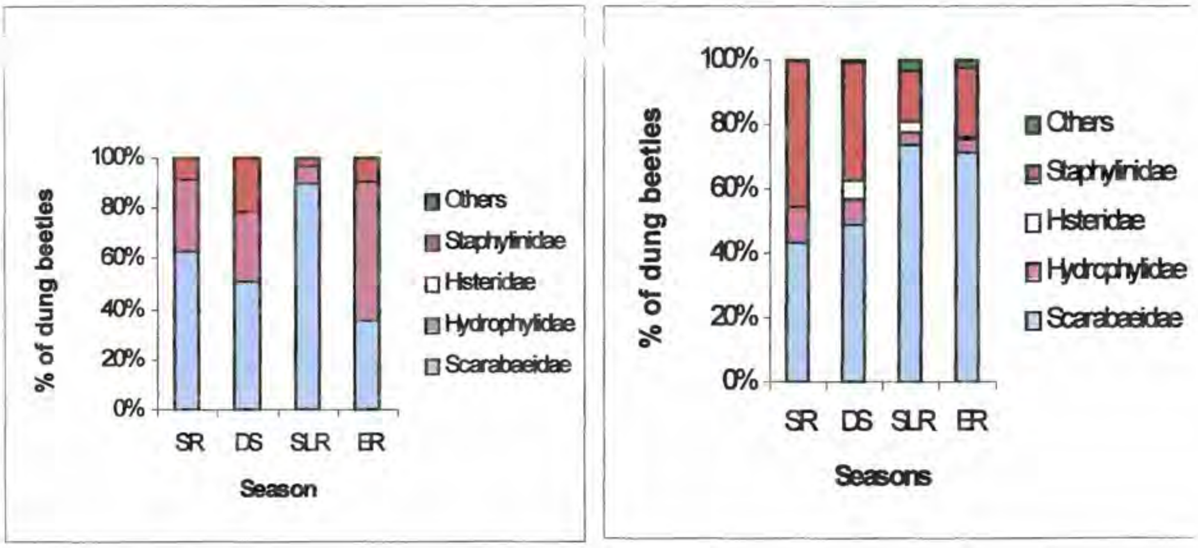
Figs 6 and 7 show the seasonal proportions of different dung beetle families in different habitats. In all the habitats (Tables 10-13) the numbers of the hydrophylids are significantly different when all the seasons are compared simultaneously (Kruskal-Wallis test $P<0.05$). However when a Dunn's pair-wise test is performed to compare abundance between any two seasons significant differences ($P<0.05$) are found only between some two seasons while in most seasons the differences were not significant (Tables 10-13).

The differences in the numbers of Staphylinids are also significantly different when all seasons are compared simultaneously ($P<0.05$, Kruskal-Wallis test) (Tables 10-13). The Dunn's pair-wise test shows that the seasonal differences in abundance is only significant between the dry season and the start of the long rain, and the short rain and the start of the long rain at nighttime in the grazed grassland (Table 10). In the primary forest, significant seasonal difference in abundance of the staphylinids is found only between the short rain and the start of the long rain seasons at nighttime (Table 11). In the secondary forest significant differences in seasonal abundance ($P<0.05$, Dunn test) is found between the end of the long rains and short rains, and between start of the long rains and the short rain seasons. Significance ($p<0.05$. Dunn test) in differences of staphylinids between any two seasons was found between the short rains and the dry season, and between the end of the long rain and the short rain seasons during daytime in the ungrazed grassland (Table 13).

Within the family Scarabaeidae significant seasonal differences in the abundance of these members was only observed in the grazed grassland and ungrazed grassland during nighttime, and the secondary forest and the ungrazed grassland during daytime ($P<0.05$, Kruskal-Wallis test) (Tables 10-13). Performing Dunn's pair-wise test (Tables 10-13) significant seasonal differences ($P<0.05$) was recorded between the short rains and the dry season, and between the dry season and the start of the long rain in the grazed grassland. In the secondary forest it was only between the short rains and the start of the short rain seasons. Most pair-wise significance in differences in seasonal abundances of Scarabaeidae was found in the ungrazed grassland (Table 13).

Gazed grassland

Primary forest



Secondary forest

Ungrazed grassland

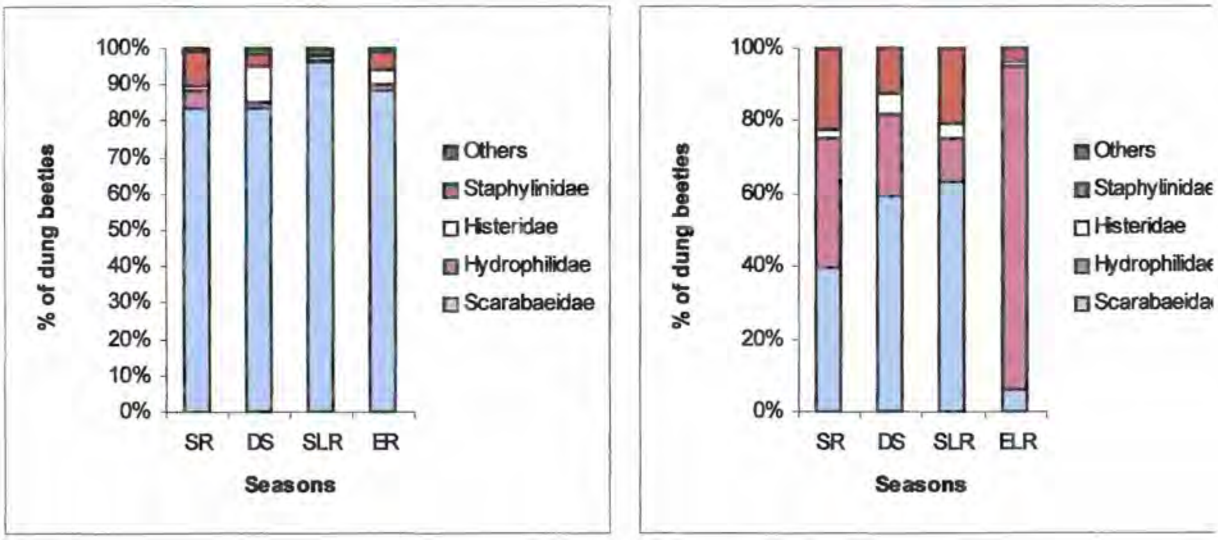
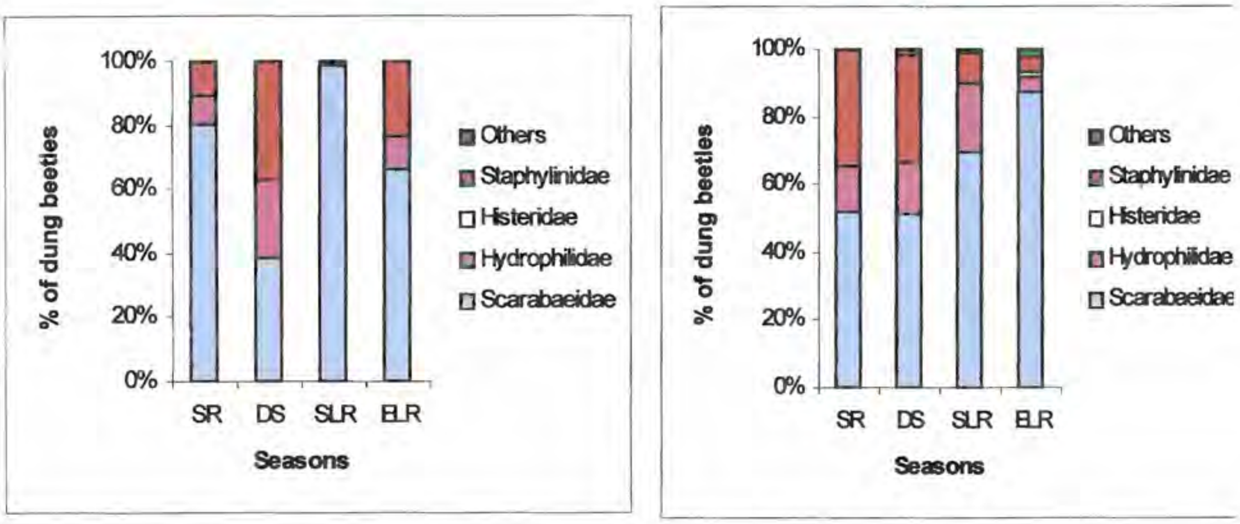
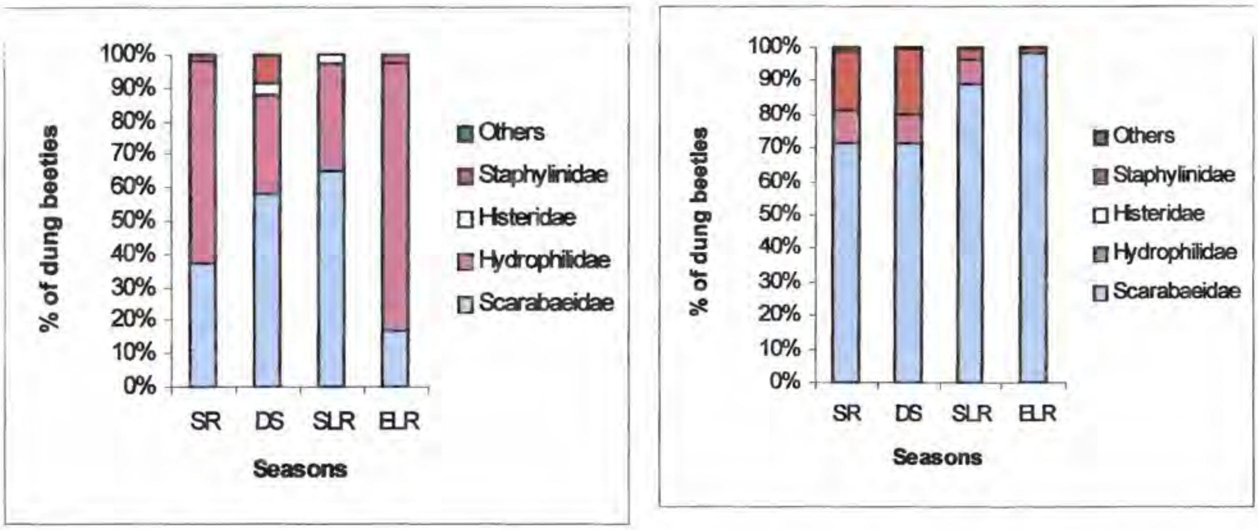


Fig 6. Abundance of dung beetle families in different seasons from the daytime sample in different habitats. SR= short rain, DS= dry season, SLR= start of long rain and ELR= end of long rain.



Grazed grassland

Secondary forest



Ungrazed grassland

Primary forest

Fig. 7. Abundance of dung beetle families in different seasons from the night samples in different habitats. SR= short rain, DS= dry season, SLR= start of long rain and ELR= end of long rain.

3.3.2 Effects of Seasons on Abundance of Dung Beetle Guilds in Different Habitats

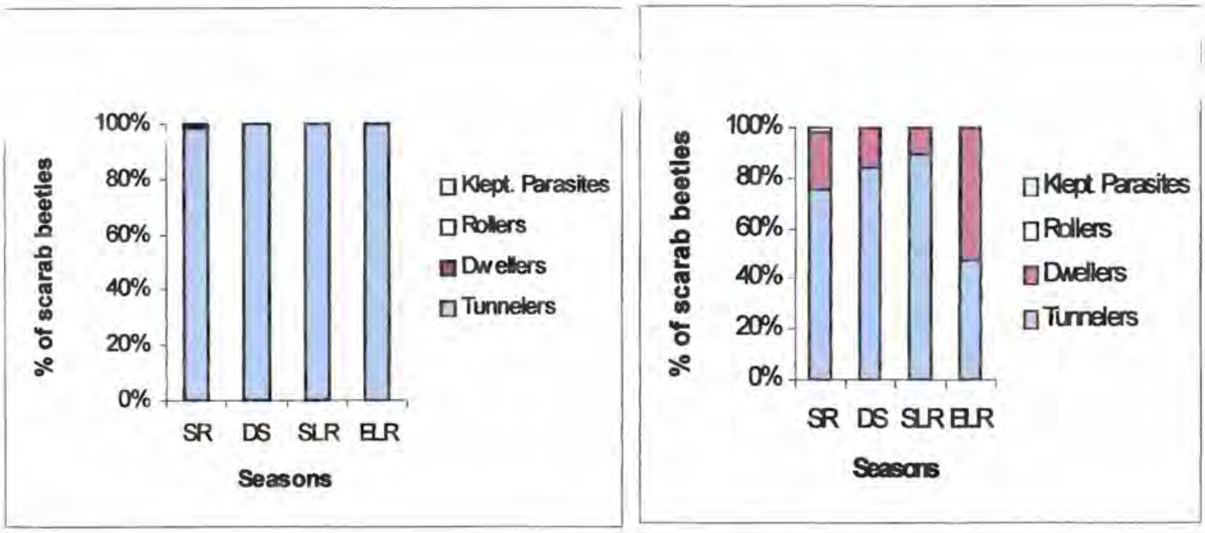
Figs 8 and 9 show the seasonal proportions of dung beetle guilds in different habitats. There is significant seasonal differences in the abundance of tunnelers ($P<0.05$, Kruskal-Wallis test) in the grazed grassland and secondary forest during the night, and the ungrazed grassland during daytime (Tables 10, 12, 13). They are not significantly different in the primary forest (Table 11). The tunnelers' abundance was significantly different ($P<0.05$, Dunn's test) between the short rain and dry season, and between the dry season and the start of the long rain. Significant differences was also between the start of the long rain and end of the long rain season, and between end of the long rain season and short rain at nighttime in the grazed grassland (Table 10). Other significant differences in seasonal abundance were observed between the short rain and the start of the long rain seasons in the secondary forest at nighttime, and the dry season and between the end of the long rain seasons in the ungrazed grassland during daytime.

Significant seasonal differences in abundance of the dwellers is found in the secondary forest and the ungrazed grassland during both daytime and nighttime, and in the grazed grassland during daytime and the primary forest during the nighttime ($P<0.05$, Kruskal-Wallis test) (Tables 10-13). The dwellers seasonal abundance were significantly different ($P<0.05$, Dunn's test) between the short rain and the dry seasons and the dry season and the start of the long rain in the grazed grassland at nighttime (Table 12). Also they are different between the start of the long rains and end of the long rains seasons and between the dry and the end of the long rains seasons (Table 12). During daytime they were significantly different between the start of the long rain and the end of the long rains seasons and between the short rains and the start of the long rains seasons in the primary forest during daytime ($P<0.5$, Dunn test) (Table 11). In the secondary forest significance in abundance is found between the short rain and the dry seasons and between the end of the long rain and the short rains during daytime.

All the other groups were very rare in the samples representing only 1% or less of all the collected specimens in the respective season both day and night. The rollers were represented during the short rainy season, dry season, and the start of the long rainy season in the ungrazed grassland and the short rainy season in the primary forest (fig 9). The kleptoparasites were totally absent in the samples in all studied seasons and habitats.

Grazed grassland

Primary forest



Secondary forest

Ungrazed grassland

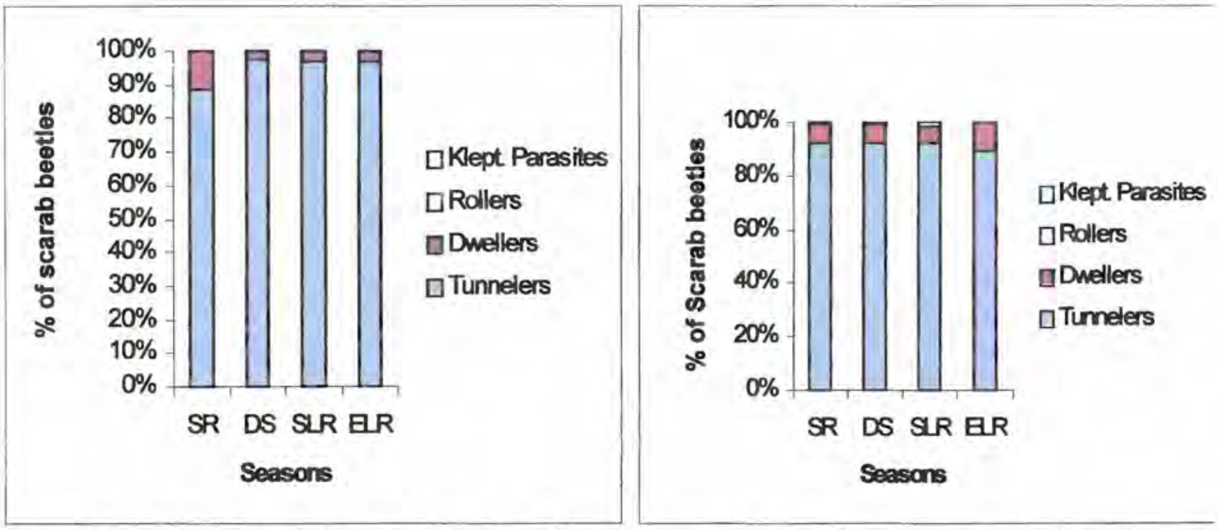
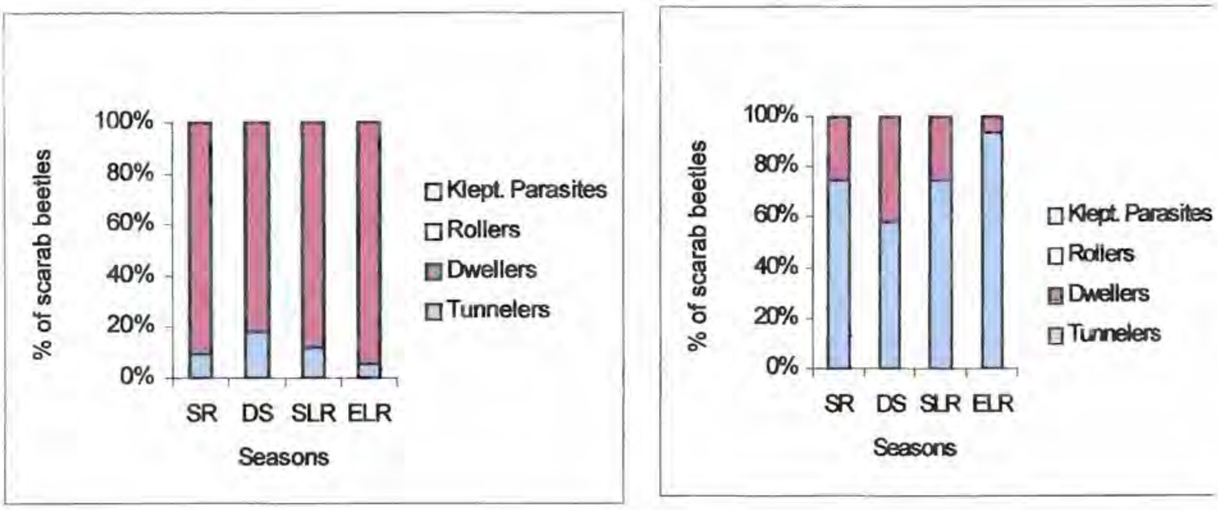


Fig. 8. Abundance of scarab dung beetle guilds in different seasons from the daytime samples in different habitats. SR= short rain, DS= dry season, SLR= start of long rain and ELR= end of long rain.

Grazed grassland

Secondary forest



Ungrazed grassland

Primary forest

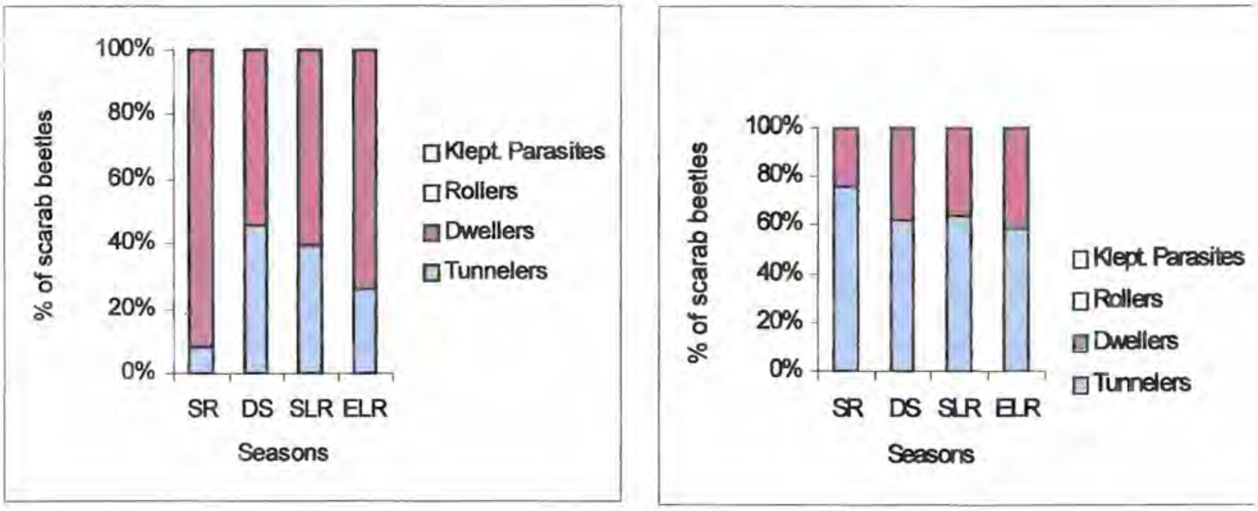


Fig. 9. Abundance of scarab dung beetle guilds in different seasons from the night samples in different habitats. SR= short rain, DS= dry season, SLR= start of long rain and ELR= end of long rain.

Families	**Sampling time**	**Kruskal-Wallis test**	**Dunn pair- wise test**					
			SR/D	**D/SLR**	**SLR/ELR**	**ELR/SR**	**SR/SLR**	**D/ELR**
Hydrophilidae	Day	*	N.S	N.S	*	N.S	N.S	*
	Night	*	N.S	*	*	N.S	*	N.S
Staphylinidae	Day	*	N.S	N.S	N.S	N.S	N.S	N.S
	Night	*	N.S	*	N.S	N.S	*	N.S
Scarabaeidae	Day	N.S	N.S	N.S	N.S	N.S	N.S	N.S
	Night	*	*	*	N.S	N.S	N.S	N.S
Tunnelers	Day	N.S	N.S	N.S	N.S	N.S	N.S	N.S
	Night	*	*	*	*	*	N.S	N.S
Dwellers	Day	N.S	N.S	N.S	N.S	N.S	N.S	N.S
	Night	*	*	*	N.S	N.S	N.S	N.S

Table 10. The statistical significance (Kruskal-Wallis test, followed by pair-wise Dunn test) of differences in abundance of the dung beetle guilds and families between seasons in the grazed grassland (SR= short rain, D= dry, SLR= start of long rain, ELR= end of long rain, N.S= not significant, and *=significant ($p<0.05$).

Families	Sampling time	Kruskal-Wallis test	Dunn pair- wise test					
			SR/D	D/SLR	SLR/ELR	ELR/SR	SR/SLR	D/ELR
Hydrophilidae	Day	*	N.S	N.S	N.S	N.S	N.S	N.S
	Night	*	N.S	N.S	N.S	N.S	N.S	N.S
Staphylinidae	Day	*	N.S	N.S	N.S	N.S	N.S	N.S
	Night	*	N.S	N.S	N.S	N.S	*	N.S
Scarabaeidae	Day	N.S	N.S	N.S	N.S	N.S	N.S	N.S
	Night	N.S	N.S	N.S	N.S	N.S	N.S	N.S
Tunnelers	Day	N.S	N.S	N.S	N.S	N.S	N.S	N.S
	Night	N.S	N.S	N.S	N.S	N.S	N.S	N.S
Dwellers	Day	*	N.S	N.S	*	N.S	*	N.S
	Night	N.S	N.S	N.S	N.S	N.S	N.S	N.S

Table 11. The statistical significance (Kruskal-Wallis test followed by pair-wise Dunn test) of differences in abundance of dung beetle guilds and families between seasons in the primary forest (SR= short rain, D= dry, SLR= start of long rain, ELR= end of long rain, N.S= not significant, and *=significant ($p<0.05$).

Families	**Sampling time**	**Kruskal-Wallis test**	**Dunn pair- wise test**					
			SR/D	**D/SLR**	**SLR/ELR**	**ELR/SR**	**SR/SLR**	**D/ELR**
Hydrophilidae	Day	*	*	N.S	*	N.S	*	N.S
	Night	*	N.S	N.S	N.S	*	N.S	*
Staphylinidae	Day	*	N.S	N.S	N.S	*	*	N.S
	Night	*	N.S	N.S	N.S	*	*	N.S
Scarabaeidae	Day	N.S	N.S	N.S	N.S	N.S	N.S	N.S
	Night	*	N.S	N.S	N.S	N.S	*	N.S
Tunnelers	Day	N.S	N.S	N.S	N.S	N.S	N.S	N.S
	Night	*	N.S	N.S	N.S	N.S	*	N.S
Dwellers	Day	*	*	N.S	N.S	*	N.S	N.S
	Night	*	N.S	N.S	*	N.S	N.S	*

Table 12. The statistical significance (Kruskal-Wallis test, followed by pair-wise Dunn test) of differences in abundance of dung beetle guilds and families between seasons in the secondary forest. (SR= short rain, D= dry, SLR= start of long rain, ELR= end of long rain, N.S= not significant, and *=significant ($p<0.05$).

Families	Sampling time	Kruskal Wallis test	Dunn pair- wise test					
			SR/D	D/SLR	SLR/ELR	ELR/SR	SR/SLR	D/ELR
Hydrophilidae	Day	*	N.S	N.S	*	N.S	*	N.S
	Night	*	*	N.S	*	N.S	*	*
Staphylinidae	Day	*	*	N.S	N.S	*	N.S	N.S
	Night	*	N.S	*	N.S	N.S	N.S	*
Scarabaeidae	Day	*	N.S	N.S	*	N.S	N.S	*
	Night	*	*	N.S	N.S	*	*	N.S
tunnelers	Day	*	N.S	N.S	N.S	N.S	N.S	*
	Night	N.S	N.S	N.S	N.S	N.S	N.S	N.S
Dwellers	Day	*	N.S	N.S	N.S	N.S	N.S	N.S
	Night	*	*	N.S	N.S	*	*	N.S

Table 13. The statistical significance (Kruskal-Wallis test, followed by pair-wise Dunn test) of differences in abundance of dung beetle guilds and families between seasons in the ungrazed grassland. (SR= short rain, D= dry, SLR= start of long rain, ELR= end of long rain, N.S= not significant, and *=significant $p<0.05$).

3.3.3 Correlation of Dung beetle Families and Guilds with Different seasons

The RDA (Fig 13) shows that during daytime the tunnelers and the rollers are associated with the dry season and not associated with the short rain season, while the dwellers are associated with the short rainy season. During nighttime (Fig 14), however, dwellers and tunnelers are associated with the start of the long rainy season and not associated with the dry season and the end of the long rains. There were no rollers collected during the night.

The RDA (Table 14) forward selection shows that all the seasons apart from the end of the long rainy seasons (p=0.068) have a significant conditional effect on the guild structure of dung beetles in Kakamega forest and the surrounding farmlands during the day (P=0.001 for the dry season, start of long rain and short rains). At night however it is the start of the long rainy (p=0.001) and the short rainy (p=0.006) that have a significant conditional effect on the structure of the dung beetle community (Table 15).

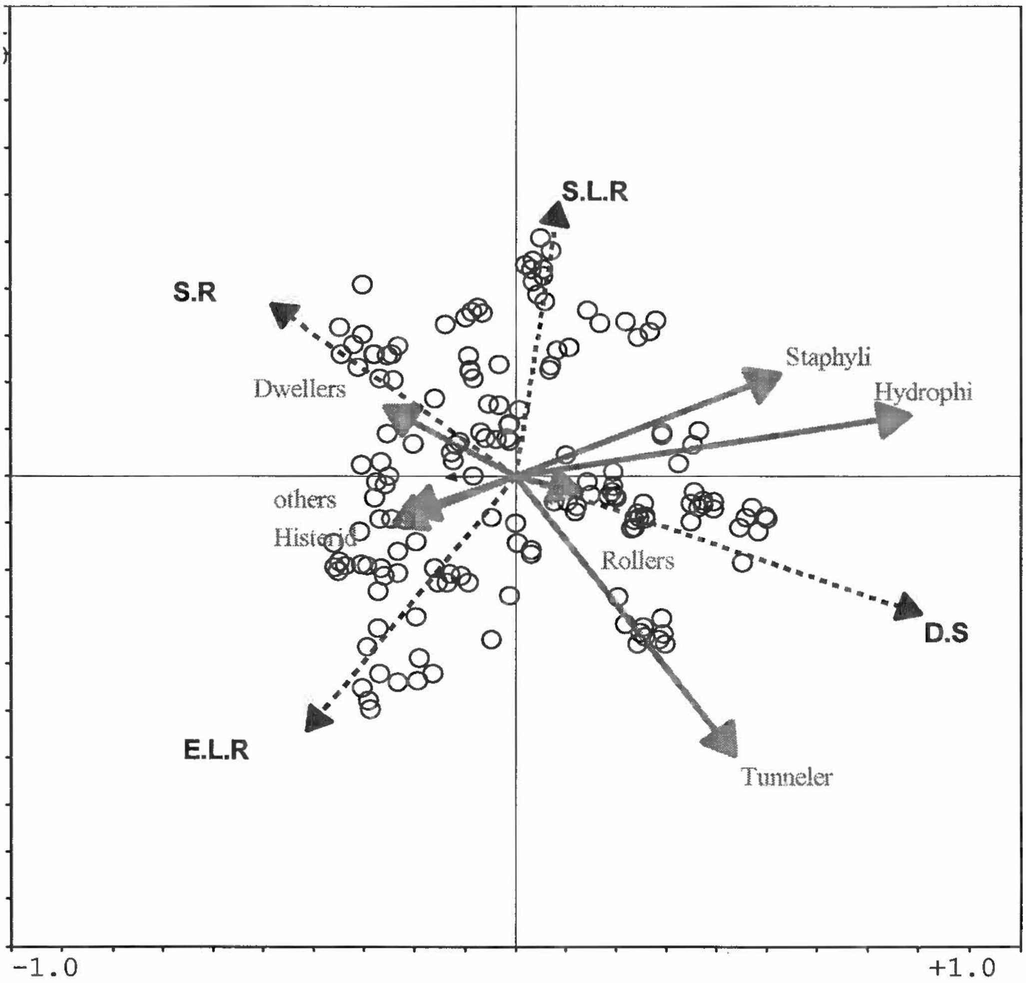


Fig. 10. RDA ordination triplot of guilds and environmental variables (Seasons) based on log transformed absolute numbers of individuals within each guild during the day. The axes represent environmental (seasonal) gradient SR= short rain, DS= dry season, SLR= start long rain and ELR= end long rain.

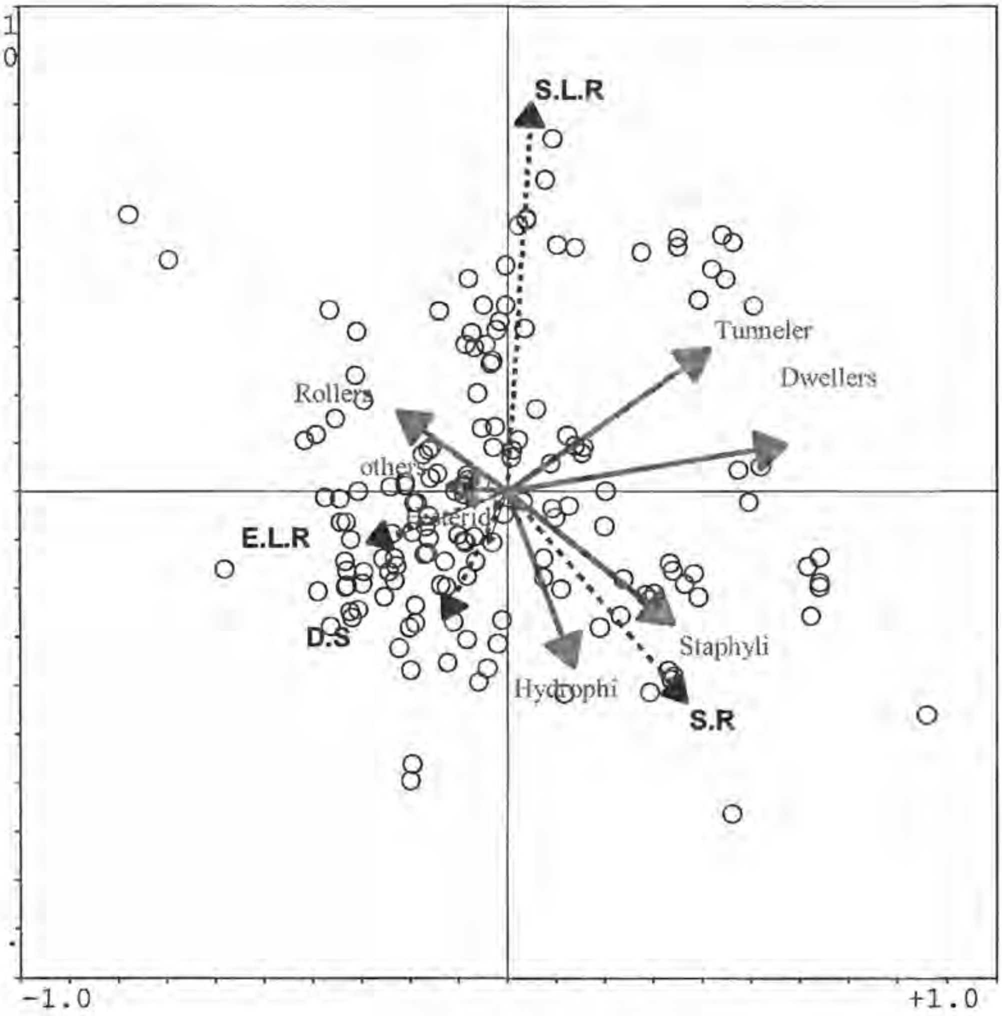


Fig. 11. RDA ordination triplot of guilds and environmental variables (seasons) based on log transformed absolute numbers of individuals within each guild during the night. The axes represent environmental (seasonal) gradient. SR= short rain, DS= dry season, SLR= start long rain and ELR= end long rain.

Marginal effects		Conditional effect		
Variable	Lambda	Variable	Lambda	P
Dry season	0.24	Dry season	0.24	0.001
Short rains	0.10	Start of long rains	0.07	0.001
End of long rains	0.09	Short rains	0.04	0.001
Start long rains	0.04	End of long rains	0.01	0.068

Table 14. Lambda values and associated statistical significance (p values) of environmental variables (Seasons) in the RDA during the day showing marginal and conditional effects. The significance of variables are tested by a Monte Carlo permutation Test (Canoco; 999 permutations).

Marginal effects		Conditional effects		
Variable	Lambda	Variable	Lambda	P
Start of Long rain	0.05	Start of long rains	0.05	0.001
Short rains	0.04	Short rains	0.03	0.006
End of Long rains	0.02	Dry season	0.01	0.196
D. season	0.02			

Table 15. Lambda values and associated statistical significance (p values) of environmental variables (Seasons) in the RDA during the night showing marginal and conditional effects. The significance of variables is tested by a Monte Carlo permutation Test (Canoco; 999 permutations).

3.4 Discussion

Seasonal differences in insect communities are well documented (Wolda 1978, Zalom *et al.* 1979, Hunter *et al* 1991, Fincher *et al.* 1986, Allsopps *et al.* 1999). This has also been reported for the dung beetle communities (Coe and Kingston 1988, Montes de Oca and Halffter 1995, Giller and Doube 1994). The results of this study also indicate that the dung beetles in Kakamega forest and the surrounding farmlands are greatly affected by seasons.

The overall variation explained by the first two axes in the RDA is rather low, indicated by low eigenvalues. This means that other factors that were not measured influence the structure of the dung beetle assemblages apart from the seasons. However the forward selection clearly shows that the seasons have a significant influence on the structure of the dung beetles and that they are important in the distribution of the beetles.

The presence of more dung beetles in the rainy seasons is in agreement with the findings in the West African rainforests (Cambefort and Hanski 1991). This could be caused by favourable microclimate and soil conditions during this period (Cambefort 1991). During this season the soils are moist, and hence soft allowing the tunnelers to expend less energy when digging nests for their offspring. This season also coincides with probably the highest dung resource availability and quality (Hanski and Cambefort 1991) and dung beetles maximise breeding and feeding during this period before the end of the rainy season. During the dry season fewer numbers of beetles collected could be due to large changes in the temperature regime between the exposure period during this season especially for the dung beetles that are sensitive to slight temperature changes.

During the day, the tunnelers' association with the dry season is not surprising, as most of the tunnelers collected during this period are members of the subgenus *Aphodius (Neocolobopterus)* (Krell *et al.* 2003) and Oniticellini that only dig shallow burrows just under the dung pat (Doube 1991). Other tunnelers were not abundant, as they prefer soft and moist soils (Cambefort 1991) which are not available during the dry season.

The presence of the rollers in most seasons could be explained by the fact that the collected rollers belong only to the tribe Sisyphini that have up to five generations per year and do not bury their dung balls. They just stick them on the basis of grass tussocks hence they are not affected by harder soils in the dry season. This makes them to be active throughout the year (Cambefort 1991) hence they are not strongly affected by seasonal changes. The absence of the rollers during the end of the long rains season could be attributed to the low prevailing temperatures especially at the end of exposure period during the day. According to Krell *et al.* (2003) most rollers prefer high day temperatures for the ball making and rolling.

The Staphylinids numbers seems to increase during the seasons when we have the lowest proportion of tunnelers in the samples. This phenomenon is however very much pronounced in the grazed grassland, the secondary forest and the primary forest at night. The above phenomena could be explained by the reduced ability of the flies to oviposit in the available dung resource (Hanski and Cambefort 1991) because the higher proportion of the tunnelers means that most of the resource is removed and buried before the dung depositing flies have had a chance to place their eggs and larvae in the dung. This implies that fewer Staphylinidae beetles, which rely on fly eggs and larvae in the dung as their food resource should be found. This phenomenon could explain the seasonal distribution of the family Staphylinidae in the study area.

It has also been found that seasons exert greater influences on the dung beetle fauna found in open habitats as compared to the closed habitats. The reason for reduced influence of seasons in the primary forest could be because of their thick vegetation canopies (Lumaret and Kirk 1991). This buffers the effects of seasonal changes, for example air temperature and humidity regimes as compared to open habitats such as the grasslands where the changes in air temperature were very pronounced especially during the day.

From this study it can be concluded that the dung beetles in Kakamega forest, as in most places in the tropics, are affected by seasons. This effect of seasons is however more pronounced as a result of the human activities on the habitats. The roller guild, generally abundant in the Afrotropics, appears to be more or less missing from our Kakamega forest, with the only representatives being the tribe Sisyphini, even after all the major seasons in Kakamega area were sampled. More research is needed to establish the reason for the fewer numbers of the rollers from this region.

Chapter 4

4.0 THE EFFECT OF FOREST DEGRADATION ON THE SPECIES DIVERSITY OF DUNG BEETLES IN KAKAMEGA FOREST, KENYA

4.1 Introduction

Ecologically, habitat characteristics are important in regulating diversity of species and population size as plants and animals are highly dependent on the quality of their habitats (Rosenzweig and Winakur 1960, MacArthur and MacArthur 1961, Pianka 1967, Ajayi 1974). Globally, habitats are continuously being altered through the forces of nature such as fires, windfall, volcanicity and floods (Wright 1974, Pickett and Thompson 1978, Foster 1980, Eldredge 1998). However the most important and large-scale cause of habitat modification is expansion and intensification of human land use (Burgess and Sharpe 1981, Adren 1994).

From the forest systems in various parts of the world it has been demonstrated that degradation and fragmentation of primary forests lead to the impoverishment of the coprophagous fauna (Howden and Nealis 1975, Klein 1989, Kirk 1989, Didham *et al.* 1998, Nummelin and Hanski 1989, Halffter *et al.* 1992, Holloway *et al.* 1992). This change in the coprophagous fauna is presumably because of radical change of vegetation structure when the habitats are altered (Howden and Nealis 1975).

This study was therefore initiated to examine the effect of forest degradation on the dung beetle species diversity in Kakamega forest. The forest and its environment have been severely impacted by human activities, such as forest depletion, crop farming and livestock grazing in the recent past. Human activities have converted this fertile tropical rain forest into a patchwork of indigenous forest patches, glades, secondary woodland and patches of exotics (Kokwaro 1988, Tsingalia 1988, Clausnitzer 1999).

4.2 Material and methods

4.2.1 Study Area

The study was conducted in the Kakamega forest is situated in Western Kenya (0°8'-0°24'N: 34°20'-34°33'E), and it covers an area of 240 km^2 and lies at altitudes 1500-1700 metres above sea level. The study sites are situated to the northern part of the forest and they included an area of the primary forest (0°21'31"N, 34°51'38"E) and Secondary forest (0°21'08"N, 34°51'55"E). The primary forest comprises an area of the forest that is dominated by the climax vegetation that has been established over a long period of time, while the secondary forest included an area of the forest that is dominated by derived vegetation as a result of human induced disturbance of the primary forest in the recent times.

4.2.2 Experiment

The collection of the dung beetles was done using the floating method with the sampling done in October 2002, January to February 2003, April 2003 and July 2003. This period coincided with the beginning of the short rainy, dry, beginning of the long rainy, and the end of the long rainy seasons respectively in the study area. During each of these periods 20 portions of 1 kg fresh cow dung (plate 6) were randomly deposited on the soil on the ground in each of the two habitats (primary forest, and secondary forest). 10 of these portions were deposited during the day (6:00 h to 16:00 h), and 10 others during the night (18:00 to 6:00h), because the flight activity of dung beetles differs strongly between night and day at guild level (Krell-Westerwalbesloh *et al.* 2004).

After the exposure period the dung-pad and the soil beneath it that was populated by dung beetles was collected into a bucket. A spade was used to dig out the dung and the soil beneath as a single cube (at least 10cm deep). This was extended in the direction of any soil hills (plate 7) and dung beetle tunnels to get the nests with the tunneling dung beetles.

The samples were processed as soon as possible after collection. The buckets containing the collected samples were filled with water and stirred vigorously to make the beetles to float (floatation method). They were then collected with a sieve from which they were picked with a pair of forceps and placed in collecting bottles containing a tissue soaked with ethyl acetate to kill the beetles.

The dead beetles were then transferred to vials for preservation using 75% ethanol. The vials were labeled accordingly.

4.2.3 Species Identification

Species determinations of the family Scarabaeidae were made in the laboratory at the Natural History Museum, London. This was done by comparing specimens against identified collection specimens. Species without corroborative specimens for comparison were classified to the generic level with species numbers. Dr. Frank Krell a taxonomic specialist with Scarabaeinae, provided or confirmed the identification.

4.2.4 Data analysis

Daytime and nighttime samples were analysed separately as the day and night assemblages of dung beetles are strongly different (Krell-Westerwalbesloh *et. al.* 2004). Species diversity, an estimate combining the number of species and the number of individuals in an area, was calculated using two general indices: the Shannon-Wiener index (H') and Margalef's index (D_{mg}) of diversity (Magurran, 1988).

$H'=-\sum p_i \ln p_i$ where pi, proportional abundance of *i*th species = (n_i/N)

$D_{mg}=(S-1)/(\ln N)$ Where S is Number of species and N is Number of individuals

Higher values of H' and D_{mg} are interpreted as higher diversity. A t -test as described in Magurran (1988) was used to test the significance of the Shannon- Wiener index.

$t=(H'_1-H'_2)/(\text{Var } H'_1+\text{Var } H'_2)^{1/2}$ Where H'_1 is the diversity of site 1 and Var H'_1 is its variance, and H'_2 is the diversity of site 2 and Var H'_2 is its variance.

Other parameters calculated were Evenness or equitability measured by the Mackintosh evenness index (U), rarefaction analysis, and similarity coefficient using Sorenson (quantitative data) measure (C_N).

$$U = \sqrt{(\sum n_i^2)}$$

Where n_i is the proportional abundance of the *i*th species

$$C_N = 2_{jN}/(aN+bN)$$

Where *aN*= the number of individuals in site A, *bN*= the number of individuals in site B, and *jN* = the sum of the lower of the two abundances of species which occur in the two sites

The computer program BioDiversity professional (version 2) of the Natural History Museum London was used to calculate these diversity indices and the species richness, while the Sorenson (quantitative data) was calculated using the method described in Magurran (1988).

4.3 Results

Table 16 shows the dung beetle in the family Scarabaeidae species collected in both the primary and the secondary forest. In both sites a total of 55 species were collected. The most dominant of all the beetles collected from both the primary forest and the secondary forest are *Diastellopalpus gilleti* d' Orbigny, *Onthophagus fuscidorsis* d'

Orbigny, *and Proagoderus multicornis* d' Orbigny. 10 species were exclusively collected in the secondary forest while 12 were exclusively collected in the primary forest. The other species were found in both the primary forest and the secondary forest.

Table 16. Total number of individuals of each species and their abundance captured in secondary and primary forest respectively.

Species	Secondary forest		Primary forest		Total
	No. of beetles	%	No. of beetles	%	
Diastellopalpus gilleti d' Orbigny	552	26.8	58	6.3	610
Onthophagus fuscidorsis d'Orbigny	269	13.1	269	29.4	538
Proagoderus multicornis d'Orbigny	354	17.2	20	2.2	374
Diastellopalpus murrayii Harold	192	9.3	23	2.5	215
Onthophagus K1	102	5	91	10	193
Diastellopalpus semirubidius d'Orbigny	113	5.5	57	6.2	170
Aphodius K2	77	3.7	47	5.1	124
Aphodius K1	37	1.8	78	8.5	115
Onthophagus denticulatus d'Orbigny	84	4.1	11	1.2	95
Aphodius K5	29	1.4	42	4.6	71
Heliocopris mutabilis Kolbe	38	1.8	20	2.2	58
Aphodius K28	7	0.35	44	4.8	51
Milichus picticollis Gerst	34	1.7	13	1.4	47
Lorditomaeus K2	4	0.2	41	4.5	45
Onthophagus sulcipennis d'Orbigny	34	1.7	1	0.1	35
Catharsius K1	20	1	8	0.9	28
Liatongus arrowi Bouc	22	1	10	1.1	32
Aphodius K4	11	0.5	11	1.2	22

Lorditomaeus K1	33	1.6	15	1.6	15
Aphodius K24	5	0.25	6	0.7	11
Onthophagus K4	1	0.05	7	0.8	8
Aphodius K10	3	0.15	5	0.5	8
Aphodius K27	2	0.1	4	0.4	6
Onthophagus K7	2	0.1	3	0.3	5
Aphodius K11	3	0.15	2	0.2	5
Aphodius K14	4	0.2	1	0.1	5
Onthophagus K6	3	0.15	1	0.1	4
Onthophagus K10	0	0	4	0.4	4
Aphodius K3	1	0.05	3	0.3	4
Lorditomaeus K3	1	0.05	3	0.3	4
Onthophagus K13	3	0.15	0	0	3
Sysyphus K1	0	0	2	0.2	2
Onitis viridulus Boheman	1	0.05	1	0.1	2
Drepanocerus K1	2	0.1	0	0	2
Aphodius K6	2	0.1	0	0	2
Aphodius K8	2	0.1	0	0	2
Lorditomaeus K4	1	0.05	1	0.1	2
Aphodius K25	1	0.05	1	0.1	2
Aphodius K26	1	0.05	1	0.1	2
Onthophagus K3	0	0	1	0.1	1
Onthophagus K5	0	0	1	0.1	1
Onthophagus K11	0	0	1	0.1	1
Onthophagus K12	1	0.05	0	0	1
Onthophagus K14	0	0	1	0.1	1
Onthophagus K15	0	0	1	0.1	1

Drepanocerus strigatus Janss	0	0	1	0.1	1
Euniticellus nasicornis Reiche	1	0.05	0	0	1
Copris K1	1	0.05	0	0	1
Aphodius K7	0	0	1	0.1	1
Aphodius K9	1	0.05	0	0	1
Aphodius K12	1	0.05	0	0	1
Aphodius K15	0	0	1	0.1	1
Aphodius K16	0	0	1	0.1	1
Lorditomaeus K5	0	0	1	0.1	1
Oniticellus K1	1	0.05	0	0	1
Number of species	43		45		55
Number of species not shared between the 2 sites	10		12		
Number of individuals	2056	100	914	100	3015

The general diversity (Table 17) as calculated by both the Shannon index (*t* test $p<0.05$) (Table 18) and the Margalef's diversity index suggest that the primary forest had a higher diversity of coprophagous scarabs overall. Species evenness as measured by the Mackintosh index shows that the dung beetle community of the secondary forest is slightly more even than that of the primary forest during both day and night. However when both day and night data are pooled together the evenness is the same (Table 17). The rarefaction plots (Fig 12 and 13) show that the primary forest has more species in a given sample size than the secondary forest. The similarity coefficient as measured by Sorenson shows that the two sites are dissimilar (Table 18).

Parameter	Secondary forest			Primary forest		
	Day	Night	Total	Day	Night	Total
Total No. of species collected	31	32	43	34	31	45
Total Scarabs collected	1451	607	2056	497	482	914
Species richness	35	48.8	51.6	53.6	55	55
Shannon-Weiner H' natural log	1.862	2.582	2.414	2.333	2.423	2.669
Margelef's Diversity (α)	17.08	19.402	16.299	20.258	20.345	18.237
Evenness (E)	1.155	1.155	1.155	1.154	1.154	1.155

Table 17. Comparison of diversity parameters for the two forest sites using different diversity indices in both day and night samples.

Sampling tine	Shannon- Weiner index t test (between primary and secondary forest)	Sorenson Similarity Index (between primary and secondary forest)
Day	$P<0.05$	0.3772
Night	$P>0.05$	0.7297
Total	$P<0.05$	0.4579

Table 18. A t-test measuring the significance of the differences in Shannon- Weiner index in measuring species diversity and the Sorenson (quantitative) measure index showing species similarity between the primary and secondary forest.

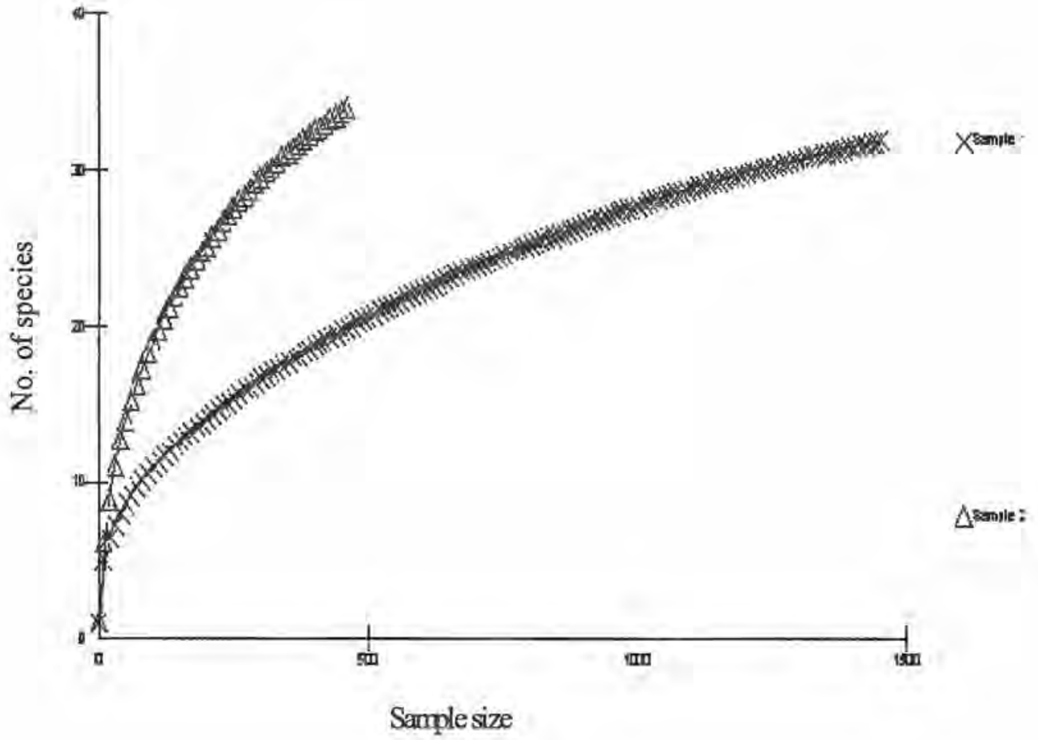


Fig.12. Rarefaction plot for the day samples showing expected number of species per sample size in both the primary and the secondary forest: Sample 1 is the secondary forest and sample 2 is the Primary forest.

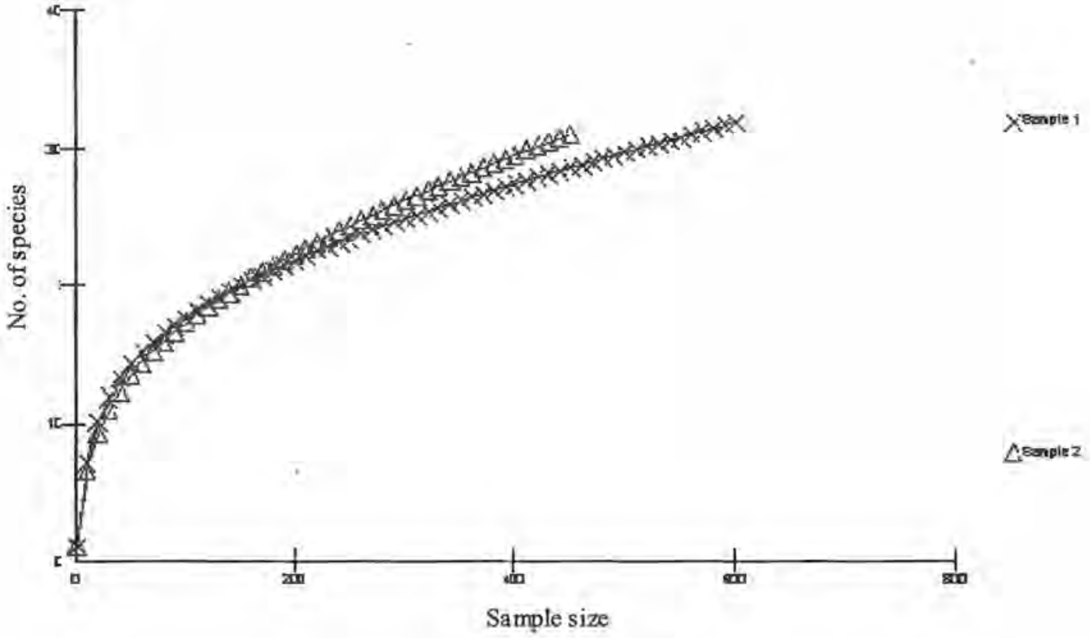


Fig.13. Rarefaction plot for the night samples showing the expected number of dung beetle species per given sample size: Sample 1 is the secondary forest and sample 2 is the Primary forest

4.4 Discussion

Work done in some parts of the tropics have found that fragmentation and degradation of forests have an adverse effect on the abundance and species composition of dung beetle assemblages (Howden and Nealis 1975, Klein 1989, Kirk 1992, Didham *et al.* 1998, Nummelin and Hanski 1989, Halffter *et al.* 1992, Holloway *et al.* 1992). Results from this study is in agreement with these findings.

Samples from the primary forest have a higher species diversity, species richness, more species in any given sample, and more evenly distributed species composition than the secondary forest, suggesting that forest degradation has some disruptive effect on dung beetle community and structure.

There are some species that are found both in the primary forest and the secondary forest (Table 15). This is an indication that there are species from the primary forest that are able to adapt and colonize new areas when their habitats are destroyed. This observation is in agreement with the findings of Halffter et al. 1992 in the Mexican rain forests. This is also a clear indication that there is some movement of forest beetles between the primary forest and the secondary forest. On the other hand, there were those species that were either found in the primary forest or the secondary forest. These species could be important indicators for any change in the respective forests as a result human disturbances in the forests. The super abundance of the *Proagoderus multicornis* and *Diastellopalpus murrayii* in the secondary forest as compared to the primary forest could also be used as an indicator of heavy disturbance in the forest systems.

The differences in the abundance and species composition of dung beetles between the primary forest and the secondary forest could be due to differences in the microclimate. Primary forest is characterised with more closed canopy as compared to the secondary forest. Shade is known to exert a very strong influence on some arthropod communities (Power 1996). The amount of shade in different systems is in turn strongly associated with the gradient of vegetation and structural diversity. Therefore, highly shaded systems like the primary forest compared to the secondary forest are likely to have more moderate temperature and moisture regimes, and this influences the dung beetle diversity (Jameson 1989, Hanski and Cambefort 1991).

Why the higher abundance of dung beetles in the secondary forest than in the primary forest is not known. Perhaps this could be attributed to the availability of more dung the secondary forest as opposed to the prevailing condition in the primary forest. In the secondary forest, there is more undergrowth as compared to the primary forest. This condition may mean that there is more food resource for the ground dwelling wild herbivores in the secondary forest than in the primary forest. This will cause more herbivores frequenting the secondary forest and in the process defecating here and hence increasing the resource for the dung beetles and thus increasing their numbers.

The differences between the sites in terms of species diversity is more pronounced in the day samples than the night ones. This might be because the microclimate at night does not differ so much between primary and secondary forest whereas during the day (with sunshine) a change in the vegetation structure, particularly in the canopy cover by logging large trees leads to a significant change in the microclimate near the ground. The primary forest has more closed canopy as opposed to the secondary forest. This in turn leads to less amount of solar radiation (light) received under the canopy in the primary forest as compared to the secondary forest thus mimicking the night condition. This condition could cause some of the night dwelling species to be active in the primary forest during the day and there by increasing the number of species collected.

The disparity in the species diversity and the uniqueness of some of the species between the primary forest and the secondary forest could be due to differences in abundance of primates and other large mammals. This is could possibly be due to reduced food resource in the degraded area. Thus if food resources is a limiting factor for dung beetles (Hanski and Cambefort 1991), then decreased mammal and bird diversity should directly decrease dung beetle species.

These studies have shown forest degradation has an effect of changing species diversity in an area and this has a consequent in the conservation of biological diversity. Due to forest degradation, some of the taxa is totally lost and no amount of regeneration of the forest will ever reclaim it. Forest degradation could also cause new species colonizing the disturbed areas. In most cases these are invasive species that could be detrimental to the survival of the original species. The management goals for our forest should therefore focus on those factors that have a potential to reduce the effect of anthropogenic disturbance that have biotic consequences like the distortion of the species balance. In the past, forest managers have been allowing for the clearing and cultivation within the forest. Most of these areas in Kakamega forest have been let to naturally regenerate hoping that they will eventually regain the former state before clearing. Changes in the dung beetle species composition as a result of anthropogenic disturbance may have a consequent of changes in the controlling gastrointestinal parasites of vertebrate, seed germination, and nutrients recycling (Bornemissza 1976, Fincher 1981, Klein 1989, Hanski and Cambefort 1991, Andresen 2002).

It is also very interesting to note that both the primary and the secondary forest have the dung beetle species *Heliocopris mutabilis*. Members of the genus *Heliocopris* are known to breed in the dung of big herbivores like elephants and buffaloes that are not present within the forest (KIFCON 1994). There is also restriction in the cattle grazing within the forest nature reserve boundaries. There is therefore need to carry out more research to establish the reasons of the presence of this species of dung beetles.

Chapter 5

5.0 GENERAL DISCUSSION, CONCLUSION AND RECOMMENDATION

5.1 General Discussion

Natural habitats are either seen as a source of unwanted pest species, weed or diseases, or hailed as a source of beneficial insects as well biodiversity in general. There are valuable published examples in support of each one of these arguments, but the impression still prevails that we only have limited notion of interaction between natural habitats and disturbed ecosystems as a result of human activities. Several countries promote and support legally the maintenance of natural habitats as ecological compensation areas in densely populated regions. In most cases however the decisions are based on speculation as most concrete figures on some important aspect are lacking.

The variation in the beetle abundance and diversity in the habitats studied is a clear manifestation that farmers face big challenge of conserving biodiversity while working to produce enough food to meet the needs of the growing population. A livestock farmer plays an important role in the dung beetle biodiversity conservation. These studies have revealed that farming practices form linkages between agriculture and biodiversity conservation, which have consequences on species diversity. Farming methods that degrade biodiversity will make human communities vulnerable because options for change are diminished.

Kakamega forest is a very important ecosystem in Kenya. It is small, isolated and under great human pressure, and we know isolated populations run a high risk of stochastic extinction. Any human activities that cause any changes in this forest have a potential to increase the risk of extinction of this forest. Insects are particularly vulnerable to changes in the environment and dung beetles are no exception. Changes in the insect community will also affect the services offered by these insects like the pollination, nutrient recycling and biological control of some pests. Lack of these services because of the deforestation will have a pronounce effect on food production especially for the communities living around the forest.

It is probable that the human forces have impacted negatively on both the guild structure and species composition in Kakamega forest and the surrounding farmlands. The human activities that intensified at the turn of the 20th century have been logging and the turning of the land into farmlands, and hunting of the wild animals. These have led into extinction of the native large mammals and this in turn has had an influence on the dung beetle community in Kakamega forest as it is the dung of this animals that the dung beetle use.

Dung beetles are only an indicator of the forest degradation in Kakamega forest. With the loss of this forest, there is a potential for the loss of other services offered by this forest. A loss of the forest will have a consequent on the rain pattern in the area, as the rain system in the area is so strongly dependent on this forest. Carbon dioxide sequestration by this forest will also be affect with an impact on the global warming.

This will destabilise the seasons and hence the dung beetle communities and other life forms that are very sensitive to seasonal changes. We should also mention the up coming tourism industry in the region that is dependent on this forest. This will collapse and hence affect the regional economy. Other values derived from the forest that will collapse include the source of medicine and the cultural values attached to the forest by the local communities.

5.2 Conclusion and Recommendation

The study has shown that the human activities have an impact on dung beetle community in Kakamega forest and the surrounding farmlands. The dung beetle guilds have shown difference preferences for different habitats along a gradient of human influence. The species composition between the primary forest and the secondary forest are different underlying the effect of deforestation on dung beetle species conservation. This gives a strong indication that dung beetles can be used as indicators of forest degradation. The managers of Kakamega forest Reserve therefore can employ dung beetles to identify areas of the forest that need immediate attention for the better conservation management of the forest.

More research also needs to be done to ascertain the reasons for the presence of the dung beetles in the *Heliocopris species*. These beetles are known to be associated with the dung of large herbivores like elephants and buffaloes that are recorded to be extinct in Kakamega forest. It was also interesting to note the absence of the kleptoparasites guild, and the low abundance of the roller guild. This is contrary to the findings other tropical rain forest in West Africa and South America. There is therefore need to carry out more investigations to explain this phenomenon.

6.0 REFERENCES

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7.0 APPENDIX

Questions and response of the local community around Kakamega forest on the use of cow dung

Date	No. Cows	Use cow dung ?	Portion of Dung	When do you collect ?	Collect all year round?	Collect only fresh dung?	Purpose	Since when did you collect?	Economic benefits?	Profit estimates
24/1/2003	3	Yes	All	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
24/1/2003	6	Yes	All	A	Yes	Yes	smear house, Manure	immemorial	Yes	No
24/1/2003	4	Yes	Half	M	Yes	Yes	Smear house, Manure	2002	Yes	No
24/1/2003	2	Yes	Half	A	Yes	Yes	Smear house, Manure	immemorial	Yes	No
24/1/2003	3	Yes	Half	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
24/1/2003	9	Yes	All	A	Yes	Fresh & old	Smear house, Manure	immemorial	Yes	No
24/1/2003	8	Yes	All	A	Yes	Yes	Smear house, Manure	immemorial	Yes	No
24/1/2003	7	Yes	Half	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
24/1/2003	8	Yes	All	A	Yes	Yes	Smear house, Manure	immemorial	Yes	No
24/1/2003	5	Yes	All	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
27/1/2003	6	Yes	All	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
27/1/2003	12	Yes	Half	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
27/1/2003	2	Yes	All	M	Yes	Fresh & old	Smear house, Manure	immemorial	Yes	No
27/1/2003	3	Yes	Half	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
27/1/2003	6	Yes	All	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
27/1/2003	4	Yes	Half	M	Yes	Fresh & old	Smear house, Manure	immemorial	Yes	No
27/1/2003	4	Yes	All	M	Yes	Fresh & old	Smear house, Manure	immemorial	Yes	No
27/1/2003	5	Yes	All	M	Yes	Fresh & old	Smear house, Manure	immemorial	Yes	No
27/1/2003	6	Yes	Half	M	Yes	Fresh & old	Smear house, Manure	immemorial	Yes	No
28/1/2003	6	Yes	All	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No

28/1/2003	7	Yes	All	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
28/1/2003	3	Yes	All	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
28/1/2003	5	Yes	All	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
28/1/2003	7	Yes	All	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
28/1/2003	3	Yes	All	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
28/1/2003	5	Yes	All	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
28/1/2003	3	Yes	All	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
28/1/2003	5	Yes	All	M	Yes	Fresh & old	Smear house, Manure	immemorial	Yes	No
28/1/2003	4	Yes	All	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
23/1/2003	3	Yes	All	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
23/1/2003	3	Yes	Half	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
23/1/2003	7	Yes	Half	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
23/1/2003	10	Yes	Half	M	Yes	Fresh & old	Smear house, Manure	immemorial	Yes	No
23/1/2003	2	Yes	All	M	Yes	Fresh & old	Smear house, Manure	immemorial	Yes	No
23/1/2003	4	Yes	All	M	Yes	Fresh & old	Smear house, Manure	immemorial	Yes	No
23/1/2003	2	Yes	All	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
23/1/2003	4	Yes	All	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
23/1/2003	5	Yes	Most	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
23/1/2003	2	Yes	Half	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No
23/1/003	5	Yes	All	M	Yes	Yes	Smear house, Manure	immemorial	Yes	No

M=Morning,
A=Afternoon