Impact of bush fire on grazing behaviour of herbivores in Masai Mara

Gräsbränders påverkan på betesbeteende hos växtätare i Masai Mara

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ABSTRACT

Fire is commonly used in African savannas to remove long, dry, low-nutritious grass and generate fresh grass, both for livestock and wildlife. Since different herbivore species have different demands on amount and quality of biomass, bush fires might change the composition of the herbivore community. I studied how grass fires on the savannah affected habitat choice and foraging behaviour of the animals in the Masai Mara Conservancy in south-western Kenya. In August and September 2005 I observed several species of animals on burnt and non-burnt areas.

Along a set of transects we recorded abundance and behaviour on burnt and non-burnt areas. Each of the 54 transects was 1000 m long and 300 m wide, thus covering an area of 0.3 km^2. The study was carried out during August and September 2005, after fires in June and October 2004 and July 2005. We placed 18 transects on areas burnt one month ago, 18 were burnt in the previous year, and 18 were controls which had not been burnt for at least two years. Recently burnt areas provided less biomass but of higher energy and protein content with less fibre than controls and areas burnt during the previous year. All observations were made between 6.30 am and 18.30 pm. This range of time was divided into 12 one-hour periods, and during the study each transect was driven once in each one-hour period.

From 35 observed species I present data from the most frequent species; blue wildebeest (*Connochaetes taurinus*), Burchell's zebra (*Equus burchelli*), Thomson's gazelle (*Gazella thomsonii*), warthog (*Phacochoerus africanus*), African elephant (*Loxodonta africana*), buffalo (*Syncerus caffer*), and topi (*Damaliscus lunatus*) were more thoroughly examined. Wildebeest, Thomson's gazelle and warthog were all found in larger numbers the burnt areas. There were more zebras on burnt areas but I failed to show a statistical significance. Zebra and Thomson were on areas with shortest grass of highest quality and wildebeest on medium-high grass. Buffalo and elephant were predominantly found on tall grass. Although the elephants were only observed on tall grass, the observations were too few to generate a significant difference. There was no significant difference in the numbers of topis on the burnt and non-burnt areas, respectively.

Differences between species can be explained in part by the anatomy and physiology of their digestive systems, and could also be affected by the increased visibility of predators in the shorter vegetation on the burnt areas. With these data we gain knowledge on how fires can be used to influence vegetation and abundance of herbivores.

SAMMANFATTNING

Anlagda gräsbränder är ett vanligt redskap på afrikanska savanner för att ersätta högt, torrt gräs med lågt näringsvärde med färskt gräs, till nytta både för boskap och vilt. Eftersom olika arter av gräsätare har olika krav på mängd och kvalitet på betet kan gräsbränder ändra sammansättningen av djurarterna.

Jag studerade hur gräsbränder på savannen påverkar val av habitat och betesbeteende hos djuren i Masai Mara Conservancy i sydvästra Kenya. I augusti och september 2005 observerade jag flera djurarter på brända och obrända områden.

Vi registrerade antal och beteende längs 54 transekter på brända och obrända områden. Varje transekt var 1000 m lång och 300 m bred, och täckte en area av 0.3 km^2. Studien utfördes under augusti och september 2005, efter bränder i juni och oktober 2004 och juli 2005. Vi lade 18 transekter på områden brända en månad tidigare, 18 på områden brända föregående år, och 18 på kontrollområden som inte bränts på minst 2 år. Nyligen brända områden erbjöd mindre biomassa men med högre energi- och proteininnehåll och mindre fibrer än kontroller och områden brända föregående år.

Från de 35 arter som observerades presenteras i denna rapport data från de vanligast förekommande arterna; strimmig gnu (*Connochaetes taurinus*), stäppzebra (*Equus burchelli*), Thomsongasell (*Gazella thomsonii*), vårtsvin (*Phacochoerus africanus*), afrikansk elefant (*Loxodonta africana*), afrikansk buffel (*Syncerus caffer*) och topi (*Damaliscus lunatus*).

Gnuer, thomsongaseller och vårtsvin föredrog de brända områdena. Det fanns fler zebror på brända områden men jag kunde inte påvisa en statistisk signifikans. Zebror och thomsongaseller fanns på områdena med det kortaste gräset med den högsta kvaliteten och gnuerna på det medelhöga gräset. Bufflar och elefanter föredrog högt gräs. Trots att elefanterna enbart observerades på högt gräs var observationerna för få för att en signifikant skillnad skulle kunna ses. Topiantiloperna föredrog inget av områdena framför det andra.

Skillnader mellan arterna kan delvis förklaras av anatomin och fysiologin hos deras matsmältningssystem, och kan också påverkas av den ökade möjligheten att upptäcka rovdjur i den kortare vegetationen på de brända områdena. Med dessa data får vi ökad kunskap om hur bränder kan användas för att påverka vegetation och förekomst av gräsätare.

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INTRODUCTION

The savannah ecosystem

A savannah is defined as grassland with a continuous layer of grasses, often interspersed with shrubs and trees. Savannas are spread over the African, American, Australian and Asian continents, mainly in tropical areas. They vary from pure grassland to woodland with much grass. Savannah ecosystems are seasonal, with the composition of vegetation and wildlife varying throughout the year reflecting mainly variations in rainfall, but also influenced by availability of nutrients, grazing and fires. Grazing by animals decreases the height of the grass and changes plant part composition, thus altering the forage available for other animals. (Belsky 1986)

Figure 1: Fire on the savannah.

Forage

The grasses in the Masai Mara National Reserve are subject to a marked seasonality in soil nutrients, rainfall and plant growth. Grasses in tropical areas are predominantly utilizing the C4 photosynthetic pathway which makes them able to grow better under conditions of high temperature and light intensity (Barbehenn et al. 2004). They differ from the grasses in temperate zones, which utilize the C3-pathway, in having a more fibrous and lignified cell wall. These grasses also have a closely-packed cell structure and a thick-walled bundle sheath which make the leaf more resistant to mechanical breakdown (Wilson 1994). Compared to C3 grasses they are of lower nutritional value (Barbehenn et al. 2004). As a plant grows and matures, more energy is needed for its mastication (Laredo & Minson 1973).

Impact of fire on vegetation and forage quality

Fire is a common strategy for clearing long, dry, low-nutritious grass and to generate fresh grass, thus creating an attractive environment for several species of herbivores. It may also change the mixture of plant species (Uys et al. 2003). The animals' foraging behaviour and habitat choice are altered by fire management, both as a result of changes in available forage and as adaptation to visibility and predators (Brashares & Arcese 2002).

This treatment will result in a significant decrease of the grass biomass on the burnt areas (Engström 2005, Gabrielsson 2005), as well as an increase in forage quality (Dörgeloh 1999). Sprouting grass has been shown to have a higher content of protein, calcium and phosphorus than the unburnt grass (Moe et al. 1990). Quantity and quality of forage are inversely related, as crude fibre content in the plant increases while the plant grows.

Intake

The energy gained from the forage must compensate for the energy spent searching and collecting the desired food. The amount of energy used during feeding depends on the spatial distribution of the food (Murray 1991). A more selective animal will spend more energy foraging, but is usually rewarded by a more nutritious diet (Murray 1991).

The bite size and the rate at which food can be chewed and swallowed are limiting factors of the intake of herbivores (Murray 1991). The forage intake is also affected by the capacity of the gastrointestinal tract (GIT) and the passage rate, as well as the body size of the animal. The characteristics of the forage, such as the compositional constituents and the digestibility, also affect the voluntary daily intake (Meissner & Paulsmeier 1995, Laredo & Minson 1973).

Teeth and jaws

The degradation of herbivore food starts with mechanical breakdown by chewing, which breaks up large particles while the food is mixed with saliva (Pond et al. 1984). It will also break up the protective structures of the grass, making it available for the ruminal microflora (Reid et al. 1979). Incisors are used for grasping and shearing whereas premolars and molars are used for crushing the food (Janis & Ehrhardt 1988).

Herbivores' teeth have been adapted to their diet. Both ruminant and equid teeth have enamel arranged in folded ridges rising over dentine basins. The dentine is more easily worn down, thus leaving the harder enamel ridge protruding. With a lower jaw more narrow than the upper, equids and ruminants chew on one side at the time, moving their jaw sideways. Chewing is performed with a rotating movement (Janis & Ehrhardt 1988).

The ruminant mouth differs from most mammals' by having no incisors in the upper jaw. Instead, the ruminants can cut their forage by pressing the incisors of the lower jaw against the paired dental pads in the upper jaw. These pads are crescent-shaped, pliable elevated parts of the gum, covered with cornified epithelium to reduce the risk of injury from the loosely implanted teeth (Dyce et al. 1996).

Warthogs have a modified skull with enlarged canine teeth and a highly specialised, high-crowned third molar which moves forward from the back of the jaw, replacing the first and second molars as these are worn and lost. These teeth seem to be adapted for grinding abrasive material such as grass and rhizomes mixed with soil particles (Mason 1984 in Woodall).

Digestion

Ruminants and hindgut fermenters have developed two different strategies for digesting their food. Since their diets are rich in cellulose they both need to degrade their food with the assistance of microbes. Monogastric animals like equids or pigs have the fermentation taking place in their gut, while the ruminants are using their forestomachs for the same purpose. (Björnhag 1990).

The ruminants are characterized by their three forestomachs; the rumen, the reticulum and the omasum. The rumen is the most voluminous compartment and the site of the main fermentation. The reticulum is located on the lower front of the rumen and connected to it by a wide opening. Ingested food can move freely between these two compartments. The uppermost part of the rumen contains a bubble of gas produced in the fermentation process; beneath is the coarse forage material most recently ingested floating on the fluid surface. The contents of the lower part of the rumen are comprised of fluid and more finely ground material with a higher specific gravity (Dyce et al. 1996). Micro-organisms such as protozoa, bacteria and fungi make up 3 to 10% of the ruminal content, and are responsible for further breakdown of the food particles (Björnhag et al 1989). They live off the nutrients in the ingested food, synthesizing amino acids while growing, which is then used by the ruminant when the micro-organisms pass with the food particles to the intestines (McDonald et al. 2002). This makes ruminants independent of essential amino acids in the food since they are able to use amino acids synthesized by bacteria (Björnhag 1990).

Ruminants and hind-gut fermenters of the same size seem to have a similar capacity to digest low-fibre foods, but the ruminant is more efficient in digesting higher-fibre diets, an effect of the selective delay in the rumen (Demment & Van Soest 1985).

Ruminants who feed predominantly on browse, like leaves and twigs, have a comparatively smaller rumen than those who eat mostly grass, and the polygonal particles in their ingesta form a homogenous frothy mass, whilst grazers' long fibre-like ingesta divide into layers in the rumen. The grass-eating ruminants' rumen are unevenly papillated and have thick, horny pillars and distinct muscle layers, indicating stronger ruminal contractions (Clauss et al. 2003b). The browsers' low selective particle retention makes escape of larger particles possible, but they are probably unable to handle the higher proportions of stratification-inducing forages in their forestomach (Clauss & Lechner-Doll 2001).

In monogastric animals the fermentation takes place in their gut, while ruminants use their forestomachs for the same purpose. Zebras, elephants and warthogs are all hindgut fermenters (Robinson and Slade 1974, Clauss et al. 2003a, Boomker & Booyse 2003).

The stomach of the equid is remarkably small in comparison to the animal's size and the volume of food it consumes. The equid abdomen is to a great extent occupied by the intestines. The large intestine is enlarged and modified to provide a reservoir for microbial fermentation (Dyce et al. 1996).

The equid colon and cecum have the capacity of harbouring a significant microbial population. These organs capacity depends on their volume relative to the rest of the GIT, which is the factor determining the time the ingested food will be allowed to remain inside and being subjected to fermentation by the microflora. Microbial digestion in the large intestine of equids is similar to that occurring in the rumen, as volatile fatty acids are produced and resorbed and gases are produced. Protein is degraded and re-formed to microbial proteins and water soluble vitamins are synthesized. However, the substrate for these organs differs from the one presented in the rumen, since most of the more readily digestible nutrients will have been removed, and endogenous material such as mucopolysaccharides and enzymes have been added (McDonald et al. 2002).

The elephant is considered having a less capacious gastrointestinal tract than other herbivorous mammals, and thus a short retention time considering its size. The advantage of being a hindgut fermenter and having a short retention time gives the elephant the possibility to increase their intake rate, thereby compensating the low grade of digestibility in their forage (Clauss et al. 2007).

Food choices

The Masai Mara is the home for many species of herbivores which all favours different kinds of forage (Hansen et al. 1985). A herbivore's choice of forage is affected by several factors, such as the availability of different kinds of forage, its quality and quantity, and the animal's adaptations to specific types of food, for example ways of intake, chewing and digestion of the food (Illius & Gordon 1987). Ruminant grazers are constrained either by the rate at which food can be cropped or the rate it can be processed. A ruminant generally needs more time for processing but can feed on forage of lower quality than equidae and pigs (McDonald et al. 2002). Food intake in equidae may be more limited by time available for intake while the ruminant is more limited by clearance of undigested food from the forestomachs (Janis 1976).

African ruminants are commonly divided into three groups with aspect to their feeding style: the bulk and roughage feeders (grazers) which mainly feed on grass, concentrate selectors (browsers but also selective grazers) which eat predominantly leaves and fruits, and the intermediate feeders eating food from both categories of differing percentages. These choices also correlate with their gastrointestinal morphology (Hofmann 1989). Among the species included in this study, cape buffalo (*Syncerus caffer*), reedbuck (*Redunca redunca*, *Redunca fulvorufula)*, Defassa waterbuck (*Kobus ellipsiprymnus defassa*), oribi (*Ourebia ourebi*), blue wildebeest (*Connochaetes taurinus*), Coke's Hartebeest (*Alcelaphus buselaphus cokii*) and topi (*Damaliscus lunatus*) all belong to the grazer group. Among the browsers we find bushbuck *(Tragelaphus scriptus*) and giraffe (*Giraffa camelopardalis tippelskirchi*) whereas impala (*Aepyceros melampus*), Thomson's gazelle (*Gazella thomsonii*), Grant's gazelle (*Gazella granti*) and Eland antilope (*Taurotragus oryx*) are found among the intermediate types (Hofmann 1989).

The elephant's diet is often made up of very coarse material. In order to eat a sufficient amount of food with acceptable spending of energy, the elephant may be forced to choose graze and browse that can be found in large quantity, even though it will be lacking in quality (Codron et al. 2006). However, the elephant may travel long distances in search for a specific type of food, possibly trying to avoid high doses of digestion-inhibiting compounds (Codron et al. 2006).

Warthogs are selective grazers, depending on high-quality food. They are dietary flexible, adding nutritious roots to their diet when grazing on low-quality forage (Treydte et al. 2006).

Aim of the study

In this study I show how grass fires on the savannah affect the wildlife, with main focus on forage selection and foraging behaviour. By studying habitat choice of different species on burned and non-burned areas, as well as the effect of fire on physical and nutritional composition of the grass, I describe how different animal species' anatomy and physiology are adapted to different forage and how this affects their choices of habitat. This gives an insight on how fires can be used to benefit different grazing species.

MATERIAL AND METHODS

The study area

The study was carried out from late August to early September 2005 in the Masai Mara National Reserve in southwestern Kenya, a part of the Serengeti ecosystem. As rainfall and availability of forage changes during the year, large numbers of wildebeests, zebras and Thomson gazelles migrate between different parts of the ecosystem. These animals tend to arrive in the Masai Mara around July, and stay there until November or December. Some carnivores follow the migration in search of prey. Very few wildebeest and zebras stay throughout the year. Other species permanently reside in the area, e.g. the Cape buffalo (*Syncerus caffer*), Maasai giraffe (*Giraffa camelopardis tippelskirchi*), topi and common eland. (Sinclair & Arcese 1985)

The Mara Conservancy, also know as Mara Triangle, is the Western part of the Reserve in-between the Mara river, the Oloololo escarpment and the Tanzanian border. This area of 520 km^2 consists mostly of savannah grassland interspersed with trees and shrubs. The area receives with about 1600 mm more rain than other areas in the Serengeti ecosystem. About 10-20% of the Conservancy is burnt by the management each year to rejuvenate forage and attract certain herbivores. Human habitation inside the Conservancy area is limited to tourist facilities.

Setting the transects

The line transect sampling method was used for the study. This means the observer carries out a survey along a set of straight lines, and records every group of animals, their behaviour and their position. All transects were 1000 m long and 300 m wide, thus covering an area of 0.3 km^2 each. Of the 54 transects were 18 transects placed on the newly burnt area, 18 on the areas burned in June or October 2004, and 18 were controls which had not been burnt for at least two years.

The three types of transects were matched according to several aspects such as type of soil, number of trees, termite mounds, rocks, and proximity to water and riverine forest. Transects were unevenly distributed throughout a study area of 30×15km. Terrain with many rocks or heavy forest was avoided to facilitate driving and make it possible to have a clear view of the whole width of the transect. Transects were put at a distance to each other of at least 500 m from their centre lines to avoid disturbance of animals when driving nearby transects as well as to minimize the risk of double counting.

Animal observations

All observations were made during full daylight between 6.30 and 18.30. This range of time was divided into 12 one-hour periods; each transect was during the study observed once in the study period. Each transect was usually driven once a day, and never twice within three hours.

Two 4WD off-road cars were used for the observations; one with two seats mounted on top of the roof rack and one with an open roof. A co-driver used a GPS (Garmin 1200XL or CX, respectively) to assist the driver in positioning the car along the centre line of the transect.

Tourist vehicles are common and animals are used to the presence of cars. Hence, they were habituated to cars during the observations.

Before entering each transect, the car stopped 200 m from the start point. Time, humidity, temperature and weather were recorded on the sheet before proceeding to the starting point. The driving speed on the transects was maximum 12 km/h.

One observer and one recorder were sitting on the roof or standing in the car while carrying out the observations. When seeing an animal or a group of animals, the species, group size and behaviour were recorded. The behaviour of members of a group was recorded individually, and for observations of larger groups, the approximate number of animals showing each behaviour was estimated. When animals changed their behaviour due to the approaching car before behaviour could be determined the behaviour was recorded as “missing behaviour”. The observer used a Leica Rangemaster 1200 scan to determine the distance, and a home-made angle board to determine the angle between the transect centre line and the animal. This data was used to determine whether the animal was positioned inside or outside the transect area. When a group of animals was observed, the position of the group's centre was recorded. The car was stopped and the engine turned off while the observations were made. The recorder noted where on the centre line the car was positioned.

When the end point of the transect was reached the car was stopped and time, temperature, humidity and weather were recorded again.

Figure 2: Observing and recording.

Species recorded in the study

The mammal species recorded were African elephant (*Loxodonta africana*), black rhinoceros (*Diceros bicornis*), blackbacked jackal (*Canis mesomelas*), blue wildebeest (*Connochaetes taurinus*), Burchell's zebra (*Equus burchelli*), bushbuck (*Tragelaphus scriptus*), cape buffalo (*Syncerus caffer*), cheetah (*Acinonyx jubatus*), common eland (*Taurotragus oryx*), common warthog (*Phacochoerus africanus*), Coke's hartebeest (*Alcelaphus buselaphus cokii*), Defassa waterbuck (*Kobus ellipsiprymnus defassa*), Grant's gazelle (*Gazella granti*), hippopotamus (*Hippopotamus amphibious*), impala (*Aepyceros melampus*), lion (*Panthera leo*), maasai giraffe (*Giraffa camelopardalis tippelskirchi*), olive baboon (*Papio anubis*), oribi (*Ourebia ourebi*), reedbuck, bohor and mountain (*Redunca redunca* and *Redunca fulvorufula*), serval (*Leptailurus serval*), spotted hyena (*Crocuta crocuta*), Thomson's gazelle (*Gazella thomsonii*) and topi (*Damaliscus lunatus*).

Several bird species were recorded; southern ground hornbill (*Bucorvus leadbeateri*), ostrich (*Struthio camelus*), secretary bird (*Sagittarius serpentarius*), Marabou stork (*Leptoptilos crumeniferus*) and some vulture species white-rumped vulture (*Gyps bengalensis*), Rüppell’s griffon vulture (*Gyps ruepellii*) Hooded vulture (*Necrosyrtes monachus*), Egyptian vulture (*Neophron percnopterus*), White-headed vulture (*Trigonoceps occipitalis*), White-backed vulture (*Gyps africanus*) and Lappet-faced vulture (*Torgos tracheliotus*).

In this report, only results in species with a sufficient amount of observations are presented. These were blue wildebeest, Burchell’s zebra, Thomson’s gazelle, common warthog, African elephant, cape buffalo and topi. In this text, some of these species may hereafter be referred to simply as wildebeest, zebra, warthog, elephant, buffalo, respectively.

Ethogram of recorded behaviours

Grazing	Standing, in short grass with the head in a downward position, in high grass with the head positioned downwards but in a more horizontal position.
Lying	Belly or side of belly on ground.
Standing	Belly off ground; the animal performs no other visible activity like grazing, grooming or moving.
Walking	Moving slowly, up to 5 km/h, without performing any other visible activity.
Running	Moving fast (more than 5 km/h) without performing any other visible activity.
Social Behaviour	Two interacting individuals of the same or different species, for example licking or grooming each other, or mother-young interactions. Two animals that possibly chase each other were recorded as running
Other Behaviour	A behaviour not listed above.

Missing Behaviour — When the behaviour of an animal was either affected by the observing vehicle or impossible to determine, missing behaviour was recorded.

Figure 3: Lions lying in an area with short, fresh grass, burnt in 2005.

Statistical analysis

The number of animals per square kilometre was computed based on the animal observations. We anticipate that if the animals prefer different types of forage, there will be a difference in the number of animals per square kilometre of the different transects. Hence, the hypothesis to be tested is whether there is a difference in number of animals per square kilometres between the different types of transects. Data was statistically analysed using MINITAB Release 14. Since the data were not normally distributed (Anderson-Darling test) they were analysed with the non-parametric Kruskal-Wallis test. Before analysing the differences between area types, we calculated the mean value of the 12 drives for each transect. Hence, n was 54 in the analysis.

RESULTS

Table 1: Total number of animals of observed species

Species	Number of observations (groups of animals)	Animals per observation (mean value of group size)	Sum of observed animals
Blue wildebeest (*Connochaetes taurinus*)	1467	22.5	33066
Burchell's zebra (*Equus burchelli*)	905	6.5	5912
Thomson's gazelle (*Gazella thomsonii*)	695	4.6	3199
Cape buffalo (*Syncerus caffer*)	21	23.4	491
Vulture (unidentified species)*	105	2.6	272
Common warthog (*Phacochoerus africanus*)	102	2.3	231
Topi (*Damaliscus lunatus*)	74	3.0	219
Rüppell's vulture (*Gyps ruepelli*)	59	3.2	186
Common eland (*Taurotragus oryx*)	20	5.3	106
Lappet-faced vulture (*Torgos tracheliotus*)	55	1.7	91
Oribi (*Ourebia ourebi*)	42	1.5	63
Whitebacked vulture (*Gyps africanus*)	18	1.9	35
Coke's hartebeest (*Alcelaphus buselaphus cokii*)	14	2.4	33
Grant's gazelle (*Gazella granti*)	9	2.7	24
African elephant (*Loxodonta africana*)	5	3.8	19
Defassa waterbuck (*Kobus ellipsiprymnus defassa*)	3	4.3	13
Ostrich (*Struthio camelus*)	10	1.2	12
Maasai giraffe (*Giraffa camelopardis tippelskirchi*)	5	2.0	10
Secretary bird (*Sagittarius serpentarius*)	8	1.1	9
southern ground hornbill (*Bucorvus leadbeateri*)	4	2.0	8
Marabou stork (*Leptoptilos crumeniferus*)	3	2.0	6
Reedbuck, bohor and mountain (*Redunca redunca and Redunca fulvorufula*)	6	1.0	6
Spotted hyena (*Crocuta crocuta*)	4	1.0	4
Cheetah (*Acinonyx jubatus*)	1	2.0	2
Impala (*Aepyceros melampus*)	1	2.0	2
Lion (*Panthera leo*)	1	2.0	2

Black rhinoceros (*Diceros bicornis*)	0	0.0	0
Bushbuck (*Tragelaphus scriptus*)	0	0.0	0
Blackbacked jackal (*Canis mesomelas*)	0	0.0	0
Hippopotamus (*Hippopotamus amphibious*)	0	0.0	0
Olive baboon (*Papio anubis*)	0	0.0	0
Serval (*Leptailurus serval*)	0	0.0	0

*Several vulture species (*Gyps rueppellii, Gyps africanus, Gyps bengalensis, Necrosyrtes monachus, Neophron percnopterus, Trigonoceps occipitalis and Torgos tracheliotus*) were recorded. However, some species were difficult to tell apart under certain circumstances, such as young vultures, far distance or sharp sunlight where the bird was only seen as a silhouette. Those vultures whose species could not be identified were gathered under "Vulture (unidentified species)".

Table 1 shows the number of times each species was observed, (each group of the species recorded as one observation, a group may consist of one animal only), and also how many individual animals were seen per observation, i.e. the mean size of the groups.

I chose to further analyse the data of those animals that were seen in largest numbers, with the exception of vultures. The vultures may be interesting as a measure of predation, since they live off what is left behind by predators. However, they were not included in this thesis. Elephants were also analysed further since they were seen exclusively on the control areas. They also represent a group of animals, the very large herbivores, otherwise not included in this thesis.

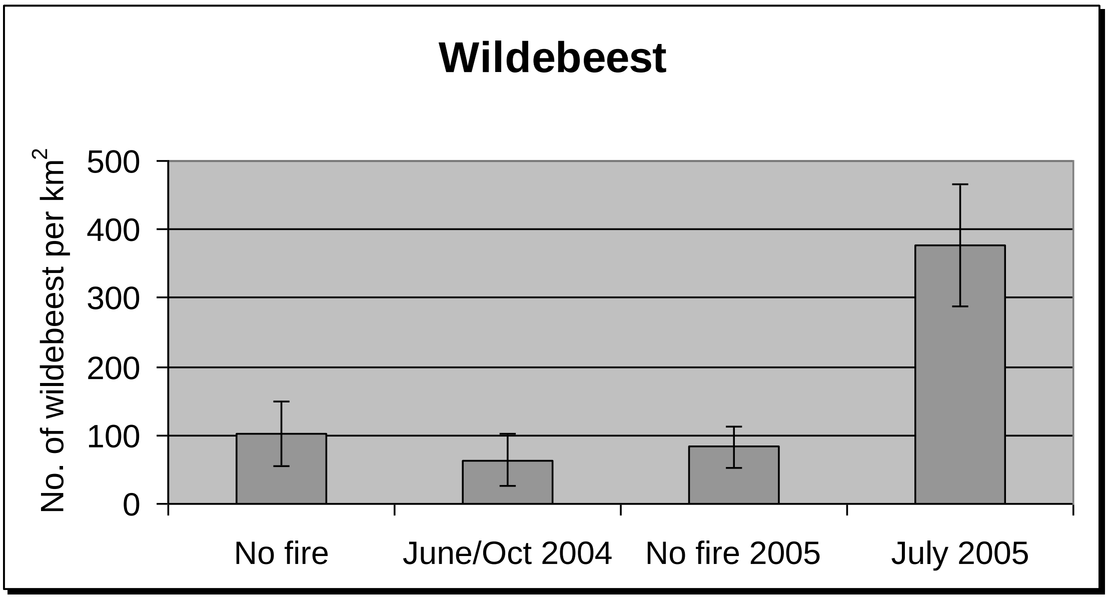

Figure 4: Number of wildebeest per km^2 for the different area types ("No fire 2005" is "No fire" and "June/Oct 2004" put together).

Figure 4 shows that blue wildebeest were predominantly found on the recently burnt areas. The data in this and the following figures are presented as means ± standard error of mean (SE), although it should be noted that since the data is not normally distributed, SE is here only used as a measure of variability rather than the actual standard error of the mean. More wildebeest were found on the areas burnt in 2005 compared to the areas burnt in 2004 ($H=15.7$, $P<0.001$) and the control areas ($H=11.0$, $P=0.001$), respectively. There was no difference in the number of wildebeest when comparing control areas with the areas burnt in 2004. Since these areas are virtually identical with respect to grass characteristics, an additional column which is labelled "No fire 2005" showing the number of animals per square kilometres for both areas combined (i.e. data from 36 transects) is included.

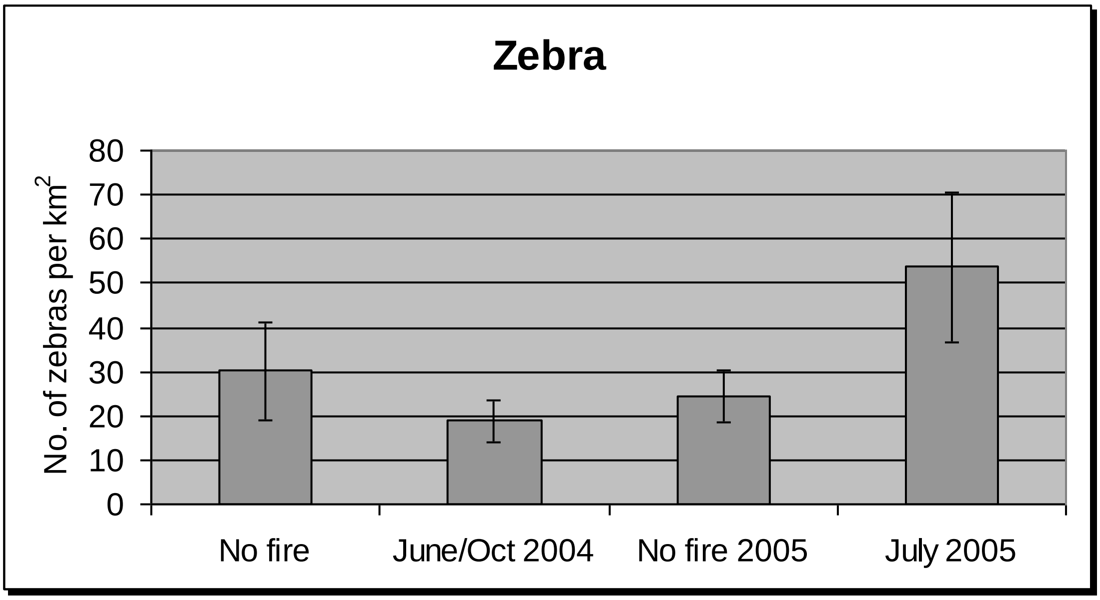

Figure 5: Number of zebras per km^2 for the different area types.

There was no significant difference in numbers of zebras between any of the area types (cf. figure 5).

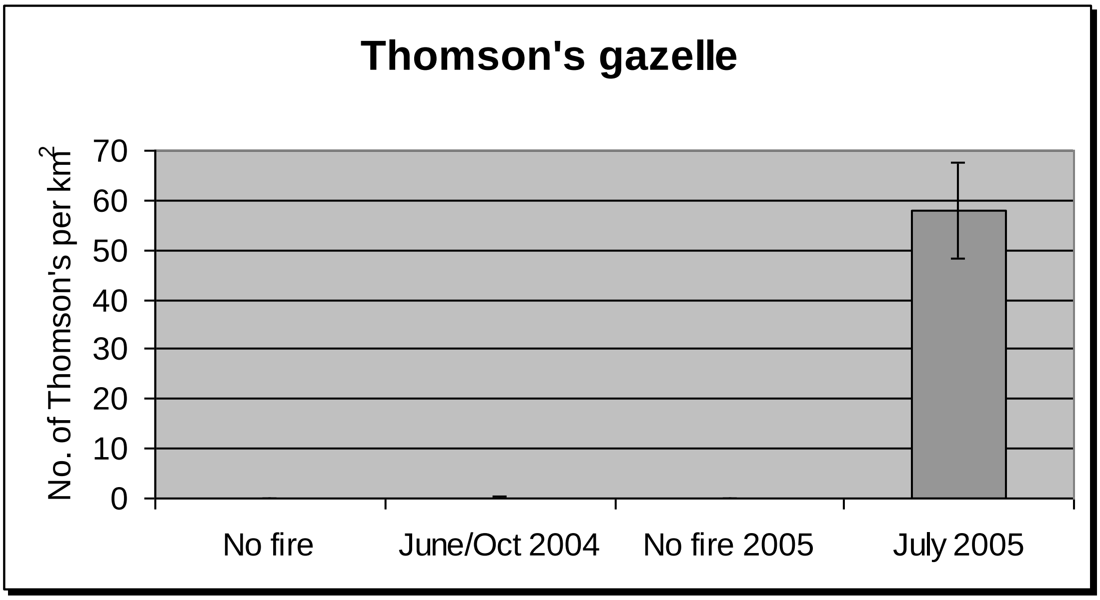

Figure 6: Number of Thomson's gazelles per km^2 for the different area types.

More Thomson gazelles were found in on the newly burnt areas than on areas burnt in the year before (H=22.50, P<0.001) and on control areas (H=22.50, P<0.001). No difference could be seen between the areas burnt in 2004 and the control areas (cf. figure 6).

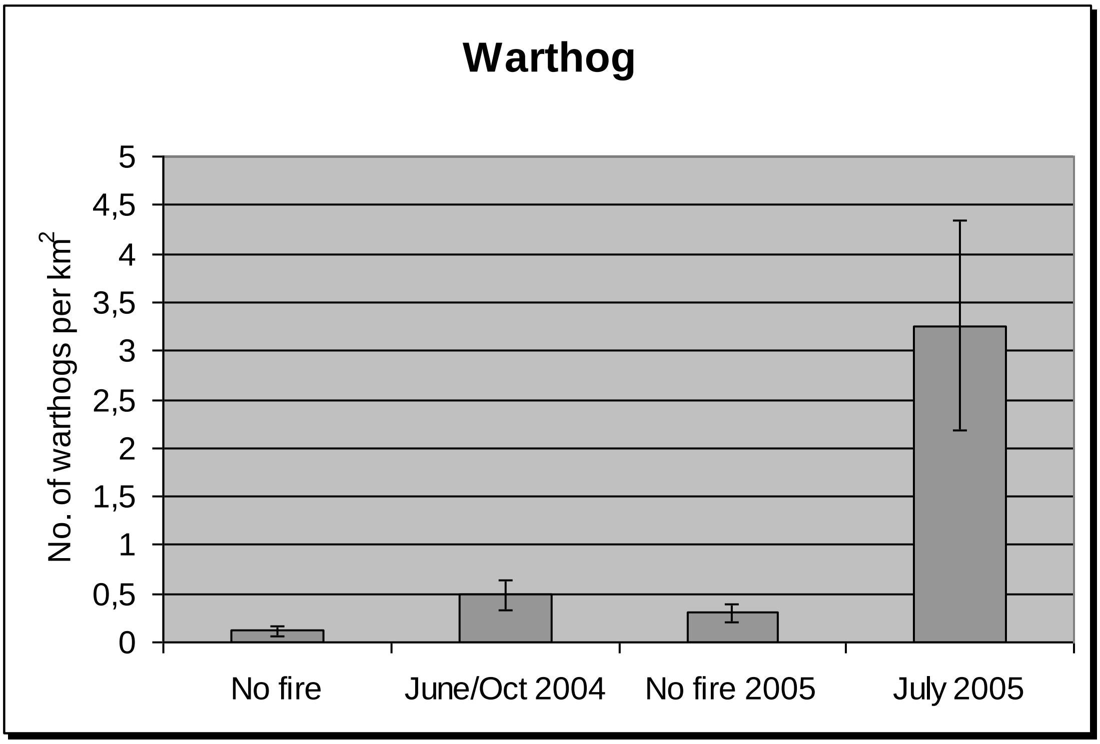

Figure 7: Number of warthogs per km^2 for the different area types.

Warthogs were more abundant in burnt areas than in control transects (H = 6.13, P = 0.013, Kruskal-Wallis test adjusted for ties). There was no difference between the number of warthogs found on the areas burnt in 2004 when compared to the control areas or the areas burnt in 2005 (cf. Figure 7).

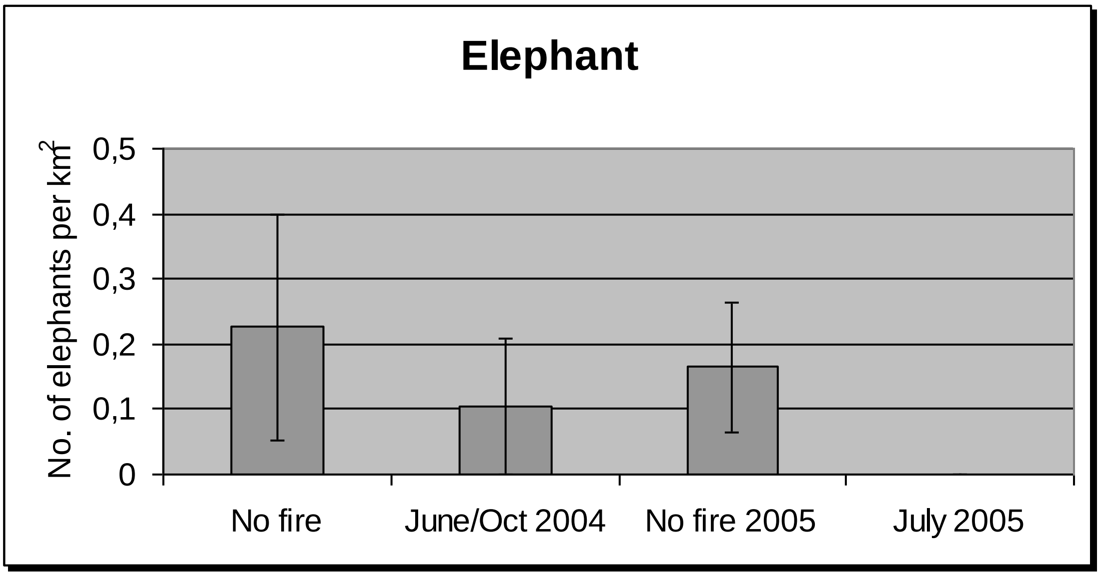

Figure 8: Number of elephants per km^2 for the different area types.

Rather few elephants were seen; those sighted were found in areas with tall grass, i.e. on previous year's fire and control areas. Despite this, there was no significant difference between any of the area types (cf. Figure 8).

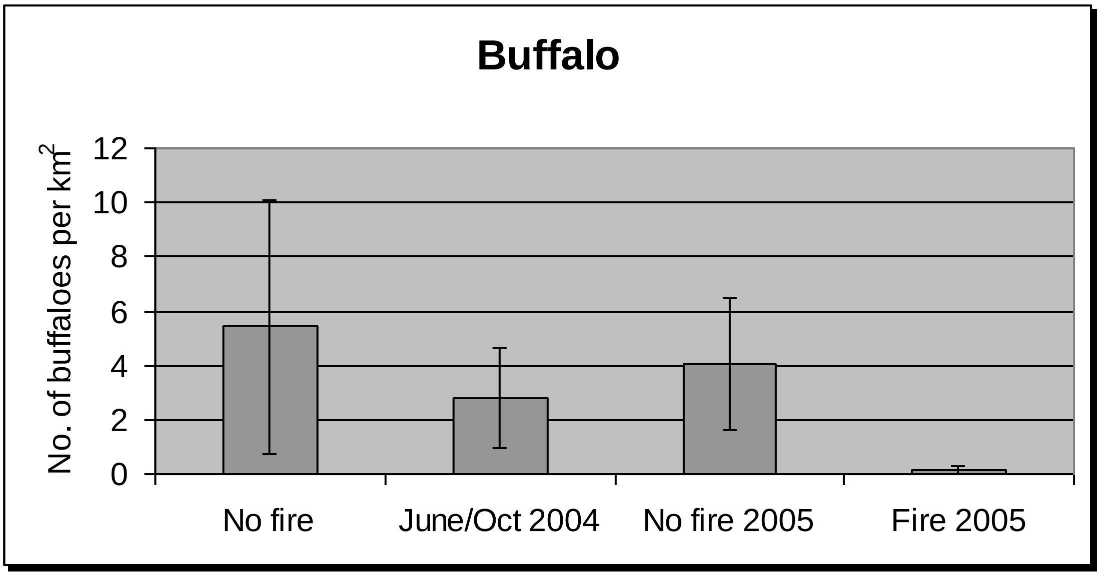

Figure 9: Number of buffaloes per km^2 for the different area types.

A tendency to be on the unburnt areas is indicated by figure 9. No significant difference was found between the number of buffaloes on the recently burnt areas and the controls. The buffaloes showed a tendency to choose the areas burnt in 2004 over the recently burnt areas ($H=2.75$, $P=0.098$). However, when ”No fire” and “Fire 2004” was combined to “No fire 2005”, there were more buffalos found on the recently burnt areas than on the other ones ($H = 3.91$ $P = 0.048$, Kruskal-Wallis test adjusted for ties). No difference was found between control areas and the areas burnt in 2004.

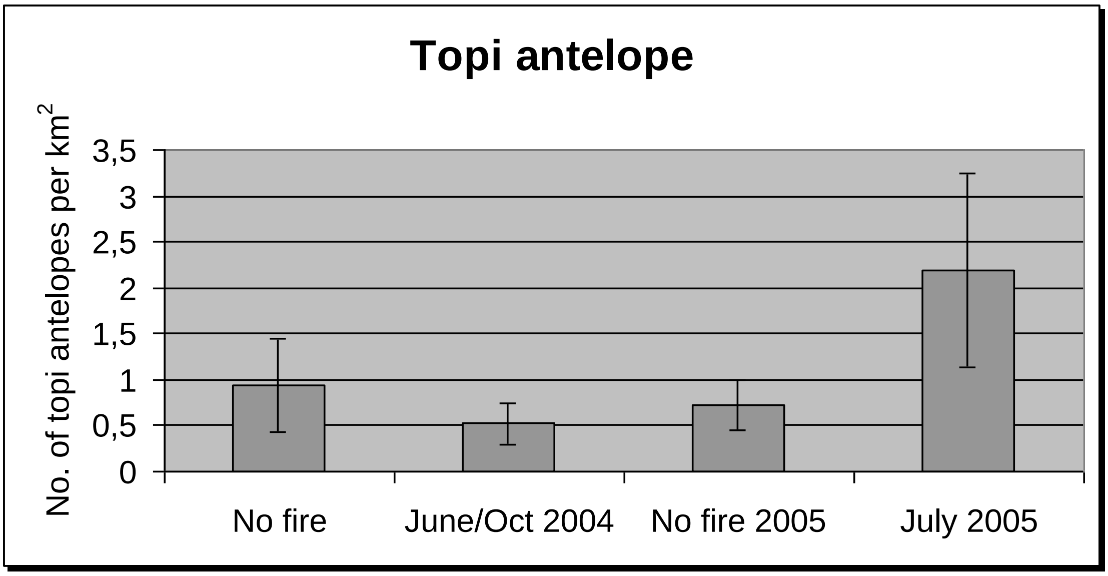

Figure 10: Number of topis per km^2 for the different area types.

The topis showed no tendency to choose either of the areas (cf. figure 10).

DISCUSSION

Grass

In this study, the animals were studied on areas of three different fire treatments. Some areas had been burnt about a month ago and were covered with short, sprouting grass of high quality. Some areas were burnt during the previous year and other areas were controls with tall and mature grass. Mature grass plants usually have low protein content (Dörgeloh 1999). Sprouting grass has up to twice the amount of protein than to mature grass (Moe et al. 1990). Grass on recently burnt or clipped areas also has significantly higher concentrations of nitrogen, phosphorus, potassium, calcium and magnesium, although this effect declines with time and, with the exception of calcium, is gone three months after the treatments (Van de Vijver et al. 1999)

As the plant matures, the cell wall thickens but the cell volume remains the same. This makes the density and percentage dry matter of the cell wall increase with age (Demment & Van Soest 1985). Forage digestibility is a function of the digestion rate acting on a particle for the duration of its retention within the gut (Demment & Van Soest 1985). Leaves and stems differ in digestibility, and thus the difference between leaves and stems offers opportunity for selective feeding (Van Soest 1996).

Wildebeest

In my study, wildebeest preferred the recently burnt areas with short grass. However, wildebeest was also recorded in considerable numbers on control and last year's burn. Alternating between the different types of grass could be a way of ensuring to get the amount of energy needed as well as enough quantity.

It was predicted that the wildebeest would choose to graze predominantly in the burnt areas, which provided short grass with good quality, but that the lower biomass in these areas may be too low for the rather large wildebeest, forcing it to graze also in the unburnt areas to get enough quantity of food.

Wildebeest is classified as a grass/roughage eater, who typically has short lips and a small mouth opening; hence, they would have difficulties picking the most nutritious parts of each plant, such as the concentrate selectors tend to do (Hofmann 1988). Despite this, wildebeest has been found selecting the leaf part of the grass, which is the least fibrous and most digestible part (Bell 1969). If this is correct, the wildebeest should be able to compensate forage of poor quality by choosing the high-quality parts.

In the first season of the study by Engström (2006) wildebeest choose the grass of intermediate height, which had much higher nutritional values than the grass in unburnt areas, but was taller than grass from the areas most recently burnt. These qualities could make it ideal for the wildebeest, offering both bulk and energy.

Figure 11: Migrating wildebeest.

The behaviour of wildebeest on burnt and unburnt areas was also recorded, to examine if they might use the areas in different ways. If a difference in grazing would be seen, that could mean that the recordings of how much time the wildebeest spent in the different areas is not representative for the time they spent feeding on the different types of forage. No such difference could be seen, suggesting that the wildebeest did in fact get more of their consumed forage from the burnt areas.

Zebra

No significant differences on recorded zebras were found in the results, even though the results suggest that the zebra chooses to be mostly on the newly burned areas. However, in a previous study the zebra was found predominantly in the burnt areas (Engström 2005).

Zebras are well adapted to digesting both types of grass. However, the burnt areas could provide them with a better opportunity of gaining energy and nutrients easily, compared to the unburnt area. Equids can compensate a low-quality food, such as the unburnt grass, by increasing their food intake. When doing this they also increase passage rates through their large intestine. The food will be less thoroughly fermented, but the small intestine can still take up the small amounts of easily digestible components in the food.

This mechanism gives zebras the possibility of, unlike the ruminants, increasing their intake rate when necessary and compensate their lesser ability to digest plant material. Zebras have a higher mean intake of forage compared to the wildebeest (Bodenstein et al. 2000) and are able to extract more nutrients per day than the ruminants of similar size (Janis 1976). They select the most fibrous part of the plant and also the tallest and oldest strands (Bell 1969). It therefore seems reasonable that the zebra wouldn’t be very dependant on the less fibrous young grass on the burnt areas. When grazing on the unburnt areas it could increase its intake rate if the grass would not be of enough quality.

Figure 12: Zebras on an unburned area.

Foraging behaviour of the zebras did not show difference between burnt and non-burnt areas. If the zebras had a strong tendency to choose one of the two types of grass as forage, and spent time in the other area for other reasons, a difference in behaviour could be expected, making the zebras spend more time grazing in either the burnt or unburnt areas, thereby getting more of their forage from that type of grass. When offered the more nutritious and digestible grass in the burnt areas the zebras chose these areas to some extent, suggesting that a combination between the two different types of grass is the most beneficial, possibly adding the bulk of the old, tall grass to the nutritional qualities of the sprouting grass.

Thomson´s gazelle

In this study, the Thomson’s gazelle was found exclusively in the burnt areas higher nutritional value, which could be expected from their physiology and food preferences, as well as earlier recordings (Gabrielsson 2005). There is also a possibility that the increased line of sight in areas with short grass has some effect on this choice.

Thomson’s gazelles usually feed on grass. Its narrow muzzle and mobile lips gives it the chance to pick the most digestible parts with high nutritional content (Hofmann 1989), while its saliva gives it the capacity to neutralize plant defence compounds and choose from a wide range of forage. The Thomson’s gazelle has parotid salivary glands of intermediate size (Hofmann 1988). Salivary glands differ in size and composition between herbivores and give the concentrate selectors better ability to deal with different types of forage than the grass/roughage eaters. These anatomical traits suggest that the Thomson’s gazelle is very selective even among different kinds and parts of the grass. The rumen of the Thomson’s gazelle is devoid of protozoa, which could indicate a very high passage rate or a very high concentrate diet (Dehority & Odenyo 2003). Selectivity makes it able to ingest a very high concentrate diet, even if most grass is of lower quality. Grazing on the burnt areas would provide Thomson’s gazelles with an opportunity to ingest their preferred diet without spending much time and energy on selecting the best parts, since most of the grass available is of the desired quality.

Warthogs

Warthogs were more often found on burnt areas, as could be expected considering that they prefer high-quality grass. They are selective grazers, choosing the highest quality of food available, and adding nutritious roots to their diet when grazing on low-quality forage (Treydte et al. 2006). During the wet season the warthogs' diet is almost completely comprised of the leaves of short grasses (Treydte et al. 2006), such as could be found on the burnt areas.

Elephants

The few elephants encountered in our study were found exclusively on the tall-grass transects. Elephants are mixed feeders, living off both graze and browse. It has been suggested that grasses are preferred to browse because of higher nutritional value. Also in previous seasons in the study, elephants were found more on non-burnt areas (Gabrielsson 2005).

Large animals, such as the elephant, have high absolute energy requirements and need abundant forage (Clauss et al. 2003a), but increasing body size should also produce higher digestibility because of longer retention times (Demment & Van Soest 1985). However, there is a limit when the long retention time will surpass the time needed to digest the forage completely. The elephant's size, and possible retention time, would be insufficient to meet its demand for energy from food. Instead, the elephant has a GIT that is shorter than could be expected from its body size, giving it a very short retention time coupled with an incomplete digestion (Clauss et al. 2005, Clauss et al. 2007). The elephant is dependent on eating large quantities of food, and since high-quality forage is scarce, it can not depend on this to maintain its needs, but has to expand their diet to include low-quality forage (Demment & Van Soest 1985). It would have little benefit from the nutritious grass in burnt areas, having to spend much time and energy to get a sufficient amount. Their way of grazing by grabbing tufts of grass with their trunk and lifting it to their mouth may also pose a problem when grazing on burnt areas, as short grass could be more difficult to grab.

Buffalo

As expected from earlier studies and its anatomy, the buffalo choose to graze from the taller grass on the unburnt areas. It grazes with a technique similar to cattle's, using their lower incisor and tongue to twist and cut the grass (Field 1976), and predominantly choosing a tall grass (Hansen et al. 1985).


Figure 13: Buffalo on tall, unburnt grass.

Grass on the burnt areas is probably too short to graze with this feeding-style. Being well adapted for digestion of fibrous grass of lower quality, using a low fermentation rate and slow passage through the GIT (Hofmann 1989), the benefits of the high-quality grass would not be enough to compensate for the difficulties of foraging effectively enough.

Topi

No significant differences on recorded topis were found in the results, even though the results suggest that more topis were seen on the newly burned areas. It is specialised in grazing from tall grass (Janis & Ehrhardt 1988), and could therefore be expected to be found mainly in the unburnt areas. The topi is probably able to benefit from the nutritious grass on the burnt areas, and at the same time it adds the selected parts from the tall grass, where it can easily find enough bulk.

General discussion

The recently burnt areas with short, high-quality grass was preferred by the wildebeest, the zebra, the Thomson's gazelle and the warthog, while the buffalo and elephant chose the unburnt areas, providing grass in higher quantity but lower quality. The topi showed no tendency to choose either area. In some species, such as the Thomson's gazelle, the results were extremely clear; other species seem less choosy, being able to adjust to both kinds of grass without much problem.

The four ruminants, although using the same principle for digesting their food, have evolved in different directions to fit different niches in the ecosystem. Ruminants are commonly divided into three main groups, the grass/roughage eaters, or grazers, the concentrate selectors, or browsers, and the mixed feeders, which covers the whole spectrum in between the other types. The grass/roughage eaters are specialised in feeding on large quantities of grass, utilising the often fibrous, indigestible material as efficiently as possible. To succeed with this, they have been fitted with teeth and mouths suitable for biting, shearing and chewing the abrasive grass, large rumens to provide room for the extensive fermentation and long intestines to delay the food enough to be thoroughly digested. The concentrate selectors, on the other hand, chooses the most nutritious parts of the forage, using their thin, mobile lips and unevenly sized teeth to pick leaves, buds or fruits, from bushes, trees or grasses. Since this diet is more digestible, they can speed up the rate of passage through their GIT. Less space is needed for the fermentation in the rumen, which is smaller than in the grass/roughage eaters, and less time is needed for digestion in the intestines, which are shorter. Since the more nutritious parts of the plants are rarer and it usually takes more energy to harvest them, the animals depending on such a diet are generally small, being able to extract the required energy from a smaller quantity of food. Larger animals tend to be grass/roughage eaters, since they would be unable to gather high-quality food in quantities large enough. The mixed feeders range from those in close resemblance to the concentrate selectors in anatomy and feeding habits to those similar to grass/roughage eaters.

The three monogastric species in this study has also different ways of meeting their nutritional needs. The elephant has reached a body size unattainable by the ruminants, since its simple stomach makes it possible to speed up the digestion, thereby forsaking the thorough digestion of the large ruminants. To keep up with its digestion it also needs a high intake rate, thus consuming large amounts of food. The zebra also has the ability to digest food faster and less thoroughly, but uses this as a resort to cope with low-quality forage, and feeds from high-quality food when it is available. The warthog digs for nutritious roots when food above ground is insufficient to meet its needs. These different strategies makes the animals more or less adapted for the different types of grass we provided them with in this study, allowing us, to some extent, to predict their choices.

To complicate matters, anatomy, physiology and feeding habits are not the only reasons for the animals to make these choices. The impact of other effects of the two fire treatments should also be taken under consideration. The short grass on the burnt areas offer the animals with an increased line of sight, making it possible to detect predators at a longer distance, which could be an incentive for the animals to stay in those areas.

People in Masai Mara, as well as in other African national parks and conservancies, are working to maintain an environment that will attract many different animal species, both for ecological as well as tourist purposes. With a better understanding of the animals’ preferences and responses to different changes in their environment, we can hopefully use rather simple tools, such as controlled fires, to create an environment suited for the needs of different animal species.

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Figure 14: Coffee break.

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