Shombe Ntaraluka Hassan

Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania

Thesis for the degree philosophiae doctor

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Norwegian University of Science and Technology
Faculty of Natural Sciences and Technology
Department of Biology

NTNU

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Preface

This thesis is an outcome of a collaborative programme between the Department of Wildlife Management (DWM) at the Sokoine University of Agriculture (SUA) in Morogoro, Tanzania, the Norwegian Institute for Nature Research (NINA) and the Department of Biology, Norwegian University of Science and Technology (NTNU), in Trondheim, Norway. The programme sought to enhance the research capacity of the teaching staff in the recently established DWM, at the Faculty of Forestry and Nature Conservation. The project was financed by the Norwegian Programme for Development, Research and Higher Education (NUFU). Nevertheless, many other institutions and individuals facilitated the work at different times, and to all of them I submit my sincere appreciation.

Foremost, I am indebted to the SUA administration for granting a study leave, Tanzania Wildlife Research Institute (TAWIRI) for granting permission to undertake research in Serengeti, and to Tanzania National Parks for conceding free of charge entry and stay in Serengeti National Park. Ngorongoro Conservation Area Authority allowed non-levied movements to and from Serengeti. Execution of this study would have been impossible without their consent. Furthermore, I wish to express my gratitude to the Department of Wildlife Management and the Faculty of Forestry and Nature Conservation at SUA for their facilitation role.

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ALLAHU AKBAR

Table of contents

List of papers

Four papers constitute this thesis:

I Shombe N. Hassan, Graciela M. Rusch, Håkan Hytteborn, Idris Kikula and Christina Skarpe. Primary production responses to early dry-season burns in western Serengeti grasslands (Manuscript).

II Shombe N. Hassan, Christina Skarpe, Graciela M. Rusch, Idris Kikula and Håkan Hytteborn. Forage quality of the grasses from burnt and non-burnt areas in western Serengeti, Tanzania (Manuscript).

III Shombe N. Hassan, Graciela M. Rusch, Håkan Hytteborn, Christina Skarpe and Idris Kikula. In press. Effects of fire on sward structure and grazing in western Serengeti, Tanzania. African Journal of Ecology.

IV Shombe N. Hassan, Graciela M. Rusch, Sigbjørn Stokke, Christina Skarpe, Eivin Røskaft and Håkan Hytteborn. Fire history and herbivore patch selectivity in Serengeti ecosystem, Tanzania (Manuscript).

Abstract

Fire is one of the major ecological factors that determines structure and function of grassland and savanna ecosystems through its effects on soil nutrient pools, floristic composition and primary production, and foraging behaviour and distribution of populations of wildlife species. Therefore, some wildlife protected area authorities in African savannas have a fire management scheme to cater for a variety of purposes such as, to prevent bush encroachment into grassland, to increase production of quality forage, to control wild fires from outside the protected areas and their spread, and to keep animals in tourist areas for visitors' enjoyment. The responses to fire of ecosystem processes can be quantified but the outcomes are generally complex depending on the nature of the fire regime, primarily the frequency and timing of the fire events. For example, while ash after fire may have a fertilising effect that will facilitate seedling establishment and increase the growth and production, there is evidence that in East Africa, fire may lead to the dominance of a few species over several other species. Fire may also lead to loss of nutrients, for example nitrogen, through volatilisation. Such variaty in responses to fire makes the use of fire as a tool in the management of wildlife and protected areas usually controversial. Therefore, the main challenge of management is to strike a fire management regime as close as possible to a natural fire regime in this ecosystem.

In the Serengeti ecosystem, fire has been regarded to have a critical role on herbivores and their forage resources. Thus, burning has been a management tool in protected areas and a common practice of range management by pastoralists. Herdsmen use fire to improve the pasture quality for cattle. Removal of old or dead grass material by fire enhances sprouting of plants, which improves, at least for a short-term, the quality of the sward. In the Serengeti National Park, early dry-season burns had been executed by the Serengeti Ecological Monitoring Program Department from end of May to mid August without clear understanding about grassland responses to the prescribed burns.

The perceived importance of fire to the management and conservation of Serengeti ecosystem has driven this thesis to focus on the effects of fire on large herbivores and their forage resources in the Serengeti National Park. To accomplish that, the thesis examines the relationships between burning and 1) above ground net primary productivity in relation to sward structure and precipitation (Paper I), 2) forage quality, i.e. the concentration of macro-nutrients (N, P, K, Na, Mg and Ca), *in vitro* organic matter digestibility and levels of acid detergent fibre per phytomass component (Paper II), and 3) the temporal and spatial patterns of herbivores' consumption (Paper III), and 4) the patch selection by ungulate species, individually and/or grouped in diet groups (Paper IV).

The result of the early dry season burns is a significantly higher daily above ground net primary production (ANPP) on burnt plots at early post-fire stages, coinciding with the dry season (July-September) and during the short rainy period (October-December). Though not significantly different, it was also high on burnt plots at the end of the main rain period (March – May), but higher on non-burnt plots in December-February, and in early dry season, June-July of the subsequent year.

Results from this area with high diversity of large herbivore species show that grazing herbivores switch between burnt and non-burnt patches by trading off between forage quantity and quality along growing season. The quality on burnt areas appears to be governed by enhanced concentrations of macronutrients, increased digestibility and reduced concentration of acid detergent fibres. The above quality variables are linked to increased ratio between live and total phytomass. Quality of forage explains the preference by grazing animals for burnt areas during some periods, and in non-burnt areas due to high phytomass in other periods.

Selection for non-burnt or burnt patches or against patches burnt more than once in a period of three years by some species of ungulates and/or diet groups are also indicative that quality and/or quantity of forage in the respective patch underlay patch choice. The cause of temporal variation in selectivity of the patches needs further investigation. However, it is unequivocal that maintenance of mosaic of burnt and non-burnt areas with adequate provision of forage amount and quality all year round is of paramount importance.

Introduction

Fire is an important ecological factor in many habitats from forests to dry grasslands (Crawley, 1986; Johnson, 1992). Several fire-evolved vegetation types are known world-wide. These include chaparral communities (Hamilton, 1997) and longleaf pine-wire grass community in North America (Noss, 1989), eucalypt woodlands and open forests in Australia tropical savannas (Andersen *et al.,* 2005), the cerrado in central Brazil (Ratter, Ribeiro & Bridgewater, 1997), and miombo woodlands and savanna grasslands in Tropical Africa (Kikula, 1986; Skarpe, 1992). The structure and function of many fire-prone communities are primarily determined through fire and herbivory (Skarpe, 1992; Hobbs, 1996; Bond & Keeley, 2005). Both factors change nutrient cycling, ecosystem composition and distribution of organic matter (Wessman, Bateson & Benning, 1997).

No grassland or savanna ecosystems have existed completely without burning and therefore, fire is considered a key factor that contribute to the natural selection on the genetic variation and features seen in the plant species today (Heady, 1972; Knapp *et al*., 1998). This has come as a result of selection for a fire tolerant and fire dependent flora (Bond, Woodward & Midgley, 2005).

Activities of humans, through use of fire as a wildlife – and later livestock management tool in savanna habitats (Trollope, 1982) have influenced the structure and function of savanna ecosystems (Harris, 1980). Deliberate use of fire by hominids started 2.5 million years ago and likely increased the fire frequency in African savannas (Brain & Sillen, 1988), which is why Africa was nicknamed the Fire Continent (Komarek, 1971). Without fire, considerable areas of African savanna could potentially develop into closed woodlands because under fire exclusion, grasslands commonly develop into tree-dominated areas (Bowman & Fensham, 1991; Hopkins, 1992; Swaine, Hawthorne & Orgle, 1992). Therefore, periodic fire maintains grassland by slowing down woody succession and stimulating grass resprout (Vesey-Fitzgerald, 1971; Anderson, 1990; Leach & Givnish, 1996) thereby helping to maintain a dynamic balance between savanna and forest (Hopkins, 1992).

In fire-prone systems the local fire regime (Fox & Fox 1987; Malanson, 1987) can strongly influence the floristic composition and the dynamics and structure of the vegetation (Whelan, 1995; Bond & Van Wilgen, 1996; Anderson, Cook & Williams, 2003). Changes in soil chemistry and microsite temperature have been found to affect phenology of many grass species, resulting in longer periods of succulence during a growing season (Daubenmire, 1968; Old, 1969). Burning may also improve forage nutritional quality (Moe, Wegge & Kapela, 1990; Dorgeloh, 1999; Van de Vijver, Poot & Prins, 1999; Paper II, Paper III) and influences aboveground net primary production in grasslands (Paper I), whereas post fire re-growth in recently burnt patches attract foraging ungulates (Moe, *et al.,* 1990; Wilsey, 1996; Tomor & Owen-Smith, 2002; Paper III). However, the use of prescribed fire, as a tool in the management of wildlife areas is usually controversial (Pratt & Gwynne, 1977). This is partly because fire is used to meet different objectives under different management schemes, and because there is insufficient knowledge about natural fire regimes. These shortcomings are exacerbated due to difficulties in extrapolating findings from other ecosystems, since the responses of ecosystem processes and community structure and composition to fire are generally complex, and vary between regions and plant communities.

Reasons for prescribed fires in and around wildlife protected areas in African savannas

In general, grasslands and savanna ecosystems are primarily managed through fire and grazing, both of which influence nutrient cycling, ecosystem composition and distribution of organic matter (Wessman *et al.,* 1997) and together with rain they influence the tree-grass dynamics in tropical savanna between tree and grass dominance (Jeltsch *et al.,* 1996; Liedloff *et al.,* 2001). Several reasons have been advanced for the use of fire in the management of African savanna. A few specific reasons and/or areas are included below:

- Early burning is practised in and around Sengwa Wildlife Research Area (SWRA), Zimbabwe, to reduce fire hazards emanating from the neighbouring village lands (Mapaure & Campbell, 2002). In this regard, burning helps to reduce fuel loads that may support wild fires.
- Herdsmen in East Africa (Vesey-FitzGerald, 1971; *Moe et al.,* 1990; Dublin, 1995) including those in Serengeti Mara ecosystem burn to control pathogens and disease vectors such as tick, and tsetse fly *(Glossina spp*) infestation, which transmit a parasite causing trypanosomiasis or sleeping sickness (Heady, 1972; Kikula, 1986). Pathogens including those that cause Malignant Catarrhal Fever (MCF) in African buffalo and cattle and Anthrax spores can as well be exterminated by fire.
- Herdsmen also burn to stimulate plant re-growth and reduce cover that harbours livestock predators (Norton-Griffiths, 1979), and it enables animals to access the green growth following removal of a mat of dead grass (Heady, 1972). This is generally considered an improvement of wildlife habitat.
- Fire may also be used to promote tourism activities by attracting and providing visibility of big mammals, and facilitating protection of wildlife by removing hiding places of illegal hunters (Mbow *et al.,* 2003).
- Fire is used to control undesirable vegetation e.g. bush encroachment of grassland (Pratt & Gwynne, 1977) which otherwise will lead to an increased competition for available water, nutrients and light between grasses and forbs on one side and bushes on the other.
- Burning often increase forage yield (Wright, 1974).

There are also other specific reasons for annual early burns in the Serengeti National Park (Mwangomo, 2003). Some of them may be uncommon to other areas:

- To induce production of re-growth, this is a favourite of grazers.
- To ensure availability of forage supplies to sustain migratory herds in dry season refuge areas.

- ☐ To prevent spread of illegitimate fires within the park by creating mosaic of burnt and non-burned patches, which fragments the landscape.
- ☐ To attract animals to burnt areas inside the park before areas outside, which are burnt by illegal hunters to lure the animals.
- ☐ To reduce the population of tsetse flies in tsetse infested areas.
- ☐ To create a fire break around sensitive and/or high diversity spots such as riverine forest, kopjes and hills to help to protect their flora and fauna.
- ☐ To enhance scenic beauty in tourist circuits and prevents fires to reach campsites. The re-growth will keep animals in the areas for tourists to enjoy. In a way this eases distribution of grazing and browsing animals in the park, through which over-grazing and under-utilization of some areas is regulated.

Therefore whatever the fire management goals, a balance needs to be struck between the possible or perceived deleterious effects of a frequent-fire regime, and the risk of intense wildfires if a regime of low frequency fires is prescribed. The appropriate use of fires in savannas is therefore an important consideration for managing these ecosystems so that expected responses of living and non-living components of the ecosystem to the fire regime are achieved. Discrepancy in results of responses of vegetation to fire suggests that use of prescribed fire as a management tool must be dictated by the objectives of the managements. Ecological, research-based information should provide guidelines for decisions about the imposed fire regime before burning is recommended or condemned.

Fire exclusion

Fire regimes are usually considered to have at least three-interrelated components; fire frequency, i.e., how often the fires occur (Hobbs, 1984; Fensham, 1990), fire intensity or heat output of the fire (Moreno & Oechel, 1991) and season of burning, what times of the year fires occur (Lonsdale & Braithwaite, 1991; Swezy & Agee, 1991). The increase in fuel loads over time in savannas which remain un-burnt for several years following fire exclusion (Gill, Hoare

& Cheney, 1990) may heighten the risk of unplanned or prescribed fire to cause substantial mortality of tress. Fire exclusion may have other ecological impacts, for example on wildlife populations. The noticeable decline in blue wildebeest numbers, but an increase in African buffalo and Burchell's zebra (Runyoro *et al*., 1995) in the Ngorongoro crater, Tanzania after eviction of Maasai pastoralists in 1974 offers a classic example. In the Ngorongoro event, exclusion of fire was said to modify the grassland community to a taller and courser structure, which favours buffalo and zebra more than wildebeest, although also the eviction of cattle grazing as such could have contributed to this. Lake Manyara National Park, in Tanzania is now under an enormous bush encroachment of grassland habitats as a result of combined effect of fire suppression and the tremendous decline of elephant population between 1970 and 1980. This situation is also being associated with local extinction (J. Koroso pers.comm.) of some mammal species such as Cheetah (*Acinonyx jubatus*), which hunts in open vegetation. Moreover, 29 years of fire suppression on Accra plains in south-eastern Ghana caused the plains to become forested, and *Ceiba pentandra*, a fire sensitive tree species became dominant (Carson & Abbiw, 1990).

Rational of thesis

High frequency burning occurs in the Serengeti-Mara ecosystem particularly in Serengeti National Park and surrounding Game Reserves on the Tanzania side (Rusch *et al.,* 2005). This includes both prescribed fires and wildfires. Table 1 shows extent of burning in the Serengeti ecosystem from May 2000 to December 2006 (Dempewolf *et al.,* 2007). Prescribed fires are set by the management authorities of the respective protected areas. However, and despite the use of fire as a management tool for decades in Serengeti, the impact of fire regimes on ecosystem processes such as primary production and on forage quality in Serengeti grasslands are poorly understood. Also, the effect of forage supply mediated by the influence of fire on herbivore foraging patterns and consumption, and use of patches of varying fire history is limited. This thesis seeks to address these issues in order to better understand how fire affects the interaction between plants and large herbivores in Serengeti. This knowledge will contribute to a knowledge-based management of the Serengeti National Park, and the surrounding protected areas.

Methods

Study system

The study area is located in the north-eastern part of the United Republic of Tanzania, more specifically in the Serengeti-Mara ecosystem. The entire Serengeti–Mara ecosystem situated in both Tanzania and Kenya is made up of about 25,000 km^2 of which 14,763 km^2 constitute the largest National Park in Tanzania, Serengeti National Park (Kideghesho *et al.,* 2006). The Serengeti–Mara ecosystem is located between latitudes 1° and 3°S and longitudes 34° and 36°E, and is defined by the boundaries of the area utilized by the migratory Blue wildebeest *Connochaetes taurinus* (over 1.3 million), Burchell's zebra *Equus burchellii* (200,000), Thomson's gazelle *Gazella thomsoni* (440,000) and eland *Taurotragus oryx* (Sinclair, 1975; 1995). Other nearby protected areas are Maswa (2,200 km^2), Grumeti and Ikorongo Game Reserves. There are about 27 species of ungulates (Sinclair & Norton-Griffiths, 1982) and Blue wildebeest, Burchell's zebra, Thomson's gazelle, African buffalo *Syncerus caffer* and topi *Damaliscus korrigum* are described as the major grazing species (McNaughton, 1985).

Open grasslands dominate in the south-east whereas *Acacia* woodlands and riverine forests dominate the western and northern parts (Senzota, 1982). Over most part of the ecosystem the herb layer is dominated by C4 grass species (Frank, McNaughton & Tracy, 1998). These include perennial bunch grass species, *Themeda triandra*, *Pennisetum mezianum* and *Digitaria macroblephara* (Clayton, Phillips & Renvoize, 1974) which dominate *Themeda* grasslands. There are two major seasons, wet season from November to May, and dry season from June to October (Norton-Griffiths, Herlocker & Pennycuick, 1975). Rainfall distribution is bimodal with short rains from November through December and long rains from March to May (Sinclair & Arcese, 1995). The average annual rainfall ranges from 600 mm per year on the South-east Plains to about 1100 mm per year in the North (Pennycuick, 1975). The temperatures in western Serengeti are generally higher than in the East and may rise above 36°C., The Western Corridor in the Serengeti National Park, which is a less known part of the National Park stretches westward nearly to Speke Gulf of Lake Victoria, and it is dominated by a mosaic of *Acacia* woodlands, grass plains and riverine forests. The area known as the Western Corridor within the Serengeti National Park provides a year round habitat for non-migratory species (McNaughton & Banyikwa, 1995).

Data collection

Forage consumption and aboveground net primary production

Herbivore forage consumption was estimated from September 2003 to July 2004 whereas aboveground primary production (ANPP) was estimated from July 2003 to July 2004. Study sites comprised six sites in medium-high *Themeda* grasslands located in the Western Corridor of the Serengeti National Park. Each site consisted of one burnt and one non-burnt patch. One large plot, 50 m x 50 m was marked out per patch (i.e. one burnt and one non-burnt plot per site), in total twelve plots. The burnt patches were burnt in the annual early dry-season burning operation in May-July 2003 executed by the Ecological Monitoring Department of the Serengeti National Park.

Repeated phytomass harvesting was done by clipping samples from randomly distributed 0.25 m x 0.25 m quadrats at ground level with a pair of scissors in each of the 12 plots at each of nine sampling occasions. Litter in the same quadrat was collected by hand and all samples were kept in separate plastic bags until processed in the laboratory. Movable cages were used to protect six quadrats from grazing by large herbivores, and six other quadrats were left open as controls. Six 'caged' and six 'open' quadrats were sampled per plot and sampling time from September 2003 to July 2004. However, at the first sampling time in July 2003, only six open quadrats were sampled. Caged quadrats sampled in September 2003 had been set up in July 2003. The six cages were placed at new random locations within the plot at each sampling from September 2003 to June 2004 avoiding previously clipped spots. The cages were of conical shape, 1 m^2 (1 m x 1 m) on the ground and 1.5 m tall. Each sample was hand-sorted into five compartments: live leaf, live stem, flower/fruit, standing dead (dead material attached to living plants) and litter. Sorted materials were first air-dried for two weeks in paper bags and later oven-dried at 70°C (Mutanga *et al*., 2004) for 48 hours and then weighed using a digital scale (Soehnle ultra, [Leifheit AG, D-56377 Nassau, Germany] with maximum 200 g, d = 0.1 g). The sward height, excluding reproductive culms, was measured at the four corners of the quadrat before collecting the phytomass sample. These data were used to calculate aboveground net primary production and consumption by large herbivores.

Monthly rainfall data at three localities with rain-gauges at Nyaruswiga, Mareo and Musabi in the neighbourhood of the study sites were retrieved from the data set of the Ecological Monitoring Department of the Serengeti National Park. Each locality has one rain gauge and the distance between the sites and the rain gauges varied between 0.5 - 1.2 km.

Forage quality

At each sampling occasions (n = 5) between July 2003 and August 2004 144 samples were collected for nutrient analyses. The periods were September 2003, December 2003, March 2004, May 2004 and July 2004. The samples consisted of the phytomass components: live leaf, live stem, flower/fruit and standing dead material. For each period, samples of the same phytomass component were merged into composite samples, one from burnt and another from non-burnt plots. For the chemical analysis the material was re-sampled by drawing six random samples from each composite sample of grass components, except for flower and fruit (n =3).

Live leaf, live stem, flower and fruit and standing dead material were analyzed for N, P, K, Ca, P and Na content for each sampling period, but only the vegetative parts were analyzed for acid detergent fibre and *in vitro* organic matter digestibility. Minerals were determined using regular procedures used by the Association of Official Analytical Chemists (A.O.A.C., 1970) with dry ashing at 550°C for 3 hours and 6N HCl instead of 1N HCl. Nitrogen content was determined with Kjeldahl analysis (Okalebo, Gathua & Woomer, 1993), and ADF determined as described by Van Soest (1982). Analysis of *in vitro* organic matter digestibility followed the method of Tilley & Terry (1963).

Herbivore patch selectivity

Ungulates were counted by species within burnt and non-burnt patches along 150 transect segments of 1 km distributed along the existing road-network in a total of 9 areas, which included areas of the Serengeti National Park, Grumeti Game Reserve, Ikorongo Game Reserve and a portion of Ngorongoro Conservation Area, but also a part outside any of the protected areas (data from the BHWI (‘*Biodiversity and the Human-Wildlife Interface in western Serengeti Project*’ database). The counts were conducted at approximately monthly intervals between May 2001 and April 2002 and from May 2003 to April 2006. Animals were scanned up to 1000 m from the road. All geographical positions were recorded in UTM system, with a Garmin XL12 GPS, geodetic map datum ARC 1960. The areas of burnt and non-burnt patches along transect segments in the period May 2000 to November 2006 (Table 1) were extracted from the fire maps in Dempewolf *et al.* (2007). The observation periods were defined from May to April the following year. Two, three and eight patch types were described based on the fire impact on an area in the year of the animal counts (‘current’) and the two preceding years. Ungulate species were grouped into three diet groups namely preferential grazers, preferential browsers and mixed feeders. The GPS position of animal counts and the burned area maps were collated in Arc GIS version 9.

Data analysis

General Linear Model-univariate ANOVAs in SPSS for windows was used to analyze the data sets in Paper I, II & III). Independent sample T-test was additionally used in Paper II. Fire (burnt/non-burnt) was consistently used in the models as fixed factor. Chi-squared goodness-of-fit test, selection ratio and confidence interval (CI) were calculated in Excel-spreadsheets.

Main results

Fire and forage availability and production

Total standing phytomass (live and standing dead plant material) achieved at all sampling times greater values in the non-burnt plots than in the burnt plots (Table 2). Biomass of nearly all live compartments and total live, and mass of dead compartments and total dead were higher on non-burnt than on burnt grassland for nearly all periods, except for the phytomass of flower/fruits, which in June was higher in the burnt plots (Table 2). However, the ratios of both live leaf and total live/total standing phytomass were significantly higher on burnt plots whereas the ratio of live stems/total standing phytomass was significantly lower (Table 3). Burnt plots also had significantly higher ratios of leaves/total live and generally lower ratios of stems plus flower-fruits phytomass/total live phytomass (Table 4). No differences between treatments in the ratios of flower and fruit phytomass/total live phytomass were observed.

A significant effect of the interaction phytomass change * fire indicated that phytomass production was dependent on the fire treatment. Daily ANPP was highest on burnt plots in July-September, October - December, and May-June, but generally higher in non-burnt plots in December - March and June - July. Significant biomass change * site in May-June and Jun-July indicated that local conditions at the sites were important determinants of production as well (Table 5). Further, only on burnt plots was ANPP positively related to leaf and total live phytomass and to the ratio between live leaf and total standing phytomass, but was negatively correlated to the ratio between the phytomass of reproductive structures (grass stems, and flower and fruits) and total live phytomass (Table 6). No significant relationships were detected between ANPP and sward structure attributes in non-burnt plots. There was no significant relationship between ANPP on burnt plots and rainfall (Table 6, Fig. 1). In contrast, ANPP was more closely related to rainfall in non-burnt plots and it increased with rainfall and attained a peak during the short rain season, after which it declined abruptly in the mid-long rain season (Table 6, Fig. 1).

Fire and forage nutritional quality

Samples from burnt areas had higher concentration of all macronutrients for all plant parts except phosphorus in live stem, and calcium and magnesium in flower and fruit (Table 7) than samples from non-burnt areas. Despite sodium concentration in the grass samples from the burnt treatment being twice that from non-burn samples for all plant parts, differences were only significantly higher in live leaf and live stem (Table 7, Fig. 2), and nitrogen significantly higher only in live leaf (Table 7, Fig. 3). On the contrary, phosphoros and potassium concentrations were significantly lower in samples from non-burnt than burnt area only in dead material (Table 7, Fig. 4). Additionally, fire increased *in vitro* organic matter digestibility of live grass components, whereas there was a significant interaction effect of fire and sampling time on digestibility of standing dead grass material (Table 7). There was also a significant interaction between fire and sampling time in the concentration of acid detergent fibre in samples from both live and in standing dead grass material (Table 7).

Fire and consumption by ungulates

Most phytomass components on non-burnt plots (including where not significant) were larger than on burnt plots for all periods, but the ratios between live leaf and total phytomass were higher on burnt plots than on non-burnt plots (Table 8). The same was true for most months for the ratio between total live phytomass and total phytomass (Table 8). The ratio of live stem and of standing dead phytomass to total phytomass tended to be higher on the non-burnt than on the burnt plots (Table 8). In December and July total phytomass consumption was mainly on the burnt plots. In June consumption was approximately the same on both burnt and non-burnt plots, while in February only non-burnt plots were grazed (Table 9, Fig. 5).

Patch fire history and herbivore patch choice

For the years fire records were available, fire areas were distributed fairly evenly in the studied area in 2003-2004 as opposed to 2004-2005 when there was comparatively a higher proportion of burnt areas in the Grumeti Game Reserve than in the rest of the study area (Fig. 6a, b). Twenty-four different ungulate species were recorded during the four years of animal counts from May 2001 to April 2002, and from May 2003 to April 2006 but the number varied from 18 to 22 between years. Six of the species are classified as mainly browsers, ten as mainly grazers and eight as mixed feeders (Table 10). Bush and Red-flanked duiker (*Cephalophus rufilatus*, and *Sylvicapra grimmia*), gerenuk (*Litocranius walleri*), klipspringer (*Oreotragus oreotragus*), oribi (*Ourebia ourebi*), spring hare (*Pedetes capensis*) and rock hyrax (*Procavia capensis*) did not have any significant preference in any of the three different contrasts, and Bohar reedbuck (Redunca redunca), Defassa waterbuck (Kobus ellipsiprymnus defassa), eland and steenbok (Raphicerus campestris) only in one year in one of the contrasts.

Grazers, except African buffalo showed a trend to prefer patches burnt in the current year during 2003-2004 in agreement with the general notion that herbivores selectively graze on post-fire vegetation. To some extent, our study reinforces the current theory concerning ungulate body weight and the expected use of burnt and non-burnt patches stating that use of burnt areas is negatively related to ungulate body size. The preference by the smallest grazer, Thomson's gazelle, conforms to a previous notion that this species makes more utilization of areas with sward of low to intermediate biomass. There are some indications in our study in support of the hypothesis that medium-sized grazers would switch between burnt and non-burnt areas. Topi and Blue wildebeest had higher preference for burnt patches but the pattern was somewhat less clear than in the case of Thomson's gazelle, with larger confidence intervals of the selection ratios, and hartebeest, had no significant preference for either currently burnt or non-burnt patches. In contrast, Burchell's zebra had a higher likelihood of occurrence in burnt patches. The largest grazer, African buffalo, on the other hand, significantly preferred non-burnt areas. In contrast to grazers, browsers and mixed feeders showed a consistent tendency to occur more frequently in not burnt patches than in patches burnt in the current year. The findings also show that ungulates generally had lower preference for areas that burnt in the current year but that had burnt repeatedly in a 3-year period compared to areas that had not burnt in the previous 3 years, which highlights that the fire history can be an important determinant of forage patch choice and can also explain part of the variability found in the preference for currently burnt areas.

Discussion

Increased ANPP in the dry season, July-September on burnt areas in western Serengeti (Paper I) ascertains that fire triggers sprouting (Vesey-FitzGerald, 1971; Norton-Griffiths, 1979, Briggs & Knapp, 2001). Moreover, significantly higher ratios between live leaf and total phytomass or total standing phytomass, and between total live biomass and total phytomass or total standing phytomass on burnt than on non-burnt grasslands (Paper I; Paper III) ascertains that fire influences the composition of sward compartments (O'Reagain & Owen-Smith, 1996). The finding that the proportion of photosynthesizing biomass, primarily leaf biomass determines ANPP in the burnt areas but not in the non-burnt areas demonstrate that fire shifts the relative importance of the factors that control ANPP. Thus, it may affect fundamental processes in the ecosystem (Williams *et al.*, 2004; Dai *et al.*, 2006; Govander, Trollope & Van Wilgen, 2006). In that way fire increases the spatial and temporal differences in supply and quality of plant material at landscape level (Vermeire *et al.*, 2004, Paper I, II & III). The small amount of biomass in burnt areas maintained for longer periods by increased grazing pressure governs under natural conditions the fuel availability and hence the spatial distribution of fires (McNaughton 1992; Dublin, Sinclair & Mcglade, 1990). To what extent the managed fire regime interferes with this pattern is not known. The positive effect of fire on primary production is crucial since biomass and net primary production are essential to ecosystem performance and function (Bourlier & Hadley, 1970), and primary production determines the energy available for other trophic levels. However, persistently low total phytomass on burnt grasslands one year after fire (Paper I & III) ascertains the negative impact of fire on aboveground phytomass. A previous study in western Serengeti reported drastic reduction in aboveground phytomass of the herbaceous vegetation (Rusch *et al.*, 2005). Low total phytomass due to fire and significant reduction in live phytomass (photosynthetic biomass) on burnt areas following consumption by large herbivores in the month October-December (Paper III) probably explains the decline in ANPP recorded on burnt grassland after December (Paper

I). The amount of photosynthesizing biomass did not fully explain the changes in ANPP in burnt plots, and it is plausible that the large increment in biomass in early post-fire stages despite the small amount of biomass depended on below-ground stored reserves (Briske & Richards 1995). Intense grazing maintaining a dependency on stored reserves may reduce this capacity of plants by depleting the store of carbohydrate reserves (McPherson & Williams, 1998). Repeated defoliation may also reduce the bud bank (Briske & Richards, 1995) thus posing limitation to re-growth (Richards & Caldwell, 1985). There is indication from other savanna ecosystems that herbivory on burnt areas can prolong the period of recovery from fire effect (Pratt, 1967; Letnic 2004). Severe reduction of photosynthetic biomass on burnt grassland hence a prolonged period of recovery is expected in Serengeti where grazing is a major shaping force of ecosystem function and structure (McNaughton, 1979; 1985; 1993) given the high abundance of grazers.

The fire mediated sward structure is characterized by increased ratios of live leaf and total live (Paper I & III) parallel with enhanced N concentration (Prins & Beekman, 1989; Van de Vijver *et al.,* 1999; Paper II). Factors such as reduced shading and raised soil temperature (Rice & Parenti, 1978; Knapp & Seastedt, 1986), enhanced rate of mineralization of soil organic material, return of soil nutrients by ash (Khanna & Raison, 1986; Kutiel & Shaviv, 1993; Thomas, Walsh & Shakesby, 1999), and a reduction of competition for nutrients as a result of the small biomass may explain the relatively high nutrient concentration in samples from the first growing season following fire. Another reason is the high proportion of young tissue and particularly of leaf. The sustained effect found in our study may have its origin in repeated grazing maintaining for a prolonged period a predominance of young photosynthesizing biomass. Some minerals, e. g., Na, may also be maintained at a high level by rapid recycling by the foraging animals (Georgiadis & McNaughton, 1990). We found higher nutrient concentration in standing dead material in samples from burnt compared to that in samples from non-burnt areas, which to our knowledge has not previously been reported. This means that translocation of nutrients to storage before wilting is weak, which might be related to high nutrient availability in the environment (Millard & Proe, 1991). Also, standing dead phytomass in burnt vegetation is younger and less leached than such in non-burnt vegetation. However, we have no conclusive explanation for the results observed.

We found significantly greater consumption on burnt than non-burnt vegetation in December and June-July despite significantly lower total phytomass (Paper III). This may explain the evidence that ungulates tend to aggregate on burnt grassland in preference to non-burnt (Rowe-Rowe, 1982; Moe *et al.,* 1990; Wilsey, 1996; Tormo & Owen-Smith, 2002). The high consumption in burnt patches was related to fire enhanced ratios of live leaf and total live/total phytomass (Paper III), live leaf and total live/total standing phytomass and live leaf/total live (Paper I), increased N and *in vitro* organic matter together with reduced acid detergent fiber (Paper II). In contrast, higher consumption on non-burnt grassland than on burnt grassland in February is related to forage quantity, i.e. significantly higher total phytomass and phytomass of most structural components (Paper III), total live biomass, total aboveground phytomass and total standing phytomass (Paper I). The findings support the prediction that herbivores would shift the preference between burnt and non-burnt patches along with the development of quality and quantity of the forage (Paper I; Paper III), which is in line with the former hypothesis that both quantity and quality of the phytomass dictates patch selection (Canon, Urness & Debyle, 1987; Van der Wal *et al*., 2000; Bergman *et al,*. 2001). Use of burnt and non-burnt areas during different periods of the year signifies the importance of maintaining mosaics of burnt and non-burnt areas to meet forage requirements of ungulates (Paper III).

It appears that the pattern of forage consumption found in the Western Corridor of Serengeti National Park represents the pattern of use of the area by migrant herds (Paper III). Consumption detected in December corresponds with the time migration moves southwards to the wet season range in the South-East Plains with some groups passing through the area (Pennycuick, 1975, Thirgood *et al.,* 2004). On the other hand, consumption in June-July relates to the time migration moves northwards to the dry season refuge areas (Pennycuick, 1975;

Musiega & Kazadi, 2004). Significantly higher probability of occurrence of all species combined, grazer diet group and the migratory grazers, topi, Thomson's gazelle, Blue wildebeest and Burchell's zebra on patches burnt in the current year than on non-burnt in the current year in 2003-2004 reinforces our notion about the relationship between temporal patterns of consumption and use of the Western Corridor by migrants (Paper III & IV). It also reinforces the view about strong relationships between animal movements and distribution in the Serengeti National Park (McNaughton 1990; Seagle & McNaughton, 1992; Paper III) and forage nutrient concentration and digestibility on burnt grasslands (Paper II) due to the functional role of different nutrients (McNaughton, 1988; 1990).

The most consistent pattern in the data on animal patch use in relation to fire history is the low probability of finding animals on repeatedly burnt patches compared to such burnt the current year only or not burnt at all in the last three years. To explain this pattern is beyond the scope of this study. However, volatilization of nutrients, primarily N, in the fires and the following heavy grazing may result in grass in frequently burn patches having relatively low nutrient concentration and relatively low biomass, thus scoring low in both trade-off criteria (high nutrient concentration vs. large biomass). The patches not burnt during the last three years likely have large grass biomass but of low quality, whereas the recently burnt patches, as discussed above, have small quantities of high nutritive quality. Our results for the different species and diet groups largely agreed with what we expected out from the "Jarman–Bell hypothesis", stating that the larger-bodied herbivores (and hind-gut fermenters) should select for large biomass whereas small bodied animals (and fore-gut fermenters) should select for high nutritive quality (Bell, 1971; Jarman, 1974; Demment & van Soest, 1985; Stokke & du Toit, 2000). Grazers and particularly the small grazers feed selectively on nutrient and energy-rich sparse food (Bell, 1971) to meet the high metabolic demands of a small body (Wilsey, 1996). Consequently, the urge for energy maximization refutes the previous notion that small grazers occupy areas of short swards as anti-predatory behaviour (Paper IV).

Variables enhanced by fire (Paper I, II & III), significantly higher consumption on burnt grassland in December, June-July (Paper III) and selection of patches irrespective of fire history (Paper IV) emphasize the relevance of early burns in maintenance of healthy animal populations as well as conservation and maintenance of grasslands in the Serengeti ecosystem. On the contrary, the variables suppressed on burnt grassland (Paper I & III) together with avoidance of repeatedly burnt patches by ungulates (Paper IV) are indicative of the detrimental effect of current fire regime, annual burns.

Conclusion

This study has provided sufficient light on the interrelationship between fire, forage and herbivores' responses to the fire mediated resources at temporal and spatial levels in the landscape. The study has demonstrated fulfilment of the desire of fire management program under the Serengeti Ecological Monitoring Program Department to supply nutritious forage to herbivores during dry season when the Western Corridor is under high use intensity by both migratory and resident populations. Parallel to that, the study has demonstrated presence of lower phytomass on burnt than on non-burnt grasslands, and slow recovery of sward on burnt grasslands as a result of annual burns, and likely due to the interactive effect of fire and grazing. Both lessons are supposed to be motive and challenge, respectively, towards reaching a fire regime suitable to the ecosystem. Equally important, this study has shed new light on quantitative use of burnt and non-burnt grasslands and has shown the response of herbivores in the selection of patches differing in fire history. On the whole, this thesis is summarized under five mega conclusions:

1. Fire changes the structure of sward, result which leads to support the expectation that herbivores could shift the preference between burnt and non-burnt patches along with the development of the sward.
2. Forage for grazers on burnt areas is of relatively higher quality than on non-burnt areas. Also the relationship between amount and quality varies along the post-fire season, and consumption shifts when the balance between amount and quality changed.
3. Early burns enhance plant sprouting during the dry season, July - September, hence higher forage supply and quality on burnt than on non-burnt patches during the dry season. Burnt areas in the Western Corridor of the Serengeti National Park appear to be largely utilised at the end of the dry period/start of the short rains (December) and after one year after the burning (July). The problem to ungulates of protein limitation

in dry season is probably to some extent alleviated through supply of the fire mediated forage.

4. Annual burns reduce total phytomass, a factor that limits large and hind-gut fermenters. Slow recovery of phytomass structure as a result of annual burns may be a draw back to animal health and reproductive success in large and hid-gut fermenters through insufficient forage available and produced. Volatilizations of N and poor browse quality may be another bottleneck to animal health and reproductive success. An alternative fire return interval that merits the ecosystem processes and functions is important. The existing knowledge about recovery period for sward on burnt areas could be a starting point while further researches continue to establish precisely the optimal interval.
5. Fire patch history influences forage patch choice in the Serengeti ungulates through spatial and temporal heterogeneity of the landscape regarding supply and quality of food for large herbivores.

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Table 1: Fire season, total fire area for the season, area of the May-August months of the fire season and percent area of May-August fires in the season in the Serengeti ecosystem.

Fire season	Total fire area for the season (sq. km)	Area covered by the May-August fires per fire season (sq. km)	Percent area of the May-August fires per season
May 2000 - April 2001	2663.7	2510.9	94.3
May 2001 - April 2002	6033.0	5184.1	85.9
May 2002 - April 2003	8841.1	6741.7	76.3
May 2003 - April 2004	6610.3	6190.2	93.6
May 2004 - April 2005	6351.8	6123.9	96.4
May 2005 - April 2006	3821.3	3513.1	91.9
May 2006 - Dec 2006	3316.4	3205.8	96.7

Table 2: Mean values of total above ground mass (including litter), and phytomass compartments: leaf, live stem, flower and fruit, total live, standing dead, and litter in fenced samples in burnt and non-burnt plots in Western Corridor grasslands, Serengeti National Park from September 2003 to July 2004.

Sampling time	Treatment	Total above ground mass	Total standing phytomass	Leaf phytomass	Live stem phytomass	Flower/ fruit phytomass	Total live phytomass	Standing dead phytomass	Litter
Sep	Burnt	71.7**	69.5**	32.0**	13.8*	-	45.8**	23.7**	2.2**
	Non-Burnt	201.7	188.3	38.2	62.9	-	101.1	87.2	13.4
Oct	Burnt	73.1**	65.4**	35.2**	4.8**	-	40.0**	25.4**	7.7**
	Non-burnt	210.1	189.3	63.4	39.8	-	103.2	86.1	20.8
Dec	Burnt	227.0	220.0	115.2	40.2	2.6	158.0	62.0**	7.0**
	Non-burnt	290.7	266.8	100.0	46.8	4.7	151.5	115.3	23.9
Feb	Burnt	145.0**	137.2**	74.3*	22.0**	0.7**	97.0**	40.2**	7.8**
	Non-burnt	373.6	341.9	110.3	64.2	3.9	178.4	163.5	31.7
Mar	Burnt	167.5**	161.0**	55.2	27.4*	0.3*	82.9*	78.1**	6.5**
	Non-burnt	340.9	316.4	61.3	53.2	1.3	115.8	200.6	24.5
May	Burnt	183.4**	173.8**	77.9	39.9*	5.1	122.9	50.9**	9.6**
	Non-burnt	363.3	324.6	89.7	57.7	5.4	152.8	171.8	38.7
Jun	Burnt	222.3	207.3	73.5	44.0	0.4*	117.9	89.4*	15.0**
	Non-burnt	323.9	296.7	63.2	65.2	0.0	128.4	168.3	27.2
Jul	Burnt	120.2**	110.0**	10.7	17.8	3.3	31.8	78.2**	10.2*
	Non-burnt	308.0	273.4	18.8	30.8	4.6	54.2	219.2	34.6

* Difference between burnt and non-burnt plots in plant mass statistically significant at $P < 0.05$; ** $P \leq 0.001$

Table 3: Mean ratios of phytomass compartments in fenced samples on burnt and non-burnt plots in six sites in the Western Corridor, Serengeti National Park, from September 2003 to July 2004. Total standing phytomass: leaf, live stem and standing dead material. Total mass: Total standing phytomass and litter.

Sampling time	Treatment	Leaf/total standing phytomass	Live stem/total standing phytomass	Total live/total standing phytomass	Standing dead/total above ground mass	Litter/ total above ground mass
Sep	Burnt	0.460	0.199*	0.659	0.331	0.031
	Non-burnt	0.203	0.334	0.537	0.432	0.066
Oct	Burnt	0.538*	0.073*	0.612	0.347*	0.105
	Non-burnt	0.335	0.210	0.545	0.410	0.099
Dec	Burnt	0.524*	0.183	0.718*	0.273**	0.031
	Non-burnt	0.375	0.175	0.568	0.397	0.082
Feb	Burnt	0.542**	0.160	0.707*	0.277**	0.054*
	Non-burnt	0.323	0.188	0.522	0.438	0.085
Mar	Burnt	0.343	0.170	0.515	0.466**	0.039
	Non-burnt	0.194	0.168	0.366	0.588	0.072
May	Burnt	0.448	0.230	0.707	0.278**	0.052*
	Non-burnt	0.276	0.178	0.471	0.473	0.107
Jun	Burnt	0.355	0.212	0.569*	0.402**	0.067*
	Non-burnt	0.213	0.220	0.433	0.520	0.084
Jul	Burnt	0.097	0.162	0.289	0.651	0.085
	Non-burnt	0.069	0.113	0.198	0.712	0.112

* Difference between burnt and non-burnt plots in biomass ratio statistically significant at $p < 0.05$; **$P \leq 0.001$.

Table 4: Mean ratios of live phytomass compartments in fenced samples on burnt and non-burnt plots in six sites in the Western Corridor, Serengeti National Park, from September 2003 to July 2004.

Sampling time	Treatment	Leaf / total live phytomass	Live stem/total live phytomass	Flower-fruit/total live phytomass	Live stem + flower-fruit/total live phytomass
Sep	Burnt	0.699	0.301**	-	0.301*
	Non-burnt	0.378	0.622	-	0.622
Oct	Burnt	0.880**	0.120**	-	0.120**
	Non-burnt	0.614	0.386	-	0.386
Dec	Burnt	0.729	0.254	0.016	0.271*
	Non-burnt	0.660	0.309	0.031	0.340
Feb	Burnt	0.766**	0.227*	0.007	0.234*
	Non-burnt	0.618	0.360	0.022	0.382
Mar	Burnt	0.666	0.331	0.004	0.334
	Non-burnt	0.529	0.459	0.011	0.471
May	Burnt	0.634	0.325*	0.041	0.366*
	Non-burnt	0.587	0.378	0.035	0.413
Jun	Burnt	0.623	0.373	0.003	0.377
	Non-burnt	0.492	0.508	0.000	0.508
Jul	Burnt	0.336	0.560	0.104	0.664
	Non-burnt	0.347	0.568	0.085	0.653

* Difference between burnt and non-burnt plots in biomass ratio statistically significant at $P < 0.05$; ** at $P \leq 0.001$

Table 5: ANOVA model factors, F statistics and P values for total live phytomass, standing dead, litter and total above-ground mass. 'Phytomass change': samples at T_n vs. T_{n+1}, 'Fire': samples on burnt vs. non-burnt plots and 'Sites': samples at 6 sites. Phytomass difference: Difference (standardised per day) between mean T_n vs. T_{n+1} on burnt and non-burnt grasslands. ANPP: mean daily aboveground net primary production (g $m^{-2}day^{-1}$) on burnt and non-burnt grasslands from July 2003 to July 2004, in six sites in the Western Corridor, Serengeti National Park.

Factor	**Total live phytomass**		**Standing dead phytomass**		**Litter**		**Total above-ground mass**		**BURNT**		**NON-BURNT**	
	F	P	F	P	F	P	F	P	**Phytomass difference ($gm^{-2}day^{-1}$)**	**Daily ANPP ($gm^{-2}day^{-1}$)**	**Phytomass difference ($gm^{-2}day^{-1}$)**	**Daily ANPP ($gm^{-2}day^{-1}$)**
Jul – Sep												
Phytomass change	2.309	0.131	0.85	0.59	2.61	0.11	3.01	0.085	0.84	0.84	-0.97	0
Fire	50.51	0.0001	84.98	0.0001	54.09	0.0001	113.45	0.0001				
Site	2.42	0.18	12.53	0.007	8.58	0.17	26.28	0.001				
Fire x phytomass change	1.23	0.27	3.39	0.068	0.01	0.924	4.29	0.04				
Site x phytomass change	4.43	0.001	1.025	0.406	4.62	0.033	0.82	0.086				
Sep - Oct												
Phytomass change	4.6	0.034	0.05	0.821	6.62	0.011	1.32	0.252	1.13	1.13	0.83	0.83
Fire	93.75	0.0001	92.08	0.0001	5.64	0.019	113.73	0.0001				
Site	6.78	0.0001	4.79	0.055	0.83	0.58	19.26	0.003				
Fire x phytomass change	5.05	0.026	0.854	0.357	8.99	0.003	0.92	0.339				
Site x phytomass change	1.87	0.1	2	0.083	7.19	0.066	0.51	0.772				
Oct - Dec												
Phytomass change	0.98	0.324	1.57	0.21	16.8	0.0001	0.46	0.497	2.45	2.45	0.68	0.68
Fire	5.17	0.025	34.11	0.0001	92.33	0.0001	26.08	0.0001				
Site	4.51	0.062	3.03	0.125	12.37	0.008	6.02	0.035				
Fire x phytomass change	7.21	0.008	0.55	0.46	12.75	0.001	7.19	0.008				
Site x phytomass change	0.98	4.33	2	0.08	1.68	0.144	1.15	0.339				

Dec - Feb												
Phytomass change	5.64	0.019	3	0.085	10.52	0.002	6.31	0.013	0.81	0.81	3.61	3.61
Fire	18.75	0.0001	58.98	0.0001	124.69	0.0001	58.05	0.0001				
Site	1.96	0.24	5.81	0.38	7.69	0.021	2.8	0.141				
Fire x phytomass change	3.41	0.067	0.54	0.465	3.54	0.021	2.85	0.094				
Site x phytomass change	0.94	0.46	0.65	0.507	2.49	0.035	1.22	0.3				
Feb - Mar												
Phytomass change	0.13	0.715	1.91	0.169	0	0.999	1.05	0.308	0.74	0.74	2.6	2.6
Fire	3.982	0.048	25.41	0.0001	28.88	0.0001	19.59	0.0001				
Site	1.89	0.25	3.922	0.08	6.76	0.028	1.74	0.279				
Fire x phytomass change	0.121	0.729	4.92	0.028	0.07	0.795	2.17	0.144				
Site x phytomass change	2.04	0.08	0.287	0.919	0.81	0.548	1.09	0.369				
Mar - May												
Phytomass change	4.65	0.033	1.59	0.209	0.77	0.383	3.87	0.05	0.68	0.68	0.34	0.34
Fire	7.704	0.006	30.55	0.0001	63.97	0.0001	24.12	0.0001				
Site	3.633	0.092	1.235	0.411	9.04	0.015	2.97	0.128				
Fire x phytomass change	8.677	0.004	0.064	0.801	0.03	0.864	2.01	0.159				
Site x phytomass change	1.2	0.084	1.277	0.278		1.25	1.01	0.414				
May - Jun												
Phytomass change	4.533	0.035	8.24	0.005	24.12	0.0001	10.73	0.001	1.25	1.25	0.17	0.17
Fire	0.002	0.968	13.12	0.0001	26.88	0.0001	5.17	0.025				
Site	0.658	0.671	0.84	0.576	3.4	0.103	0.84	0.57				
Fire x phytomass change	4.31	0.04	3.68	0.057	16.314	0.0001	6.65	0.011				
Site x phytomass change	2.76	0.021	4.12	0.002	5.48	0.0001	4.53	0.001				
Jun - Jul												
Phytomass change	0.19	0.66	14.61	0.0001	18.7	0.0001	8.74	0.004	-1.22	0	2.31	2.31
Fire	1.86	0.176	0.59	0.446	1.61	0.208	1.523	0.22				
Site	1.33	0.38	0.482	0.779	0.95	0.523	0.44	0.803				
Fire x phytomass change	0.82	0.368	0.104	0.747	13.96	0.0001	0.085	0.771				
Site x phytomass change	1.11	0.36	7.72	0.0001	4.2	0.002	4.94	0.0001				

Table 6: Pearson correlation (r) and P values between sward structural attributes in fenced samples (as in Tables 2, 3 and 4) and rainfall (as in Table 1) on daily above-ground net primary production (as in Table 5) in burnt and non-burnt grasslands for the period September 2003 to July 2004.

Net primary production	Structural attributes	Burnt		Non-burnt	
		r	P	r	P
ANPP	Leaf phytomass	0.787**	0.010	0.155	0.357
	Live phytomass	0.696*	0.028	0.095	0.411
	Standing dead phytomass	-0.041	0.461	0.550	0.079
	Leaf/Total standing phytomass	0.626*	0.048	-0.170	0.344
	Live / Total standing phytomass	0.614	0.053	-0.370	0.183
	Stem-Flower-Fruit/Live phytomass	-0.552	0.078	-0.074	0.863
	Leaf / Live phytomass	0.517	0.095	0.078	0.427
	Rainfall	0.087	0.419	0.486	0.111

*Pearson correlation significant at P <0.05; ** P <0.01.

Table 7: Concentration of N, K, P, Mg, Ca and Na, and ADF and INVOMD in percent of dry weight of grasses in burnt and non-burnt grassland patches. Values higher in non-burnt area are boldfaced.

Element	Plant component	Treatment				Fire * sampling time interaction
		Burnt	Non-burnt	SE[b]	P value	P value
N	Live leaf	1.76	1.36	0.04	<0.001**	0.983
K		2.29	2.07	0.09	0.209	0.375
P		0.35	0.31	0.02	0.071	0.820
Mg		0.19	0.18	0.01	0.261	0.514
Ca		0.35	0.32	0.01	0.596	<0.001**
Na		0.46	0.25	0.03	0.003*	0.551
N	Live stem	0.75	0.69	0.06	0.632	0.001**
K		1.04	0.94	0.04	0.732	<0.001**
P		0.15	0.15	0.01	0.978	0.207
Mg		0.08	0.06	0.01	0.190	0.370
Ca		0.13	0.08	0.02	0.054	0.780
Na		0.22	0.10	0.01	0.010*	0.003*
N	Flower & Fruit	1.47	0.99	0.13	0.169	0.239
K		1.09	0.94	0.12	0.406	0.612
P		0.23	0.21	0.02	0.630	0.507
Mg		0.11	**0.14**	0.01	0.131	0.573
Ca		0.13	**0.21**	0.01	0.168	0.031*
Na		0.09	0.04	0.02	0.355	0.102
N	Standing dead	0.76	0.59	0.03	0.111	0.006*
K		0.68	0.42	0.04	0.040*	0.024*
P		0.15	0.11	0.01	0.002*	0.905
Mg		0.13	0.11	0.01	0.148	0.116
Ca		0.43	0.35	0.02	0.353	<0.001**
Na		0.22	0.10	0.01	0.010*	0.081
ADF	Live leaf	37.19 (± 0.36)	40.73 (± 0 37)		0.309	<0.001**
INVOMD		56.60 (± 1.52)	46.83 (± 1.55)		0.003*	0.745
ADF	Live stem	47.01 (± 0.59)	51.56 (± 0.59)		0.256	<0.001**
INVOMD		41.47 (± 1.23)	30.45 (± 1.21)		0.014*	0.061
ADF	Standing dead	49.18 (± 0.55)	55.00 (± 0.55)		0.107	<0.001**
INVOMD		36.94 (± 1.10)	30.02 (± 1.10)		0.083	0.009*

* Significant at the 0.05 level; ** significant at P ≤ 0.001 (Univariate ANOVAs); ± SE = standard error.

[b] Applies to both treatments.

Table 8: Effects of fire on total phytomass, on the four phytomass components (i.e.live leaf, live stem, flower/fruits and standing dead), on the interaction between fire and site, and on weight ratios (i.e. live leaf/total phytomass, live stem/total phytomass, standing dead/total phytomass, and live phytomass/total phytomass) during eight periods, September 2003-July 2004 (as in Table 1) in the Western Corridor, Serengeti National Park.

Period	Phytomass	Phytomass (g/m^2)		Fire	Fire*Site interaction	Phytomass ratio	Phytomass (g/m^2)		Fire	Fire*site interaction
		Burrnt plots	Non-burnt plots	P value	P value		Burnt plots	Non-burnt plots	P value	P value
September	Total	32.2	175.4	0.007*	0.367	Leaf/Total	0.469	0.192	0.034*	< 0.001**
	Live leaf	15.1	33.6	0.125	0.533	Stem/Total	0.022	0.329	0.007*	0.028*
	Live stem	0.7	57.7	0.022*	0.093*	Stand.d/Total	0.509	0.479	0.551	< 0.001**
	Flower/Fruit					Live/Total	0.491	0.521	0.185	< 0.001**
	Stand.d	16.4	84.133	0.022*	0.347					
October	Total	71.3	201.9	0.007*	0.388	Leaf/Total	0.338	0..248	0.074*	0.121
	Live leaf	24.1	50.0	0.078*	0.088*	Stem/Total	0.098	0.178	0.132	0.073*
	Live stem	7.0	35.9	0.005*	0.685	Stand.d/Total	0.564	0.575	0.210	0.214
	Flower/Fruit					Live/Total	0.436	0.425	0.079*	0.489
	Stand.d	40.2	116.0	0.012*	0.244					
December	Total	109.0	218.5	0.090*	0.267	Leaf/Total	0.534	0..317	0.015*	0.025*
	Live leaf	58.2	69.2	0.887	0.088*	Stem/Total	0.132	0.149	0.550	0.027*
	Live stem	14.4	32.6	0.237	0.421	Stand.d/Total	0.332	0.531	0.006*	0.058*
	Flower/Fruit	0.2	0.7	0.541	0.464	Live/Total	0.668	0.469	0.008*	0.020*
	Stand.d	36.2	116.0	0.012*	0.248					
February	Total	139.2	232.5	0.009*	0.094*	Leaf/Total	0.490	0.382	0.186	0.092*
	Live leaf	68.2	88.8	0.037*	0.150	Stem/Total	0.172	0.182	0.816	0.062*
	Live stem	24.0	42.2	0.062*	0.006*	Stand.d/Total	0.328	0.427	0.268	0.012*
	Flower/Fruit	1.3	2.3	0.144	0.022*	Live/Total	0.672	0.573	0.189	0.007*
	Stand.d	45.7	99.2	0.009*	0.206					
March	Total	137.0	322.2	0.010*	0.487	Leaf/Total	0.318	0.231	0.462	< 0.001**
	Live leaf	43.5	74.4	0.035*	0.794	Stem/Total	0.130	0.200	0.247	0.127
	Live stem	17.8	64.6	0.083*	0.166	Stand.d/Total	0.552	0.564	0.982	0.012*
	Flower/Fruit	0.1	1.6	0.081*	0.167	Live/Total	0.448	0.436	0.920	0.004*
	Stand.d	75.6	181.6	0.011*	0.401					
May	Total	177.8	301.3	0.071*	0.049*	Leaf/Total	0.404	0.305	0.077*	0.072*
	Live leaf	71.9	91.8	0.182	0.492	Stem/Total	0.204	0.154	0.578	0.024*
	Live stem	36.3	46.4	0.385	0.015*	Stand.d/Total	0.360	0.521	<0.001**	0.964
	Flower/Fruit	5.6	6.0	0.892	< 0.001**	Live/Total	0.640	0.479	0.001*	0.904
	Stand. d	64.0	157.1	0.027*	0.035*					
June	Total	139.5	198.7	0.506	0.081*	Leaf/Total	0.219	0.136	0.025*	0.983
	Live leaf	30.5	27.0	0.777	0.275	Stem/Total	0.193	0.230	0.672	0.002*
	Live stem	26.9	45.7	0.595	0.053*	Stand.d/Total	0.588	0.634	0.989	0.007*
	Flower/Fruit	0.1	0.1	0.103	0.558	Live/Total	0.412	0.366	0.843	0.003*
	Stand.d	82.0	125.9	0.365	0.121					
July	Total	57.1	253.0	0.483	0.039*	Leaf/Total	0.046	0.024	0.707	0.276
	Live leaf	2.6	6.1	0.469	0.693	Stem/Total	0.103	0.215	0.660	0.082*
	Live stem	5.9	54.3	0.599	0.143	Stand.d/Total	0.851	0.761	0.845	0.014*
	Flower/Fruit	0.0	0.0	0.500	0.500	Live/Total	0.149	0.239	0.726	0.053*
	Stand.d	63.4	205.9	0.495	0.092*					

*Significant at P < 0.1, ** P < 0.001.

Table 9: Total phytomass and phytomass components in caged and open samples in burnt and non-burnt plots in the Western Corridor, Serengeti National Park, during eight periods, September 2003-July 2004 (as in Table 1). Consumption in each period is based on significant differences in phytomass between caged and open samples. Interaction between fire* grazing and between fire*grazing * site are shown.

Period	Phytomass	Burnt plots, (g/m^2)				Non-burnt plots, (g/m^2)				Fire*Grazing interaction P value	Fire*Grazing* Site interaction P value
		Caged samples (I)	Open samples (J)	Consumption (I-J)	P value	Caged samples (I)	Open samples (J)	Consumption (I-J)	P value		
Sept.	Total	69.5	32.2	37.3	0.238	188.2	175.4	12.8	0.767	0.650	0.244
	Live leaf	32.0	15.1	16.9	0.278	38.2	33.6	4.6	0.351	0.420	< 0.001**
	Live stem	13.8	0.7	13.1	0.304	62.9	57.7	5.2	0.727	0.661	0.771
	Flow./Fruit										
	Stand.d	23.7	16.4	7.3	0.499	87.2	84.1	3.1	0.912	0.903	0.076*
Oct.	Total	65.5	71.3	-5.8	0.692	189.3	201.9	-12.6	0.813	0.898	0.101
	Live leaf	35.2	24.1	11.1	0.110	63.4	50.0	13.4	0.416	0.868	0.116
	Live stem	4.8	7.0	-2.2	0.422	39.8	35.9	3.9	0.802	0.726	0.268
	Flow./Fruit										
	Stand.d	25.4	40.2	-14.8	0.170	86.1	116.0	-29.9	0.326	0.580	0.120
Dec.	Total	220.0	109.0	**110.9**	0.055*	266.9	218.5	48.4	0.223	0.310	0.352
	Live leaf	115.2	58.2	**57.0**	0.009*	100.0	69.2	**30.8**	0.040*	0.125	0.596
	Live stem	40.2	14.4	**25.7**	0.072*	46.8	32.6	14.2	0.220	0.525	0.171
	Flow./Fruit	2.6	0.2	**2.4**	0.013*	4.7	0.7	4.0	0.322	0.672	0.250
	Stand.d	62.0	36.2	25.8	0.259	115.3	116.0	-0.7	0.965	0.334	0.550
Feb.	Total	137.2	139.2	-2.0	0.911	341.9	232.5	**109.4**	0.043*	0.032*	0.656
	Live leaf	74.3	68.2	6.1	0.476	110.3	88.8	**21.5**	0.043*	0.261	0.550
	Live stem	22.0	24.0	-2.0	0.709	64.2	42.2	**22.0**	0.014*	0.016*	0.960
	Flow./Fruit	0.7	1.3	-0.6	0.170	3.9	2.3	1.6	0.134	0.056*	0.891
	Stand.d	40.2	45.7	-5.5	0.417	163.5	99.2	**64.4**	0.091*	0.062*	0.308
March	Total	160.9	137.0	23.9	0.391	316.4	322.2	-5.8	0.932	0.733	0.077*
	Live leaf	55.2	43.5	11.7	0.269	61.3	74.4	-13.1	0.338	0.252	0.015*
	Live stem	27.4	17.8	9.6	0.308	53.2	64.6	-11.4	0.619	0.367	0.304
	Flow./Fruit	0.3	0.1	0.2	0.363	1.3	1.6	-0.3	0.686	0.563	0.585
	Stand.d	78.1	75.6	2.5	0.811	200.6	181.6	19.0	0.675	0.765	0.065*
May	Total	173.8	177.8	-4.0	0.838	324.7	301.3	23.4	0.667	0.628	0.257
	Live leaf	77.9	71.9	6.0	0.735	89.7	91.8	-2.1	0.869	0.708	0.159
	Live stem	39.9	36.3	3.6	0.562	57.7	46.4	11.3	0.456	0.470	0.754
	Flow./Fruit	5.1	5.6	-0.5	0.250	5.4	6.0	-0.6	0.495	0.809	0.998
	Stand.d	50.9	64.0	**-13.1**	0.074*	171.8	157.1	14.7	0.644	0.368	0.270
June	Total	207.3	139.5	67.8	0.140	296.6	198.7	97.9	0.249	0.324	0.213
	Live leaf	73.5	30.5	**43.0**	0.080*	63.2	27.0	**36.2**	0.029*	0.931	0.056*
	Live stem	44.0	26.9	**17.1**	0.018*	65.2	45.7	19.5	0.400	0.462	0.449
	Flow./Fruit	0.4	0.1	0.3	0.109	0.0	0.1	-0.1	0.374	0.066*	0.629
	Stand.d	89.4	82.0	7.4	0.686	168.3	125.9	42.4	0.409	0.269	0.096*
July	Total	109.9	57.1	**52.8**	< 0.001**	273.4	253.0	20.4	0.853	0.204	0.795
	Live leaf	10.7	2.6	**8.1**	0.003*	18.8	6.1	12.7	0.471	0.667	< 0.001**
	Live stem	17.8	5.9	**11.9**	0.001**	30.8	54.3	-23.5	0.613	0.600	0.848
	Flow./Fruit	3.3	0.0	3.3	0.374	4.6	0.0	4.6	0.423	0.500	0.874
	Stand.d	78.2	48.6	**29.6**	0.022*	219.2	192.6	26.6	0.709	0.502	0.411
Sign. Total				**223.8**				**176.4**			
Sign. Living				**165.2**				**110.5**			
All eight periods	Total									0.950	< 0.001**
	Live phyt.									0.274	< 0.001**

*significant at $P < 0.1$; ** at $P \leq 0.001$

Table 10: The twenty-four mammalian herbivores recorded during animal counts in Serengeti NP and its surroundings along nine transects during four years, May 2001-April 2002, May 2003-April 2004, May 2004-April 2005, May 2005-April 2006. Diet groups: B = browser, G = grazer and MF = mixed feeder. Animal counts: O = observed during the respective year, NO = not observed during the respective year.

Scientific name	**English name**	**Diet group**	**Investigated periods**			
			May 2001-April 2002	**May 2003-April 2003**	**May 2004-April 2005**	**May 2005-April 2006**
Aepyceros melampus	Impala	MF	O	O	O	O
Alcelaphus buselaphus	Coke's hartebeest,	G	O	O	O	O
Cephalophus rufilatus	Red-flanked duiker,	B	NO	NO	O	O
Connochaetes taurinus	Blue wildebeest	G	O	O	O	O
Damaliscus lunatus korrigum	Topi	G	O	O	O	O
Equus burchelli	Burchell’s zebra	G	O	O	O	O
Gazella granti	Grant’s gazelle	MF	O	O	O	O
Gazella thomsoni	Thomson’s gazelle	G	O	O	O	O
Giraffa camelopardalis	Giraffe	B	O	O	O	O
Kobus ellipsiprymnus defassa	Defassa waterbuck	MF	O	O	O	O
Litocranius walleri	Gerenuk	B	NO	NO	O	NO
Loxodonta africana	African elephant	MF	O	O	O	O
Madoqua kirkii	Kirk's dik-dik	B	O	O	O	O
Oreotragus oreotragus	Klippspringer	B	O	O	O	O
Ourebia ourebi	Oribi	G	NO	O	NO	NO
Pedetes capensis	Spring hare	G	O	O	O	NO
Phacochoerus aethiopicus	Warthog	G	O	O	O	O
Procavia capensis	Rock hyrax	MF	O	O	O	NO
Rahicerus campestris	Steenbok	MF	NO	O	NO	NO
Redunca redunca	Bohor reedbuck	G	O	O	O	O
Sylvicapra grimmia	Common duiker,	B	NO	O	O	O
Syncerus caffer	African buffalo	G	O	O	O	O
Taurotragus oryx	Eland	MF	NO	O	O	O
Tragelaphus scriptus	Bushbuck	MF	O	NO	O	O
Total (all species)			**18**	**21**	**22**	**19**

Figure legends

Figure 1: Above ground daily net primary production (ANPP) and precipitation on burnt and non-burnt grasslands from July 2003 to July 2004 in six sites in the Western Corridor, Serengeti National Park.

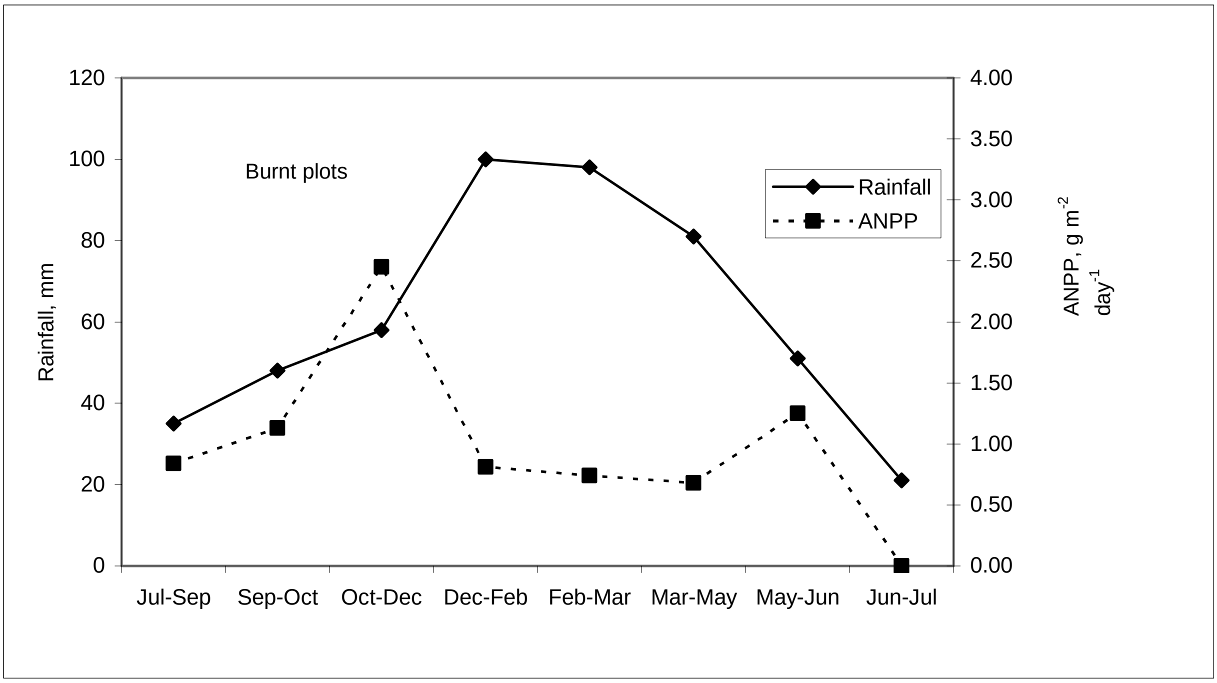
Figure 2: Sodium in percent dry weight in live leaf and live stem in burnt (dark bars) and non-burnt (open bars) plots from September 2003 to July 2004. Asterisk indicates significant difference between means (independent sample t-test, ** $P \leq 0.001$). Error bars represent 95 % confidence interval (CI).

Figure 3: Nitrogen in percent dry weight in live leaf in burnt (dark bars) and non-burnt (open bars) plots from September 2003 to July 2004. Asterisk indicates significant difference between means (independent sample t-test, * $P < 0.05$; ** $P \leq 0.001$). Error bars represent 95 % confidence interval (CI).

Figure 4: Phosphorus and potassium in percent dry weight in standing dead in burnt (dark bars) and non-burnt (open bars) plots from September 2003 to July 2004. Asterisk indicates significant difference between means (independent sample t-test, * $P < 0.05$; ** $P \leq 0.001$). Error bars represent 95 % confidence interval (CI).

Figure 5: Amount of phytomass of the field layer vegetation consumed in burnt and non-burnt plots from September 2003-July 2004 (periods as in Table 1) in the Western Corridor, Serengeti National Park.

Figure 6: Map of the fire patches (Dempewolf et al. 2007) and Thomson's gazelle counts along transects segments in the period (a) May 2003 to April 2004 and (b) May 2004 to April 2005


Burnt plots
Rainfall
ANPP
Rainfall, mm
ANPP, g m^{-2} day^{-1}
0
20
40
60
80
100
120
0.00
0.50
1.00
1.50
2.00
2.50
3.00
3.50
4.00
Jul-Sep
Sep-Oct
Oct-Dec
Dec-Feb
Feb-Mar
Mar-May
May-Jun
Jun-Jul

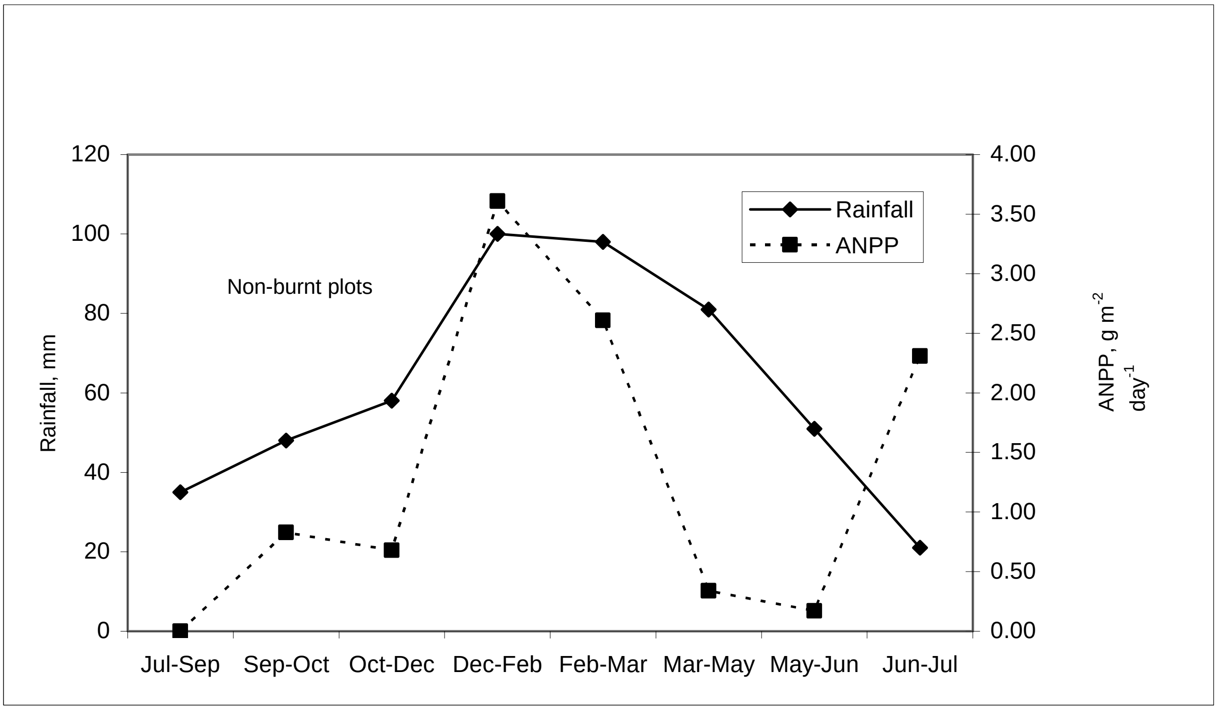
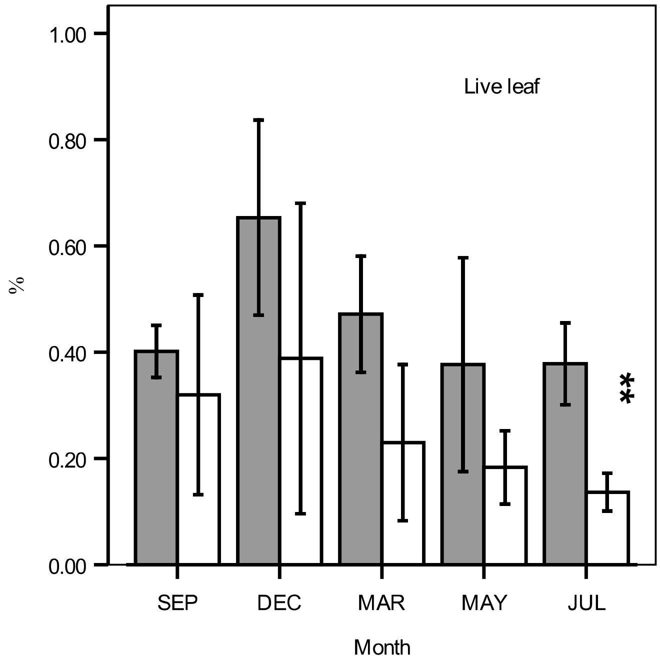

Non-burnt plots
Rainfall
ANPP
Rainfall, mm
ANPP, g m^{-2} day^{-1}
0
20
40
60
80
100
120
0.00
0.50
1.00
1.50
2.00
2.50
3.00
3.50
4.00
Jul-Sep
Sep-Oct
Oct-Dec
Dec-Feb
Feb-Mar
Mar-May
May-Jun
Jun-Jul

Figure 1


1.00
0.80
0.60
0.40
0.20
0.00
%
Live leaf
*
*
SEP
DEC
MAR
MAY
JUL
Month

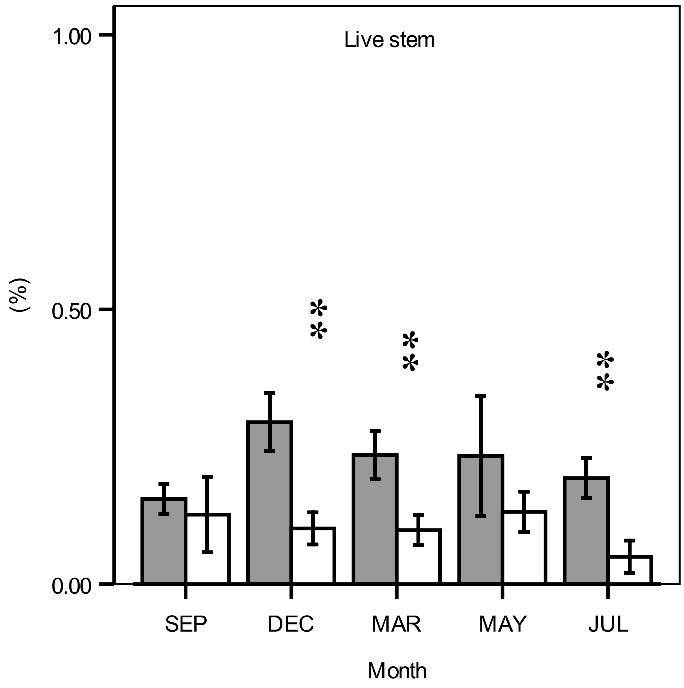

1.00
0.50
0.00
(%)
Live stem
*
*
*
*
*
*
SEP
DEC
MAR
MAY
JUL
Month

Figure 2

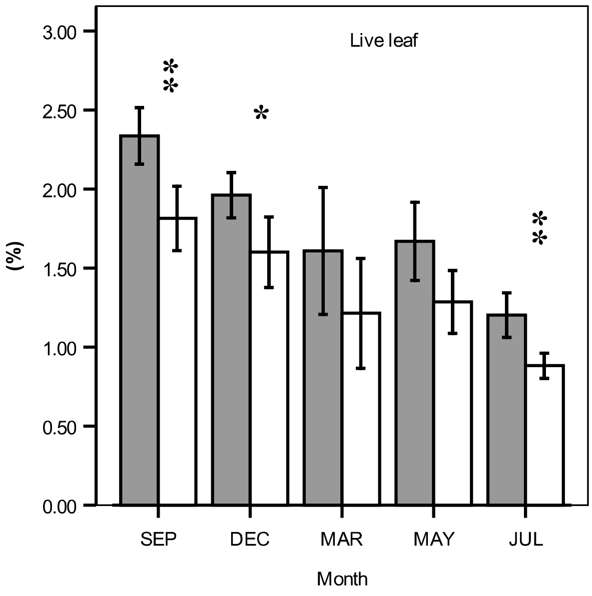
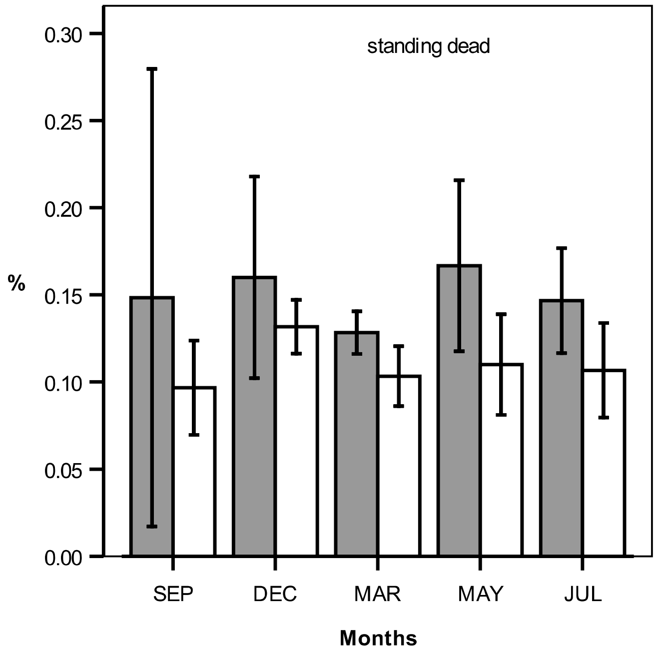


Figure 3


standing dead
%
0.30
0.25
0.20
0.15
0.10
0.05
0.00
SEP
DEC
MAR
MAY
JUL
Months

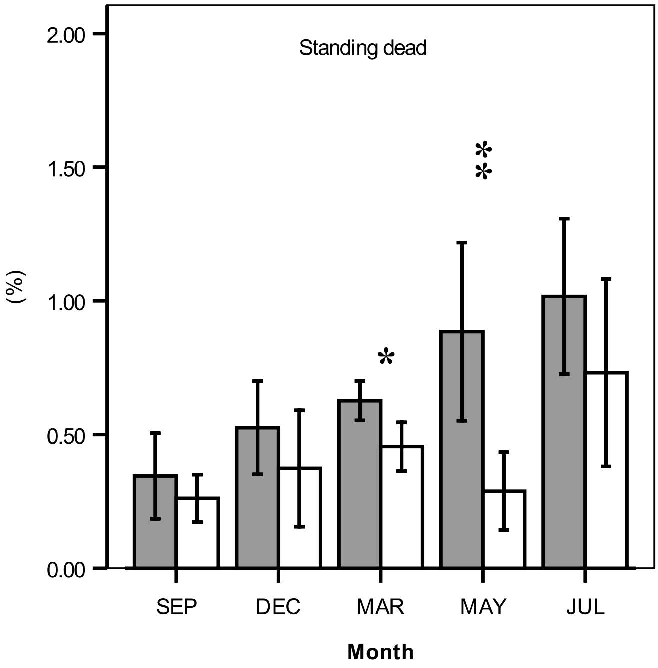

Standing dead
(%)
2.00
1.50
1.00
0.50
0.00
*
**
SEP
DEC
MAR
MAY
JUL
Month

Figure 4

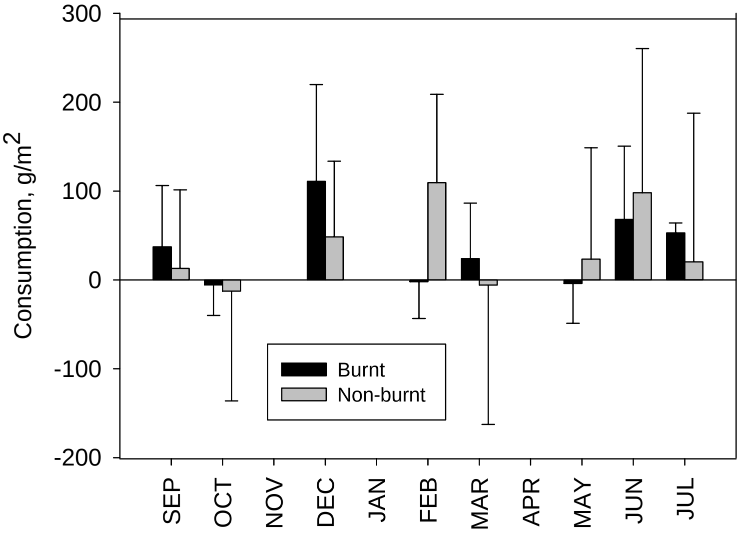

300
200
100
0
-100
-200
Consumption, g/m2
Burnt
Non-burnt
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL

Figure 5

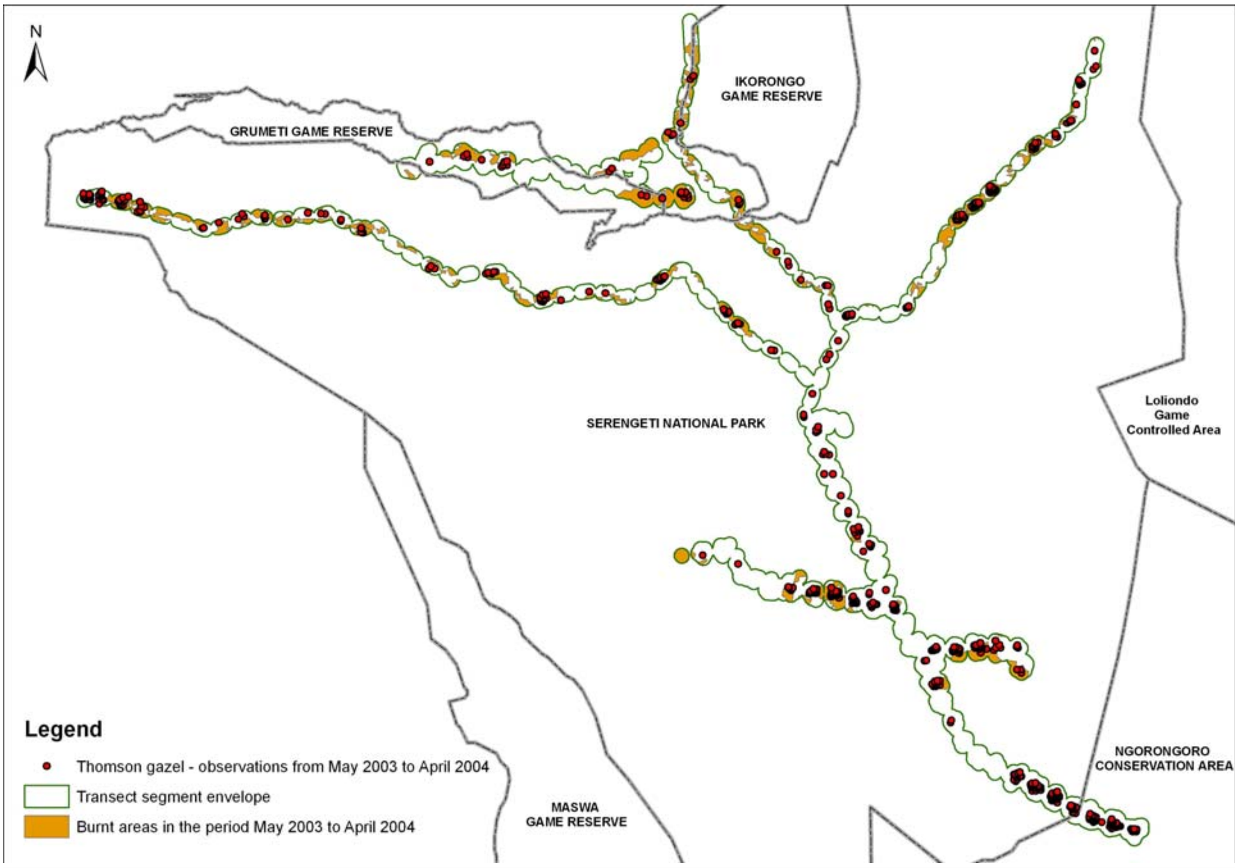

N
GRUMETI GAME RESERVE
IKORONGO
GAME RESERVE
SERENGETI NATIONAL PARK
Loliondo
Game
Controlled Area
NGORONGORO
CONSERVATION AREA
MASWA
GAME RESERVE
Legend
Thomson gazel - observations from May 2003 to April 2004
Transect segment envelope
Burnt areas in the period May 2003 to April 2004

Figure 6a

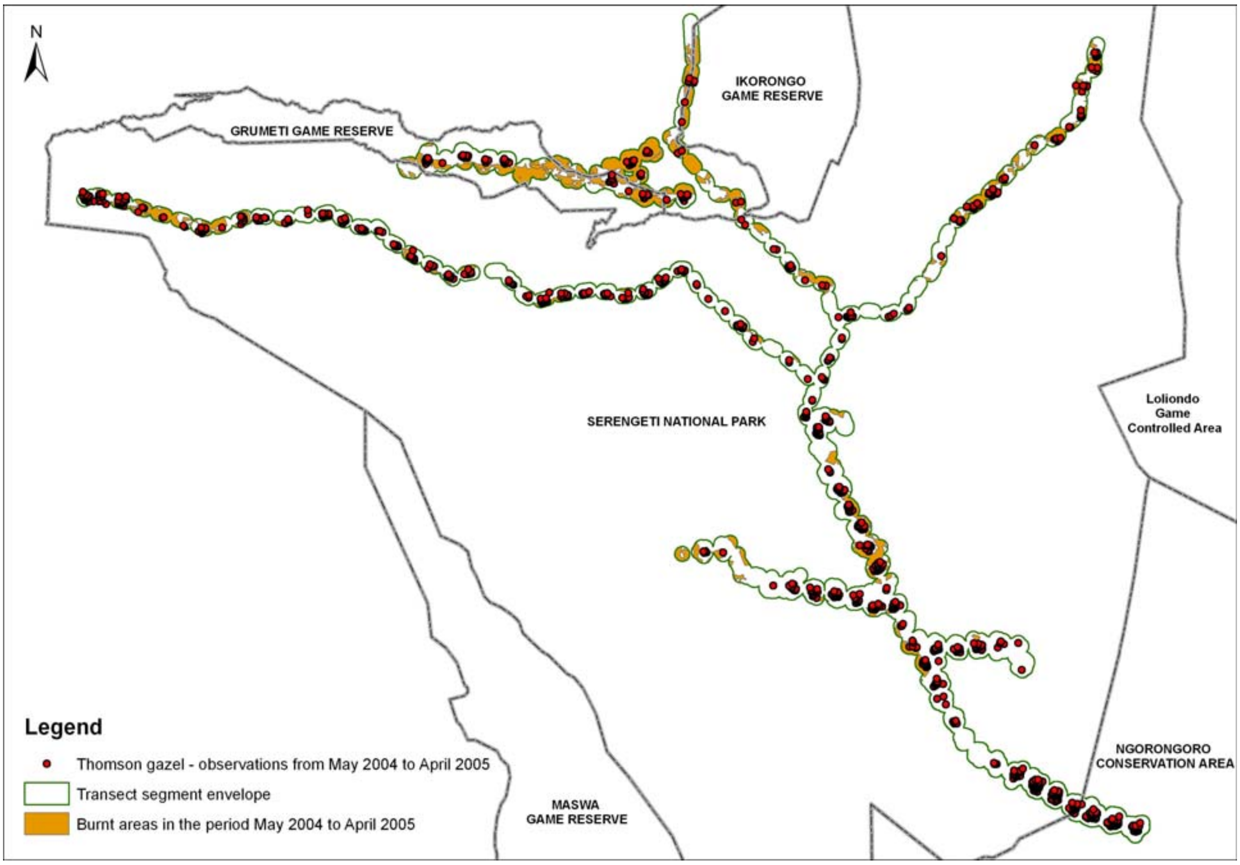

N
GRUMETI GAME RESERVE
IKORONGO GAME RESERVE
SERENGETI NATIONAL PARK
Loliondo Game Controlled Area
NGORONGORO CONSERVATION AREA
MASWA GAME RESERVE
Legend
Thomson gazel - observations from May 2004 to April 2005
Transect segment envelope
Burnt areas in the period May 2004 to April 2005

Figure 6b

PAPER I

Primary production responses to early dry-season burns in western Serengeti grasslands

Shombe N. Hassan[1,2], Graciela M. Rusch[3], Håkan Hytteborn[1], Christina Skarpe[3,4] and Idris Kikula[5]

Corresponding author: Shombe N. Hassan, Department of Biology, Norwegian University of Science and Technology (NTNU), NO-7491 Trondheim, Norway

Tel: + 47 73550348, FAX: +47 73596100

E-mail:shombe.hassan@bio.ntnu.no and hassanshombe@yahoo.co.uk

[1] Department of Biology, Norwegian University of Science and Technology (NTNU), NO-7491 Trondheim, Norway.

[2] Department of Wildlife Management, Sokoine University of Agriculture, P.O. Box 3073, Morogoro, Tanzania

[3] Norwegian Institute for Nature Research, Tungasletta 2, NO-7485, Trondheim, Norway

[4] Faculty of Forestry and Wildlife Management, Hedmark University College, NO-2480 Koppang, Norway.

[5] Vice-Chancellor, The University of Dodoma, P.O. Box 259 Dodoma, Tanzania.

Abstract

We assessed the extent to which fire changes the short-term (4-9 weeks) temporal patterns of ANPP during the first post-fire year in western Serengeti National Park and examined potential differences in the factors that limit ANPP (water availability and energy (photosynthetic)) between burnt and non-burnt grasslands. Our results show temporal differences in phytomass structure between burnt and non-burnt grasslands. Sward phytomass structure and the litter do not recover to non-burnt levels within the first post-fire year. Fire stimulated growth at early post-fire stages, even during the dry season (July-October) and led to larger increments in green phytomass compared to the non-burnt grassland at the start of the short rain period (Oct-Dec). Fire shifted the relative importance of the factors that control ANPP. ANPP in burnt plots was unrelated to rainfall. In contrast, the results support the hypothesis that the amount of photosynthetic biomass constrains ANPP during the first post-fire year. Also, the positive relationship between ANPP and the ratio leaf/total standing phytomass is indicative that the accumulation of standing dead material can be a limiting factor to ANPP in burnt grasslands. ANPP in burnt plots reached an early peak and declined early in the rain season, which could be a consequence of the interactive effects of fire and grazing in a system with high impact of herbivory. In non-burnt plots, the temporal change in ANPP was more related to water availability, at least until mid-growing season. The results underpin the notion that current fire regime in areas of Serengeti (fire return frequency < 1.25 years) are probably ecologically unsustainable.

Key words**:** Above-ground net primary production, energy limitation, rainfall, fire-grazing interactions, savanna.

Introduction

Fire can alter fundamental biogeochemical processes and functions in ecosystems, affecting nutrient and carbon budgets and fluxes (Williams *et al.,* 2004; Dezzeo & Chacon, 2005; Dai *et al.,* 2006; Govender, Trollope & Van Wilgen*,* 2006). The effect on primary production is crucial since biomass and net primary production are essential to ecosystem performance and function (Bourlier & Hadly, 1970), and primary production determines the energy available for other trophic levels. Frequent fires are inherent some ecosystems such as tropical savannas (Beerling & Osborne, 2006). Thus, in such systems the understanding of its effects, in interaction with other ecological determinants, on primary production is critical to guide management practices that can maintain ecosystem's sustainability *sensu* Chapin, Torn & Tateno (1996): "an ecosystem that, over the normal cycle of disturbance events, maintains its characteristic diversity of major functional groups, productivity, and rates of biogeochemical cycling".

There is evidence that fire affects primary productivity, but with apparently contradictory results. The variety in responses appears to depend on the biomes in question, the characteristics of the fire regime (Knapp, Conard & Blair, 1998) and the spatial scales and temporal scopes at which the studies have been conducted (Blair, 1997; Kang, Kimball & Running, 2006; Dai *et al.,* 2006). Important to these differences are the factors that limit primary production in each case and the time lags in the responses to the controlling biophysical processes (Williams *et al.,* 2004).

Nitrogen and soil water availability are important determinants of grass growth in East African savannas (Georgiadis *et al.,* 1989) and fire can change the amounts of these resources available for the vegetation. Through the effect on soil mineralization rates and the volatilization of N from combusted plant material, fire can reduce the availability of N in frequently burnt grasslands compared to long-term non-burnt grasslands (Ojima *et al.,* 1994, Blair, 1997; Turner *et al.,* 1997). However, despite the observed reduced N availability, frequently burnt grasslands, can sustain significantly higher productivity than non-burnt grasslands (Blair, 1997; Turner *et al.,* 1997) likely, as a consequence of fire releasing energy limitations to photosynthesis and soil temperature through the removal of phytomass (Blair, 1997; Turner *et al.,* 1997). Fire affects the structure of the sward (O'Reagain & Owen-Smith, 1996) by removing old leaves, dead material and litter (Snyman, 2005a) and through post-fire regrowth (Vesey-FitzGerald, 1971; Van de Vijver, Poot & Prins, 1999). Further, although the mechanisms are poorly understood, the removal of dead matter by fire appears to stimulate re-growth in grasslands (Norton-Griffiths, 1979), particularly by grasses (Briggs & Knapp, 2001). Contrarily, fires can reduce above-ground net primary production (ANPP) by controlling the amount of total biomass and photosynthetic area, which are typically low immediately after the fire (Reich *et al.,* 2001). During this phase primary production can increase steadily before levelling off at a full-developed sward (Gholz, 1982).

Water availability is a critical factor controlling biomass and primary production in savannas (Bourliere & Hadley, 1970; Norton-Griffiths, Herlocker & Pennycuick, 1975; Sinclair, 1975; Prins & Loth, 1988; Sawadogo, Tiveau & Nygård, 2005). Above-ground net primary production is strongly correlated with mean annual precipitation in Serengeti grasslands (McNaughton, 1985) and also in other African grasslands, and phytomass production follows within-year (monthly) variation in rainfall (Wiegand *et al.,* 2004). Further, the rate of post-fire recovery of the vegetation is known to be related to rainfall (Govender *et al.,* 2006; Nippert, Knapp & Briggs, 2006). However, fire, likely through its effect on the vegetation and litter cover (Snyman, 2005a), can reduce the amount of water availability in the soil by increasing runoff and reducing infiltration (O'connor, Haines & Snyman, 2001) which can lead to comparatively lower net primary production in burnt grasslands (Turner *et al.,* 1997; Snyman, 2005b).

Despite the relatively large number of studies about the effects of fire on semi-arid grasslands and savannas, the current understanding of the processes that determine fire-mediated ANPP is incomplete and insufficient to establish the key controlling factors in each case. Most evidence refers to long term differences among fire regimes (in terms of frequency of burning). Fewer studies have focused on the development during early (first year) stages of the sward recovery when important differences in the amount of green biomass and in the degree of sward shading are expected to be determinants of production. This knowledge is critical to understand the factors that limit carbon fixation in frequently burnt systems.

Although Serengeti National Park has probably been the centre of more quantitative ecological research than any other ecosystem in Africa, comparatively little work has been directed to understand the effects of fire in this system. So far, burning practices in the area are conducted without proper understanding about grassland responses to the prescribed burns, and the relationship between the post-fire sward development and ANPP is unknown. The combined effects of fire, other disturbances (i. e. grazing) and water availability on grassland ANPP are also largely unknown for the Serengeti and for other semi-arid systems with large wild herbivore populations.

The purpose of the study was to assess the effect of early dry-season burning on grassland productivity in western Serengeti National Park by establishing short-term (4-9 weeks) temporal patterns of ANPP during the first post-fire year. We aimed to test hypotheses about water availability and energy (photosynthetic) limitations to ANPP (Blair, 1997) by establishing whether there is a correspondence between ANPP and rainfall, and of ANPP and sward structure attributes in terms of the amount and proportions of leaf biomass, reproductive structures and standing dead material, and whether factors limiting ANPP differed between burnt and non-burnt grasslands We hypothesised that: i) The small amount of photosynthetic biomass is a constraint to ANPP during the early stages of post-fire sward recovery. We predicted that at this time, ANPP would be higher in the non-burnt grassland. ii) In agreement with the energy limitation hypothesis (Blair, 1997) ANPP would increase in burnt grasslands along with sward development and would reach levels higher than in non-burnt grasslands due to the combination of larger photosynthetic biomass and smaller amounts of dead material and plant debris. iii) Also in agreement with the energy limitation hypothesis, and assuming that fire did not affect soil water availability, we predicted that in the burnt grassland ANPP would increase with rainfall. In contrast, energy limitation (shading) would set a limit for productivity (Sims & Singh, 1978) in the non-burnt grassland. Therefore ANPP would be more closely related to monthly precipitation in burnt-grassland than in non-burnt grasslands. iv) In agreement with predictions about the time needed for full canopy recovery of Serengeti grasslands (McNaughton, 1985), burnt grasslands in the study will not reach steady-state levels within one year of post-fire sward recovery.

Methods

Study system

The study was conducted in the Western Corridor of Serengeti National Park (SNP). The SNP (14763 km^2) is the main part of the 25000 km^2 large Serengeti ecosystem which extends to the Masaai Mara in Kenya (Serneels & Lambin, 2001), and is characterised by annual movements of migratory wildebeests (*Connochaetes taurinus*), zebras (*Equus burchelli*), Thomson's gazelles (*Gazella thomsoni*) and elands (*Taurotragus oryx*) (Sinclair, 1975; Sinclair, 1995). Generally, the migrants spend the wet season (Dec-May) in the South East Plains and the dry season (Aug–Oct) in northern Serengeti and Masaai Mara area in southern Kenya. The Western Corridor is primarily used by migrating herds while moving between dry and wet season grazing grounds. Serengeti is situated between latitude 1° and 3°30'S, and longitude 34° and 36°E (Sinclair, 1995). Wildebeest, Burchell's zebra, Thomson's gazelle, African buffalo (*Syncerus caffer*) and topi (*Damaliscus korrigum*) are the key grazing species (McNaughton, 1985). Annual average rainfall ranges between *ca* 600 mm in the Southeast Plains and *ca* 1100 mm in the north (Pennycuick, 1975). The rainfall distribution is bimodal, with a period of short rains from November to December and the main rain season from March to May (Norton-Griffiths *et al.,* 1975).

Data set

Phytomass dynamics and ANPP were assessed in the period 5th July 2003 to 21st July 2004 by repeated harvesting of samples taken at intervals of 2 to 9 weeks (Table 1). Study sites were in the main area of the wildebeest migratory route. The sites (n = 6) were selected in medium-high *Themeda* grasslands with *Themeda triandra, Pennisetum mezianum* and *Digitaria macroblephara* (Clayton, Phillips & Renvoize 1974) as dominant grass species. Each site consisted of one burnt and one non-burnt patch, each patch at least 10 ha in size and as similar as possible to each other in terms of the general aspect of the landscape. One plot (50 m x 50 m) was established in each burnt and non-burnt patch at each of the 6 sites, in total twelve plots. The distance between the sites ranged between 1 and 40 km, and the distance between the plots and the closest road ranged between 0.45 and 0.75 km. The burnt patches were burnt in the annual early dry-season burning operations in May-July 2003 performed by the Serengeti Ecological Monitoring Program (SEMP) unit.

Phytomass samples and the litter were collected in 6 randomly distributed quadrats (0.0625 m^2) (Taylor Jr., Brooks & Garza, 1997), in total 72 samples. Movable cages were used to temporarily exclude large herbivores from the quadrats between samplings occasions. At the first sampling time (T0), in each of the twelve plots, phytomass samples were hand-clipped to ground level. At the same time six cages were erected over other randomly selected quadrats. The cages were conical in shape with 1m^2 (1 m x 1 m) base on the ground and 2 m tall. From each of the twelve plots, at each sampling time from T1 onwards (time T1-T8), six "fenced" and six "open" phytomass samples were collected (in total 144 samples). After clipping the cages were moved to new randomly selected quadrats.

Phytomass samples were hand-sorted into five compartments: live leaf, live stem (for the purpose of the study: grass reproductive culms without the leaves), flower/fruit, standing dead (dead material attached to living plants) and litter. Sorted materials were air-dried for two weeks in paper bags and later oven-dried at 70°C (Mutanga *et al*., 2004) for 48 h and then weighed using a digital scale (Soehnle ultra, [Leifheit AG. D-56377 Nassau, Germany] with maximum 200 g, d = 0.1g). A total of 1152 samples were collected. Seventy-two samples were lost due to two wildfires which burnt four plots, the first one in May and the second one in June. Monthly rainfall data from the stations Nyaruswiga, Mareo and Musabi with the Serengeti National Park Ecological Monitoring Department (Table 1) were averaged for the months on which ANPP was calculated (Table 5). Each station consists of one rain gauge and the distance between the sites and the rain gauge varied between 0.5 - 1.2 km.

Data analyses

Differences in phytomass between open (at T*i*) and fenced (at T*i*+1) samples were tested with univariate ANOVAs independently for each phytomass component and sampling occasion (T*i* from *i* = 0 to 8). Since the length of the interval between two consecutive samplings varied among samplings, 'Sampling interval' (in days) was included in the model as a covariate (Table 1). The model included 'Fire' (burnt vs. non-burnt), 'Phytomass change' (fenced T*i*+1 vs. open T*i*), 'Site', the interaction term 'Phytomass change * Fire' and 'Sampling interval'. 'Fire' and 'Phytomass change' were fixed factors, and 'Site' random. The analyses were conducted with the General Linear Model – Univariate ANOVA routine in SPSS v. 15 for windows. Significant positive differences in total above-ground phytomass (including litter) between fenced samples at T*i*+1 and open samples at T*i* indicated phytomass gain (production). A significant interaction effect of 'Phytomass change*Fire' indicated differences in production between burnt and non-burnt plots.

Daily ANPP in each fire treatment was calculated as the phytomass increment, i. e. the positive difference in total phytomass (live, standing dead and litter) between consecutive samplings divided by the number of days between samplings. Phytomass increments were based on plot averages, i.e. on 6 open and 6 fenced samples at Ti and Ti+1, respectively.

The structural attributes of the sward, i.e. the amount of leaf, stem, flower-fruits, standing dead material and litter, and the ratios of phytomass compartments were computed for the eight sampling periods (T1-T8) on the 'fenced' samples. Spearman correlations (one-tailed significance test) were calculated between the daily ANPP and the average sward attributes per treatment using the correlations routine in SPSS v. 15.0.

Phytomass ratios were calculated on each sample and arcsine transformed for the ANOVAs and Pearson correlations. Other data were square-root transformed to improve normality and variance homocedasticity (Underwood, 2002).

Results

Fire, sward structure and phytomass allocations

Total standing phytomass (live + attached dead plant material) was at all sampling times higher in the non-burnt plots than in the burnt plots with averages of ca 275 g $^{-2}$ and ca 143 g m^{-2}, respectively (Table 2). The differences were significant in six of the eight periods. Total live phytomass was also generally larger in non-burnt plots, differing significantly at four occasions. Phytomass of leaf, stem and flower/fruit were significantly higher in non-burnt plots at 3, 5 and 2 sampling times, respectively. Only in June was the phytomass of flower/fruits higher in the burnt plots (Table 2). Mean total live biomass was 123 g m^{-2} and 87.0 g m^{-2} for non-burnt and burnt plots, respectively.

Fire had an effect on the temporal distribution of live phytomass. The peaks for live leaf and total live phytomass differed between treatments, in December in burnt plots and in February in non-burnt plots (Table 2 and Fig. 1). Also the first peak in live stem phytomass, related to the reproductive phase in grasses, was earlier in burnt plots (December) than in non-burnt plots (February) (Table 2). In contrast, the phytomass of flowers/fruits followed similar temporal patterns in burnt and non-burnt plots with peaks in December, May and July.

Fire had also an effect on the amount of plant debris. There was more standing dead phytomass and litter in non-burnt plots than in burnt plots at all times (Table 2 and Fig. 1). In both treatments, standing dead phytomass increased steadily during the early stages of the growth season with a peak and a significant net accumulation in March (Fig. 1), after the short rain-period in December-February (Table 1). Non-burnt plots had a second peak at the end of the long rain-season, in July.

Fire also changed the relative phytomass composition of the sward (Table 3). Burnt plots had significantly higher ratios of live leaf/total standing phytomass in Oct, Dec and Feb; significantly lower ratios of live stem/total standing phytomass at early post-fire stages (Sep and Oct), and higher ratios of total live/total standing phytomass (Dec and Feb). Non-burnt plots had generally higher standing dead/total phytomass ratios.

Fire also changed the relative distribution of live phytomass, between vegetative and reproductive structures (Table 4). Burnt plots had significantly higher ratios of leaves/total live phytomass (Oct and Feb) and generally lower ratios of stems plus flower-fruits phytomass/total live phytomass, significantly lower at five sampling times. There were no differences between treatments in the ratios of flower and fruit phytomass/total live phytomass.

Variation in productivity

Green phytomass changed significantly between sampling periods at the end of the dry season (Sep – Oct), during the short rains (Dec – Feb) and during the long rains (Mar – Jun) (Table 5 and Fig. 1). In four periods, the production of green phytomass differed between the fire treatments (significant interaction fire x phytomass change). There was also in some periods, a significant site effect on biomass change (site x phytomass change) (Table 5).

Standing dead phytomass changed, demonstrated by significant effect of phytomass change and/or of the interactions of phytomass change with fire and/or site, during the short dry period (Feb-Mar) and at the end of the main rain period (May-Jul) (Table 5, Fig 1). Burnt plots had significantly lower amounts and less variability of the litter compartment compared to non-burnt plots (Fig. 1). The mass of litter changed significantly from September to March and in May-July, shown as a significant effect of phytomass change and/or of its interactions with fire and site (Table 5), with net accumulation in non-burnt plots in Sep-Oct and Mar-May, and a decrease in Oct-Dec and in Jun-Jul. In burnt plots net accumulation occurred in May-June (Fig. 1).

Total above-ground phytomass (total standing plus litter) changed in most periods (significant main effect of phytomass change and/or of its interactions with fire and/or with site), except in Sep-Oct and in Feb-Mar (Table 5). A significant effect of the interaction phytomass change times fire indicated that phytomass production was dependent on the fire treatment. These effects were significant at $p < 0.05$ in Jul-Sep, Oct-Dec and May-Jun. In non-burnt plots, total above-ground phytomass decreased in the long dry season (Jul-Sep) and increased steadily during the growth season showing net accumulation in Dec-Feb. The amount of total biomass attained in this period in fenced samples was maintained until the end of the rain period (May-Jun). In contrast, burnt plots had net phytomass accumulation at early stages of the post-fire period (Jul-Dec) even during the dry season (Jul-Sep and Sep-Oct). Total standing phytomass declined after this period and also production, and increased again at the end of the rain period (May-Jun) (Fig. 1, Table 5). Daily ANPP (increment of live, standing dead and litter) in burnt plots was on average 1.0 $gm^{-2} d^{-1}$ (range 0.0 to 2.5 $gm^{-2} d^{-1}$) and in non-burnt grassland 1.2 $gm^{-2} d^{-1}$ (range 0.0 to 3.6 $gm^{-2} d^{-1}$). Significant biomass change x site in May-June and Jun-July indicates that local conditions at the sites were important determinants of production in these periods.

Relationship between sward structure and productivity

There was a significant relationship between sward properties and ANPP, but only in the burnt treatment. ANPP was positively related to leaf and total live phytomass and to the ratio leaf/total standing phytomass. ANPP was negatively correlated ($P = 0.078$) to the ratio between the phytomass of reproductive structures (live stems, flower and fruits) and total live phytomass (Table 6). In contrast, no significant relationships were detected between ANPP and sward structure attributes in non-burnt plots.

Relationship between precipitation and productivity

ANPP in burnt plots was not significantly related to rainfall (Table 6 and Fig. 2). ANPP showed high biomass increment rates at early post-fire stages, during the dry season (Oct-Dec). After December, ANPP declined and was generally maintained low during the rest of the growth season, with a small increase at the end of the rain season (May-Jun). In contrast, ANPP was more closely related to rainfall in non-burnt plots (Table 6, Pearson rho 0.486; P = 0.111). It increased with rainfall until reaching a peak at the short rain season and declined abruptly in the mid-long rain season (Fig. 2).

Discussion

In agreement with other studies in African savannas, our results show that early-dry season fires in Serengeti affect the grassland structure by removing dead material including litter (Snyman, 2005a) and through post-fire regrowth (Vessey-FitzGerald, 1971; Van de Vijver *et al,* 1999). Our results further show temporal differences in phytomass structure between burnt and non-burnt grasslands. Fire stimulated growth at early post-fire stages, even during the dry season (July-October) and led to larger increments in green phytomass compared to the non-burnt grassland at the start of the short rain period (Oct-Dec). These findings agree with results from other studies in grasslands showing that fire stimulates regrowth (Norton-Griffiths, 1979; Briggs & Knapp, 2001) and the standing crop of leaves (McNaughton, 1985).

Generally, the daily ANPP values in our study (between 0 and 3.6 g m^{-2}) are comparable to those found in other savanna communities (mean range 1-4 g m^{-2}, Bourliere & Hadley, 1970) and to previous studies in Serengeti (Sinclair, 1975; McNaughton, 1985). However, our results demonstrate that fire shifts the relative importance of the factors that control above-ground net primary production and agree with the general idea that fire can affect fundamental processes in the ecosystem (Williams *et al.,* 2004; Dai *et al.,* 2006; Govender *et al.,* 2006). The significant relationship between leaf phytomass and ANPP in burnt plots generally supported our hypothesis that, in western Serengeti grasslands, the amount of photosynthetic biomass constrains primary productivity during the first post-fire year.

However, the amount of live phytomass did not fully explain the changes in ANPP in burnt plots. The large increments in live phytomass at early post-fire stages despite the small amounts of initial photosynthetic biomass indicates that regrowth in this period could in part have depended on below-ground reserves (Briske & Richards, 1995). Further, in agreement with other studies, the comparatively higher allocation to leaf phytomass (Gwynne, 1966; Bowen & Pate, 1993) and the lower allocation to reproductive structures, i. e., stems and flowers /fruits, found in the burnt plots at the early post-fire stage can be a strategy to compensate for the lost mass (Heichel & Turner, 1983; Trumble, Kolodny-Hirsch & Ting, 1993) which could additionally have contributed to the high live biomass increments assessed in this period.

Above-ground net primary productivity in burnt plots had an early peak and declined after December despite that this period corresponds to the main rain season. The increase in live phytomass declined until May and we found no significant accumulation of standing dead material and litter in this period. These results contradict earlier findings showing that the rate of post-fire recovery of the vegetation responds to rainfall (Govender *et al.,* 2006; Nippert *et al.,* 2006). Two reasons may explain these apparently contradictory results. Fire can reduce the amount of water availability in the soil by increasing runoff and reducing infiltration (O'Connor *et al.,* 2001) with negative effects on net primary production in burnt grasslands (Turner *et al.,* 1997; Snyman, 2005b). Alternatively, the decline in ANPP in burnt grassland could be a consequence of the interplay between grazing and fire. Results from a parallel study (Hassan *et al.,* 2007) showed that consumption by herbivores in burnt plots in the period October-December led to a significant reduction in live phytomass. Fire in interaction with other disturbances can importantly affect plant growth by increasing the rate and the magnitude of biomass loss in the vegetation, and hence by intensifying the disturbance regime, with consequences for the capacity of the vegetation to restore biomass loss and to grow. Although re-growth in grasses appears to depend only marginally on stored carbohydrates (Chapin, Schulze & Mooney, 1990; Richards & Caldwell, 1985), repeated defoliation, can reduce the amount of carbohydrate reserves, affecting post-disturbance leaf area and plant vigour (McPherson & Williams, 1998). Repeated defoliation can also deplete the bud bank (Briske & Richards, 1995) and it has been shown that meristematic limitations in grasses appear to be of prime importance in determining re-growth after defoliation (Richards & Caldwell, 1985). The interactive effects of fire and other disturbances, such as grazing, are incompletely understood but earlier studies support the idea that herbivory on burnt patches can prolong the period for recovery from fire (Pratt, 1967; Letnic, 2004). These effects are expected to be of importance in the Serengeti and other savanna ecosystems where large herbivores are a major shaping force of ecosystem function and structure (McNaughton, 1979; 1985; 1992).

In contrast to the pattern found in burnt plots relating sward structure and ANPP, we found no correspondence in non-burnt plots between ANPP and the amount of live biomass or any of the assessed sward structural attributes. In non-burnt plots, the temporal change in ANPP was more related to water availability, at least until February. Beyond this period, the decline in the rate of live phytomass increments could be attributed to two factors. First, similarly to the effect of herbivory on burnt plots, Hassan *et al.* (2007) found a significant decline in standing biomass due to herbivory in the same grasslands in the period December-February. The reduction in the amount of photosynthetic matter could explain the low ANPP at the peak rain season. However, our results also show a significant increment in the amount of standing dead phytomass after this period (February-March) which suggests less favourable conditions for plant growth after the production peak in February. Possible factors could be shading (Sims & Singh, 1978) or the allocation of resources to belowground parts towards the end of the growth period (Snyman, 2005b).

Conclusions

Early-dry-season fires in the Serengeti Western Corridor have important effects on the composition of the grassland phytomass during the first post-fire growth season both in terms of the total standing crop, and of the amount of leaf and total live phytomass. Our study shows that the sward phytomass structure and the litter do not recover to non-burnt levels within one year, a finding which is in agreement with earlier studies in Serengeti (McNaughton, 1985) indicating that full recovery of sward standing crop should be expected two-three years after the fire. Fire frequency in Serengeti, particularly in the game reserve areas and along the SNP borders is currently high. Within the period August 2000 to December 2006, the total part burnt within SNP was 76.2 % and between 82 and 87 % for the adjacent game reserves, Ikorongo, Maswa and Grumuti (calculus based on data in Dempewolf *et al.,* 2007). In a large portion of the area, fire return frequency during the same period was lower than 1.25 years (Dempewolf *et al.,* 2007) an indication that the current fire regime in areas of the Serengeti is too frequent to maintain steady state functions and ecosystem sustainability (*sensu* Chapin *et al.,* 1996). Further, our results show that, in contrast to non-burnt grasslands, leaf phytomass limits ANPP in burnt Serengeti grasslands and that the interaction of fire and grazing can intensify the disturbance regime with effects on ANPP in the Serengeti grasslands and likely on other savanna ecosystems where large herbivores are a major shaping force.

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Tables

Table 1: Periods for phytomass change assessments from July 2003 to July 2004, with shortenings and mean time interval in days between consecutive samplings on burnt and non-burnt plots in six sites in the Western Corridor, Serengeti National Park. Average rainfall for whole months in the sampling period calculated on monthly records at the stations Nyaruswiga, Mareo and Musabi in Serengeti National Park.

Period	Shortenings of sampling periods	Burnt	Non-burnt	Rainfall
		days		mm/month
Jul-Sep	T1-TO	45	54	35
Sep-Oct	T2-T1	33	33	48
Oct-Dec	T3-T2	66	67	58
Dec-Feb	T4-T3	37	37	100
Feb-Mar	T5-T4	32	31	98
Mar-May	T6-T5	61	61	81
May-Jun	T7-T6	37	38	51
Jun-Jul	T8-T7	19	11	21

Table 2: Mean values (gm^{-2}) of total aboveground mass (including litter), total standing phytomass and phytomass compartments: live leaf, live stem, flower and fruit, total live, standing dead, and litter in fenced samples in burnt and non-burnt plots in Western Corridor grasslands, Serengeti National Park from September 2003 to July 2004.

Sampling time	Treatment	Total above-ground mass	Total standing phytomass	Live phytomass				Dead phytomass	
				Leaf	Stem	Flower/ Fruit	Total live	Standing	Litter
Sep	Burnt	71.7**	69.5**	32.0**	13.8*	-	45.8**	23.7**	2.2**
	Non-Burnt	201.7	188.3	38.2	62.9	-	101.1	87.2	13.4
Oct	Burnt	73.1**	65.4**	35.2**	4.8**	-	40.0**	25.4**	7.7**
	Non-burnt	210.1	189.3	63.4	39.8	-	103.2	86.1	20.8
Dec	Burnt	227.0	220.0	115.2	40.2	2.6	158.0	62.0**	7.0**
	Non-burnt	290.7	266.8	100.0	46.8	4.7	151.5	115.3	23.9
Feb	Burnt	145**	137.2**	74.3*	22.0**	0.7**	97.0**	40.2**	7.8**
	Non-burnt	373.6	341.9	110.3	64.2	3.9	178.4	163.5	31.7
Mar	Burnt	167.5**	161.0**	55.2	27.4*	0.3*	82.9*	78.1**	6.5**
	Non-burnt	340.9	316.4	61.3	53.2	1.3	115.8	200.6	24.5
May	Burnt	183.4**	173.8**	77.9	39.9*	5.1	122.9	50.9**	9.6**
	Non-burnt	363.3	324.6	89.7	57.7	5.4	152.8	171.8	38.7
Jun	Burnt	222.3	207.3	73.5	44.0	0.4*	117.9	89.4*	15.0**
	Non-burnt	323.9	296.7	63.2	65.2	0.0	128.4	168.3	27.2
Jul	Burnt	120.2**	110.0**	10.7	17.8	3.3	31.8	78.2**	10.2*
	Non-burnt	308.0	273.4	18.8	30.8	4.6	54.2	219.2	34.6

* Difference between burnt and non-burnt plots in plant mass statistically significant at $P < 0.05$; ** $P \leq 0.001$.

Table 3: Mean ratios of phytomass compartments in fenced samples on burnt and non-burnt plots in six sites in the Western Corridor, Serengeti National Park, from September 2003 to July 2004. Live leaf, live stem and total live is shown in relation to total standing phytomass, and standing dead material and litter in relation to total above-ground mass.

Sampling time	Treatment	Live leaf/total standing phytomass	Live stem/total standing phytomass	Total live/total standing phytomass	Standing dead/total above-ground mass	Litter/ total above-ground mass
Sep	Burnt	0.460	0.199*	0.659	0.331	0.031
	Non-burnt	0.203	0.334	0.537	0.432	0.066
Oct	Burnt	0.538*	0.073*	0.612	0.347*	0.105
	Non-burnt	0.335	0.210	0.545	0.410	0.099
Dec	Burnt	0.524*	0.183	0.718*	0.273**	0.031
	Non-burnt	0.375	0.175	0.568	0.397	0.082
Feb	Burnt	0.542**	0.160	0.707*	0.277**	0.054*
	Non-burnt	0.323	0.188	0.522	0.438	0.085
Mar	Burnt	0.343	0.170	0.515	0.466**	0.039
	Non-burnt	0.194	0.168	0.366	0.588	0.072
May	Burnt	0.448	0.230	0.707	0.278**	0.052*
	Non-burnt	0.276	0.178	0.471	0.473	0.107
Jun	Burnt	0.355	0.212	0.569*	0.402**	0.067*
	Non-burnt	0.213	0.220	0.433	0.520	0.084
Jul	Burnt	0.097	0.162	0.289	0.651	0.085
	Non-burnt	0.069	0.113	0.198	0.712	0.112

* Difference between burnt and non-burnt plots in biomass ratio statistically significant at $p < 0.05$; **$P \leq 0.001$.

Table 4: Mean ratios of live phytomass compartments in fenced samples on burnt and non-burnt plots in six sites in the Western Corridor, Serengeti National Park, from September 2003 to July 2004.

Sampling time	Treatment	Live leaf/ total live phytomass	Live stem/ total live phytomass	Flower-fruit/total live phytomass	Live stem + flower-fruit/total live phytomass
Sep	Burnt	0.699	0.301**	-	0.301*
	Non-burnt	0.378	0.622	-	0.622
Oct	Burnt	0.880**	0.120**	-	0.120**
	Non-burnt	0.614	0.386	-	0.386
Dec	Burnt	0.729	0.254	0.016	0.271*
	Non-burnt	0.660	0.309	0.031	0.340
Feb	Burnt	0.766**	0.227*	0.007	0.234*
	Non-burnt	0.618	0.360	0.022	0.382
Mar	Burnt	0.666	0.331	0.004	0.334
	Non-burnt	0.529	0.459	0.011	0.471
May	Burnt	0.634	0.325*	0.041	0.366*
	Non-burnt	0.587	0.378	0.035	0.413
Jun	Burnt	0.623	0.373	0.003	0.377
	Non-burnt	0.492	0.508	0.000	0.508
Jul	Burnt	0.336	0.560	0.104	0.664
	Non-burnt	0.347	0.568	0.085	0.653

* Difference between burnt and non-burnt plots in biomass ratio statistically significant at $P < 0.05$; ** at $P \leq 0.001$

Table 5: ANOVA model factors, F statistics and P values for total live phytomass, standing dead, litter and total above-ground mass. 'Phytomass change': samples at T_i vs. $T_{i+1,}$ 'Fire': samples on burnt vs. non-burnt plots and 'Sites': samples at 6 sites. Phytomass difference: Difference (standardised per day) between mean T_i vs. T_{i+1} on burnt and non-burnt grasslands. ANPP: mean daily aboveground net primary production (g $m^{-2}day^{-1}$) on burnt and non-burnt grasslands from July 2003 to July 2004, in six sites in the Western Corridor, Serengeti National Park.

Factor	**Total live phytomass**		**Standing dead phytomass**		**Litter**		**Total above-ground mass**		**BURNT**		**NON-BURNT**	
	F	P	F	P	F	P	F	P	**Phytomass difference ($gm^{-2}day^{-1}$)**	**Daily ANPP ($gm^{-2}day^{-1}$)**	**Phytomass difference ($gm^{-2}day^{-1}$)**	**Daily ANPP ($gm^{-2}day^{-1}$)**
Jul – Sep												
Phytomass change	2.309	0.131	0.85	0.59	2.61	0.11	3.01	0.085	0.84	0.84	-0.97	0
Fire	50.51	0.0001	84.98	0.0001	54.09	0.0001	113.45	0.0001				
Site	2.42	0.18	12.53	0.007	8.58	0.17	26.28	0.001				
Fire x phytomass change	1.23	0.27	3.39	0.068	0.01	0.924	4.29	0.04				
Site x phytomass change	4.43	0.001	1.025	0.406	4.62	0.033	0.82	0.086				
Sep - Oct												
Phytomass change	4.60	0.034	0.05	0.821	6.62	0.011	1.32	0.252	1.13	1.13	0.83	0.83
Fire	93.75	0.0001	92.08	0.0001	5.64	0.019	113.73	0.0001				
Site	6.78	0.0001	4.79	0.055	0.83	0.58	19.26	0.003				
Fire x phytomass change	5.05	0.026	0.854	0.357	8.99	0.003	0.92	0.339				
Site x phytomass change	1.87	0.1	2	0.083	7.19	0.066	0.51	0.772				
Oct - Dec												
Phytomass change	0.98	0.324	1.57	0.21	16.8	0.0001	0.46	0.497	2.45	2.45	0.68	0.68
Fire	5.17	0.025	34.11	0.0001	92.33	0.0001	26.08	0.0001				
Site	4.51	0.062	3.03	0.125	12.37	0.008	6.02	0.035				
Fire x phytomass change	7.21	0.008	0.55	0.46	12.75	0.001	7.19	0.008				
Site x phytomass change	0.98	4.33	2	0.08	1.68	0.144	1.15	0.339				

Dec - Feb												
Phytomass change	5.64	0.019	3	0.085	10.52	0.002	6.31	0.013	0.81	0.81	3.61	3.61
Fire	18.75	0.0001	58.98	0.0001	124.69	0.0001	58.05	0.0001				
Site	1.96	0.24	5.81	0.38	7.69	0.021	2.8	0.141				
Fire x phytomass change	3.41	0.067	0.54	0.465	3.54	0.021	2.85	0.094				
Site x phytomass change	0.94	0.46	0.65	0.507	2.49	0.035	1.22	0.3				
Feb - Mar												
Phytomass change	0.13	0.715	1.91	0.169	0	0.999	1.05	0.308	0.74	0.74	2.6	2.6
Fire	3.982	0.048	25.41	0.0001	28.88	0.0001	19.59	0.0001				
Site	1.89	0.25	3.922	0.08	6.76	0.028	1.74	0.279				
Fire x phytomass change	0.121	0.729	4.92	0.028	0.07	0.795	2.17	0.144				
Site x phytomass change	2.04	0.08	0.287	0.919	0.81	0.548	1.09	0.369				
Mar - May												
Phytomass change	4.65	0.033	1.59	0.209	0.77	0.383	3.87	0.05	0.68	0.68	0.34	0.34
Fire	7.704	0.006	30.55	0.0001	63.97	0.0001	24.12	0.0001				
Site	3.633	0.092	1.235	0.411	9.04	0.015	2.97	0.128				
Fire x phytomass change	8.677	0.004	0.064	0.801	0.03	0.864	2.01	0.159				
Site x phytomass change	1.2	0.084	1.277	0.278		1.25	1.01	0.414				
May - Jun												
Phytomass change	4.533	0.035	8.24	0.005	24.12	0.0001	10.73	0.001	1.25	1.25	0.17	0.17
Fire	0.002	0.968	13.12	0.0001	26.88	0.0001	5.17	0.025				
Site	0.658	0.671	0.84	0.576	3.4	0.103	0.84	0.57				
Fire x phytomass change	4.31	0.04	3.68	0.057	16.314	0.0001	6.65	0.011				
Site x phytomass change	2.76	0.021	4.12	0.002	5.48	0.0001	4.53	0.001				
Jun - Jul												
Phytomass change	0.19	0.66	14.61	0.0001	18.7	0.0001	8.74	0.004	-1.22	0	2.31	2.31
Fire	1.86	0.176	0.59	0.446	1.61	0.208	1.523	0.22				
Site	1.33	0.38	0.482	0.779	0.95	0.523	0.44	0.803				
Fire x phytomass change	0.82	0.368	0.104	0.747	13.96	0.0001	0.085	0.771				
Site x phytomass change	1.11	0.36	7.72	0.0001	4.2	0.002	4.94	0.0001				

Table 6: Pearson correlation (r) and P values between sward structural attributes in fenced samples (as in Tables 2, 3 and 4) and rainfall (as in Table 1) on daily above-ground net primary production (as in Table 5) in burnt and non-burnt grasslands for the period September 2003 to July 2004.

Net primary production	Structural attributes	Burnt		Non-burnt	
		r	P	r	P
ANPP	Leaf phytomass	0.787**	0.01	0.155	0.357
	Live phytomass	0.696*	0.028	0.095	0.411
	Standing dead phytomass	-0.041	0.461	0.55	0.079
	Leaf/Total standing phytomass	0.626*	0.048	-0.17	0.344
	Live / Total standing phytomass	0.614	0.053	-0.37	0.183
	Stem-Flower-Fruit/Live phytomass	-0.552	0.078	-0.074	0.863
	Leaf / Live phytomass	0.517	0.095	0.078	0.427
	Rainfall	0.087	0.419	0.486	0.111

*Pearson correlation significant at P <0.05 ** P <0.01.

Figure legends

Figure 1: Mean live, standing dead, litter and total above-ground phytomass in burnt and non-burnt plots at the start (light grey bars) and the end (dark grey bars) of the sampling period. Bars show 95% confidence interval.

Figure 2: Above-ground daily net primary production (ANPP) and precipitation on burnt and non-burnt grasslands from July 2003 to July 2004 in six sites in the Western Serengeti Corridor, Serengeti National Park.

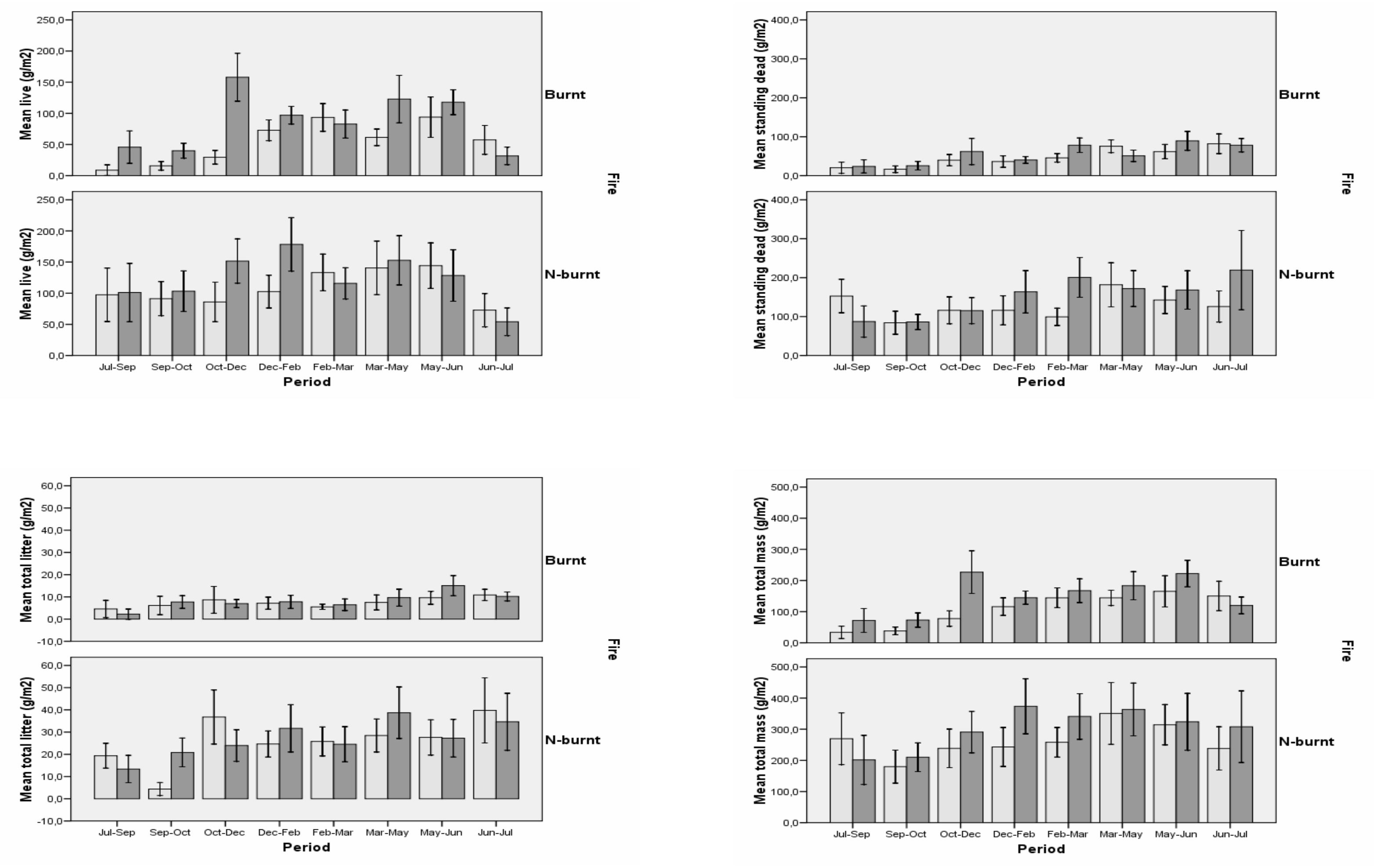
Mean live (g/m2)
Mean standing dead (g/m2)
Mean total litter (g/m2)
Mean total mass (g/m2)
Burnt
N-burnt
Fire
Period
Jul-Sep
Sep-Oct
Oct-Dec
Dec-Feb
Feb-Mar
Mar-May
May-Jun
Jun-Jul
0,0
50,0
100,0
150,0
200,0
250,0
300,0
400,0
500,0
-10,0
10,0
20,0
30,0
40,0
50,0
60,0

Figure 1

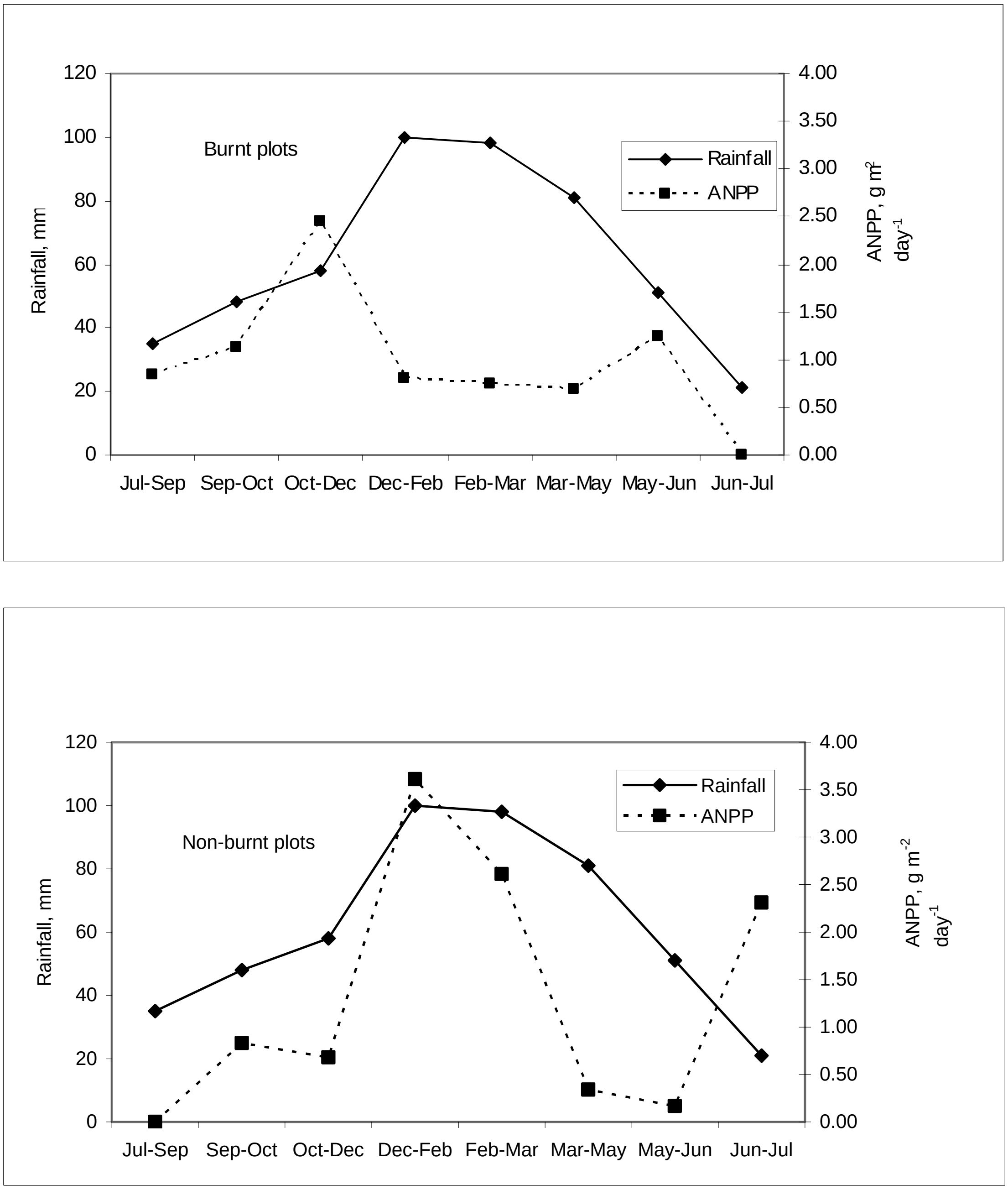
Burnt plots
Rainfall
ANPP
Rainfall, mm
ANPP, g m^{-2} day^{-1}
120
100
80
60
40
20
0
4.00
3.50
3.00
2.50
2.00
1.50
1.00
0.50
0.00
Jul-Sep
Sep-Oct
Oct-Dec
Dec-Feb
Feb-Mar
Mar-May
May-Jun
Jun-Jul
Non-burnt plots
Rainfall
ANPP
Rainfall, mm
ANPP, g m^{-2} day^{-1}
120
100
80
60
40
20
0
4.00
3.50
3.00
2.50
2.00
1.50
1.00
0.50
0.00
Jul-Sep
Sep-Oct
Oct-Dec
Dec-Feb
Feb-Mar
Mar-May
May-Jun
Jun-Jul

Figure 2

PAPER II

Forage quality of the grasses in recently burnt and non-burnt areas in western Serengeti, Tanzania.

Shombe N. Hassan[1,2], Christina Skarpe[3,4], Graciela M. Rusch[3], Håkan Hytteborn[1] and Idris Kikula[5]

Corresponding author: Shombe N. Hassan, Department of Biology, Norwegian University of Science and Technology (NTNU), NO-7491 Trondheim, Norway

Tel: + 47 73550348, FAX: +47 73596100

E-mail:shombe.hassan@bio.ntnu.no and hassanshombe@yahoo.co.uk

[1] Department of Biology, Norwegian University of Science and Technology (NTNU), NO-7491 Trondheim, Norway. Fax:+47 73596100

[2] Department of Wildlife Management, Sokoine University of Agriculture, P.O. Box 3073, Morogoro, Tanzania. Fax: +255 23 2604648

[3] Norwegian Institute for Nature Research, Tungasletta 2, NO-7485, Trondheim, Norway

[4] Faculty of Forestry and Wildlife Management, Hedmark University College, NO-2480 Koppang, Norway

[5] Institute of Resources Assessments, University of Dar-es-Salaam, P.O. Box 35097, Dar -es-Salaam, Tanzania.

Abstract

In Serengeti National Park, fire is used as a tool in maintenance and conservation of the ecosystem, including managing grasslands for high quality forage. This study evaluates forage quality in terms of concentration of nitrogen, phosphorus, potassium, magnesium, calcium, sodium and acid detergent fibre and *in vitro* organic matter digestibility in grass from burnt and non-burnt grasslands in five periods between July 2003 and August 2004. Grass samples were hand-clipped in six burnt and six non-burnt plots situated in medium-high *Themeda* grasslands in the wildebeest migratory route. We found indications that fire increased concentration of all macronutrients for all plant parts except phosphorus in live stem, and calcium and magnesium in flower and fruit. Sodium concentration in grass samples from burnt plots was double that in sample from non-burnt plots for all plant parts. Further, fire increased *in vitro* organic matter digestibility in samples of live grass components, whereas an interaction between fire and sampling time explained increased digestibility of samples of standing dead grass material. The interaction between fire and sampling time also explained a reduction in concentration of acid detergent fibre in samples of both live and standing dead grass material. Our results suggest that increased digestibility and concentration of macronutrients and reduced concentration of fibres could be part of the explanation for the differential preference by large herbivores for recently burnt and non-burnt areas.

***Key words*:** Acid detergent fibre, *in vitro* organic matter digestibility, macronutrients, Serengeti National Park

Introduction

Many grassland ecosystems including African savannas depend on periodic fire for maintenance and conservation (Brigs & Knapp, 1995; Anderson, Cook Williams, 2003). Following fire, sprouting of some plants ensues even in dry season (Vesey-FitzGerald, 1971) leading to higher forage quality in burnt than in non-burnt grasslands (Canon, Urness & Debyle, 1987; Van de Vijver, Poot & Prins, 1999). Grazing animals are often attracted to burnt patches (Rowe-Rowe 1982; Moe, Wegge & Kapela, 1990; Wilsey, 1996; Tomor & Owen-Smith, 2002).

The effect of fire on nutrient cycling particularly soil nutrients available to plants remains controversial. Because ash is the least mobile product of fire mineralization, it returns large quantities of K^{+}, Ca^{++}, Mg^{++} and NH4 , and $PO4^{3-}$ and NO3 to the soil system (Christensen, 1977; Khanna & Raison, 1986). Some authors argue that ashes (Grogan *et al.,* 2000) and fire-induced increase in mineralization rate (Singh, 1993) result in higher soil nutrient content in burnt compared to non-burnt patches (Kutiel & Shaviv, 1993). Conversely, volatilisation may result in significant losses of nitrogen (N), sulphur (S) and carbon (C), and a considerable proportion of N is lost to the atmosphere as N2 (McNaughton, 1985; Thornley & Cannell, 2004).

There is an indication that the effect of fire on plant nutrient concentration differs between plant components (Duffey *et al.,* 1974), causing larger increase of N in leaves than in the whole plant (Gwynne, 1966) after the growth resumes. The dominant mechanism for increase of nutrients in post burn vegetation depends on whether the system is nutrient-rich or nutrient poor (Van de Vijver *et al.,* 1999). In nutrient-poor systems, ash (Christensen, 1977; Grogan, Bruns & Chapin, 2000) and translocation of stored nutrients from roots to shoots (Singh, 1993; Van de Vijver *et al.,* 1999) raise nutrient concentration in the aboveground plant components. Contrary, in nutrient-rich systems much of the increase in nutrient concentration is ascribed to an increase in leaf/stem biomass ratios and in rejuvenation effects (Kauffman, Cummings & Ward, 1994; Van de Vijver *et al.,* 1999) and distribution of nutrients over less plant biomass (Van de Vijver *et al.,* 1999).

In vitro organic matter digestibility (INVOMD) is an essential determinant of forage quality, both in relation to nutrients and energy (Dorgeloh, 1999). *In vitro* organic matter digestibility is positively related to N concentration (Crampton & Harris, 1969) and negatively related to concentration of acid detergent fibre (ADF) (Pehrson & Faber, 1994).

In Serengeti National Park, the area burnt yearly in the period May 2001 to March 2005 ranged between 42% and 24% with a higher concentration and frequency in border areas and neighbouring game reserves. In a large portion of the area fire return frequency is less than 1.25 years (Dempewolf *et al.,* 2007). The frequent fires include such set for management of grasslands for high quality forage (E.A Mwangomo, unpublished). Burnt grassland patches tend to begin new seasonal production earlier than non-burnt grasslands (Pratt, 1967; Vesey-Fitzgerald, 1971; Hassan *et al.,* 2007). Subsequently, grazers are attracted to the re-growth (Wilsey, 1996) although the overall consumption of forage does not appear to be higher in burnt than in non-burnt areas (Hassan *et al.,* 2007). Minerals such as phosphorus (P), potassium (K), calcium (Ca), sodium (Na), zinc (Zn), magnesium (Mg) and copper (Cu) are required by herbivores (McNaughton, 1988; 1990) and their distribution in vegetation influences animal food selection in different spatial and temporal scales (McNaughton, Banyikwa & McNaughton, 1997).

The proportions of different grass biomass components, particularly leaf to stem ratio and the variation in forage nutrient concentration and digestibility have strong impact on seasonal animal movement and distribution in the Serengeti National Park (McNaughton, 1990; Seagle & McNaughton, 1992; Hassan *et al.,* 2007). However, the relation of the nutritive status of the vegetation in Serengeti to fire has received little attention. A better knowledge of these relationships can improve the understanding of the effects of fires on wildlife usage of the landscape particularly regarding resident herds in the western Serengeti (McNaughton, 1985; McNaughton & Banyikwa, 1995). The resident herbivores meet their dietary requirements within the region throughout the year (Seagle & McNaughton, 1992) by alternating between burnt and non-burnt patches based on trading off between quality and quantity (Hassan *et al.,* 2007). These responses have implications for the fire management program in the Serengeti National Park.

The objective of this study was to evaluate the effect of fire on forage quality in terms of digestibility and concentration of macronutrients and fibre of grass phytomass components in burnt and non-burnt plots over time. Specific questions were: 1) what is the effect of fire on the concentration of macronutrients and acid detergent fibre and on *in vitro* organic matter digestibility in grass phytomass components?, 2) is there an interaction between fire and time explaining part of the variation in grass chemistry following fire?, and 3) how does fire effect on grass chemistry vary between grass components?

Methods

Study system

This study was conducted in the western corridor of Serengeti National Park (14763 km^2). Serengeti National Park is the core area of the Serengeti ecosystem, which spans over 25000 km^2 (Serneels & Lambin, 2001). The system is situated between latitude 1° and 3°30′S, and longitude 34° and 36°E (Sinclair, 1995). The climate is sub-humid, and rainfall pattern is bimodal, with one peak in December and another peak in April (Norton-Griffiths, Herlocker & Pennycuick, 1975). Annual means increase from 600 mm on the Southeast Plains to about 1100 mm in the north (Pennycuick, 1975). Norton-Griffiths *et al.* (1975) describe the vegetation as grasslands, woodlands, and woodlands with remnant forest/bush. Open grassland dominates in southeast whereas woodland dominates the western and northern parts (Senzota, 1982). In most of Serengeti, the field layer vegetation is dominated by perennial bunch grasses with C4 photosynthesis (Frank, Mcnaughton & Tracy, 1998).

Data collection

Study sites (n = 6) were selected in medium-high *Themeda* grasslands in the western corridor in the Serengeti National Park, which is an important part of the wildebeest migration route (Thirgood *et al.,* 2004; Rusch *et al.,* 2005). *Themeda triandra, Pennisetum mezianum* and *Digitaria macroblephara* (Clyaton, Phillips & Renvoize, 1974) are the dominant grass species in all the sites. Each site consisted of one burnt and one non-burnt patch, of at least 10 ha in size. One 50 m x 50 m plot was established in each burnt and non-burnt patch, in total 12 plots. The distance between the sites ranged between 1 km and 40 km. The burnt patches were burnt in the annual early burning Park operations in May-July 2003.

In each of the twelve plots, 12 samples of grass phytomass were hand clipped to ground level from 0.0625 m^2 randomly located quadrats, in total 144 samples for each sampling period (n = 5) between July 2003 and August 2004. The periods were September 2003, December 2003, March 2004, May 2004 and July 2004. Each sample was put in a separate plastic bag and later hand-sorted into four compartments, live leaf, live stem, flower/fruit and standing dead material, and then air-dried for two weeks in paper bags. For each period, samples of the same grass phytomass component were merged into composite samples, one from burnt and another from non-burnt plots. For the chemical analysis the material was re-sampled, by drawing six random sub-samples from each composite sample and each grass biomass component, except for flower and fruit (n =3).

Chemical analysis

The samples were dried at 70 C (Mutanga *et al.,* 2004) for 48 hours and then weighed using a digital scale (Soehnle ultra, [Leifheight AG, D-56377 Nassau, Germany] with maximum 200g, d = 0.1g). Live leaf, live stem, flower and fruit and standing dead material were analysed for N, P, K, Ca, P and Na content for each sampling period, but only the vegetative parts were analysed for acid detergent fibre and *in vitro* organic matter digestibility. Minerals were determined using A.O.A.C (1970) procedures with dry ashing at 550 C for 3 hours and 6N HCl instead of 1N HCl. Nitrogen concentration was determined with Kjeldahl analysis (Okalebo, Gathua & Woomer, 1993), and ADF determined as described by Van Soest (1982). Analysis of *in vitro* organic matter digestibility followed the method of Tilley & Terry (1961). All laboratory works were undertaken at the Sokoine University of Agriculture, Morogoro, Tanzania.

Data analysis

Although variation in chemistry between the sub-samples drawn from the composite samples will not necessarily be related to the variation between the original samples, we carried out statistical analyses in order to describe size and direction of differences. Nutrient concentration, digestibility and fibre concentration are expressed as percent dry weight of the grass material. Subsequently, data were arcsine transformed prior to analysis (Underwood, 2002). Data were analysed using the General Linear Model, univariate analysis of variance (ANOVAs) routine in the SPSS 14 for windows statistical package, each plant component separately. The effect of fire was tested in a mixed model with fire as a fixed factor, sampling time as a random factor and the interaction term fire x sampling time. Independent sample T-test was used to test equality of treatment means.

Results

Patch difference in macronutrient concentration

There was a general tendency that concentrations of macronutrients were higher in grass samples from burnt than from non-burnt plots, although few of the differences were significant (Table 1). Sodium concentration in grass material from burnt plots was twice as high as in grass from non-burnt plots for vegetative grass components.

Temporal variation in macronutrient concentration

The interaction between fire and sampling time had a significant influence on N in live stem and standing dead material (Table 1). In the samples of live leaf N concentration declined successively from September to July. Leaves from burnt areas tended to have higher N concentration than such from non burnt areas, and the difference was significant in three periods, September, December and July (Figure 1). N concentration in live stem, showed a general decline along the season in the sample from the non-burnt treatment, but this pattern was not evident in the burnt treatment, which maintained relatively constant N concentrations with time. There were significant differences in N concentration in live stems between treatments approximately one year after the fire, and coinciding with the end of the rain season (Figure 1). Such pattern was not displayed for burnt plots. There were also temporal differences in N concentration in the standing dead material, but the temporal fluctuation had a different pattern than that of the live material. In grass from non-burnt plots, N concentration peaked in December, coinciding with the short rain period, whereas in grass from burnt plots, N concentration was highest in May, towards the end of the rain season (Figure 1).

The interaction between fire and sampling time had a significant influence on K in live stem and standing dead material (Table 1). The response to fire of the concentration of K in live stem and standing dead material was dependent on the sampling time (Table 1). Potasium concentration in live stems followed similar temporal patterns in samples from burnt and non-burnt plots, with peaks in December and May in both cases. However, temporal fluctuations were larger following fire than in non burnt areas. Differences between treatments were only significant at early stages after the fire (September) (Figure 2). The concentration of K in standing dead material from burnt areas increased steadily from mid dry season (two months after fire) and peaked ten months later in early dry season, approximately one year after fire. In contrast, non-burnt standing dead material showed a low value in K concentration in May. Difference between treatments occurred at the beginning of long rains (March) (Figure 2).

There was an interaction between fire and sampling time for Ca in the samples of live leaf, flower and fruit and standing dead (Table 1). In live leaves from burnt areas, the concentration of Ca was highest in September, ca. 2 months after the fire and declined steadily the following year, from September to July. In contrast, live leaves from non-burnt areas showed a peak in Ca towards the end of the wet season, in May (Figure 3). In flower and fruit, the Ca concentration differed between treatments at the beginning of the long rains, eight months after burns (Figure 3). In standing dead material, the Ca concentration increased in burnt plots from two to ten months after fire with the difference between treatments at eight and twelve months after fire (Figure 3).

The interaction between fire and sampling time had a significant influence on the Na concentration in live stem (Table 1). Peak concentration of Na in post burn live stem occurred in the short rainy period five months after fire, and then declined in the subsequent months to early dry season. In samples from non-burnt plots Na concentrations were relatively uniform throughout the season, with a minimum at the start of the dry season in July. At all sampling occasions Na concentrations were lower in samples from non burnt areas than in samples from burnt areas. Differences between treatments were at five, eight and ten months after fire (Figure 4).

Fire influence on acid detergent fiber content and in vitro organic matter digestibility

There were no significant differences in ADF between treatments but the values were for all plant parts consistently greater in grass from non-burnt compared to burnt areas (Table 1). Conversely, INVOMD was greater for all plant components from burnt compared to that of non-burnt areas but the difference was significant only for live parts (Table 1).

Temporal variation in acid detergent fiber concentration and in vitro organic matter digestibility

The interaction between fire and sampling time shows that ADF varies in grass from burnt and non-burnt areas along sampling time for both live and standing dead grass material (Table 1). ADF concentration in live leaves showed a peak at mid-growth season (March-May) in samples from non-burnt areas. In contrast, ADF concentration showed a minimum in grass from burnt areas in March. ADF concentration was generally lower in grass from burnt areas than in grass from non-burnt, except at the start of the dry season, ca 1 year after the fire. Significant differences were observed in March, May and July (Figure 5). Acid detergent fibre in live stem was also generally higher in grass from non-burnt than from burnt areas, and showed a minimum in burnt areas in March. Differences between grass from burnt and non-burnt areas were significant at two and eight months after fire (Figure 5).

Acid detergent fibre concentration in standing dead material was relatively constant in samples from non burnt areas. Acid detergent fibre concentration fluctuated more in samples from burnt areas with a minimum in March, when it was also significantly lower than in samples from non burnt areas (Figure 5). Common to all three grass components was low ADF in March for plant material from burnt areas and a drop in the concentration for grass material from non-burnt areas in July (Figure 5).

An interaction between fire and sampling time was also observed for INVOMD on standing dead material (Table 1). *In vitro* organic matter digestibility increased in samples from burnt plots from two months to twelve months after fire with significant differences between treatments at two and ten months after fire (Figure 6).

Discussion

We here discuss the differences in nutrient concentration in grass phytomass components between the compound samples from burnt and from non-burnt plots. Although the variation of the measured variables within and between the sampled plots is unknown, we find it plausible that large and significant differences between the samples to some extent reflect differences between the sampled plots.

Differences in macronutrient concentration between samples from burnt and non-burnt areas

In this study, N concentration in live leaf was highest in samples from burnt areas two months after fire and the fire enhancement effect was sustained until twelve months (Figure 1). However, results of the study on the Maasai steppe, an ecosystem adjacent to Serengeti indicated highest concentration of N one month after fire and that the enhancement was short lived, decreasing to the same level as the control by the end of three months after fire (Van der Vijver *et al.*, 1999). Thus the time of commencement of the enhancement effect on N reported in this study is comparable to that found by Van de Vijver *et al.,* (1999), but our results demonstrate a more long lived fire enhancement effect. Rejuvenation effect of fire, a cause advanced for high N concentration in post burn aboveground vegetation on the Maasai steppe soon after fire (Van de Vijver *et al.,* 1999), may be a plausible explanation in our study as well. However, the sustained effect of fire observed in our study suggests that other fire-mediated processes related to the plant-soil N circulation operate in western Serengeti. These might be related to the interactive effect of fire and herbivory causing continued rejuvenation from grazing and/or deposition of N in herbivore urine (Duffey *et al.,* 1974) which can be larger in burnt than in non-burnt areas if herbivores are more attracted to burnt patches (Rowe-Rowe, 1982; Moe *et al.,* 1990; Wilsey, 1996; Tomor & Owen-Smith, 2002). Alternatively, higher N concentrations could be due to an enhancement by fire of soil organic matter mineralization rates. For example, Fisher and Binkley (2000) have shown that the addition of ash to soil and increased microbial mineralization rate after fire can cause the build up of ammonium.

The high N concentrations in both live and standing dead grass material (Table 1) suggest that fire induced growth in these grasslands may not be N-limited. The N concentrations observed, in fact have the potential during much of the year to provide large herbivores with N above minimum level (0.8 %) required by ruminants for body maintenance (Agric. Res. Council, 1965). Moreover, enhanced N concentration in live leaf (Figure 1) suggests that resident herbivores in western Serengeti may have ccess to adequate N even in mid-dry season when poor forage quality cause N limitations in herbivores in East Africa (Sinclair, 1975).

Sodium is the primary animal attractant at many natural mineral licks (Moe, 1993) and is required particularly at pregnancy, lactation and growth of infants (McNaughton *et al.,* 1997). Significantly higher concentration of Na in live leaf and live stem material in samples from burnt compared to non-burnt areas means that Serengeti herbivores may accrue Na by grazing on vegetation developed after fires. With concentration of Na concentration in samples from burnt areas about twice as high as in those from non-burnt plots, we suspect that several processes may be responsible for the effect. According to McNaughton (1988) and Georgiadis and McNaughton (1990), areas in the Serengeti that are frequently visited and grazed by ungulates have high Na concentration in soils and in grass biomass, which they interpret as enhanced recycling of Na by the grazing herbivores. Thus, high concentration of Na in post burn grass material observed in this study may partly be attributable to greater forage consumption and/or more time spent by ungulates in burnt than in non-burnt plots (Rowe-Rowe, 1982; Moe *et al.,* 1990; Wilsey, 1996; Tomor & Owen-Smith, 2002). Also, as reported in other studies the increased Na concentration in post fire re-growth can be caused by increased Na available to plants in the soil nutrient pools as a result of release from sodium enriched ashes following the fire (Christensen, 1977; Khanna & Raison, 1986). In consequence, combined effect of the two processes is probably responsible for the observed results in this study.

We found increased nutrient concentration in post burn standing dead material, which has not been reported b before for East African Savannas. This means that translocation of nutrients to storage before wilting is weak, which might be related to high nutrient availability (Millard & Proe, 1991). Also, standing dead in burnt vegetation is younger and less leached than that in non-burnt, but, as far as the scope of this study is concerned, no conclusive explanation is available for the effect.

Temporal difference in macronutrient concentration

The significant interaction between fire and sampling time suggests that the effect of fire on the concentration of N in grass material depends on the time of sampling. The decline over time of N concentration in live stem in non-burnt samples (Figure 1) conforms to evidences elsewhere (Acosta *et al.,* 1991; Mustafa & Seguin, 2003; 2004) that N concentration drops as growing season advances.

Concentration of K in live stem was significantly higher in grass from burnt compared to non-burnt areas, two months after fire (Figure 2). This is comparable to the findings of Van de Vijver et *al*. (1999) who found increased K concentration one month after fire in live leaves from burnt plots in the Maasai steppe. According to Van de Vijver *et al.* (1999) high concentration of K one month after fire was due to distribution of the element over less grass material due to reduced production (mass per time per area) following fire.

Concentration of Ca in post burn live leaf was highest in samples from the first sample occasions after fire (Figure 3), which is also comparable to one month after fire reported for the Maasai steppe (Van de Vijver *et al.,* 1999). They suggested that higher Ca in post burn re-growth was due to rejuvenation effect of fire, which may be the cause also in our study. On the other hand, the cause for low content of calcium in flower and fruit in samples from burnt compared to non-burnt areas (Figure 3) is uncertain. Another study in the same area revealed higher flower and fruit production in non-burnt compared to burnt patches (Hassan *et al.,* 2007), invoking a link between fire and Ca metabolism related to flower and fruit development, either indirectly or directly. Calcium is required for flower and fruit development (Kiss, 1996). Apparently, addition of ash to soil and increased microbial mineralization rate after fire cause build up of ammonium (Fisher & Binkley, 2000), which may impair Ca availability to plants (Kessel, 2005). We think that the uptake of Ca in burnt plots is probably impaired at the time of flowering/fruiting due to cumulative effect of ammonium during short rains in November-December.

Na concentration in samples of live stem from burnt patches peaked five months after fire and then a declined during the next seven months (Figure 4). This is in accordance with the understanding that in Serengeti, forage is Na-deficient in the dry season (McNaughton, 1990).

The duration of fire enhancement effect on concentration of some nutrients in samples of both live and dead plant components in our results is different to previous notion that the effect starts shortly after fire (Christensen, 1977; Singh, 1993; Van de Vijver *et al.,* 1999; Snyman, 2003) and is of brief duration (Van de Vijver *et al.,* 1999). In our study increased concentrations of several elements have demonstrated that the enhancement effect can persist from three to twelve months after fire.

In vitro organic matter digestibility in samples from burnt and non-burnt areas

Although INVOMD was significantly higher in samples from burnt compared to non-burnt areas only for live parts, greater INVOMD value for standing dead from burnt areas demonstrates that fire can enhance INVOMD in both live and dead grass material (Table 1). Increased digestibility following fire is known from studies in other ecosystems (Pearson, Davis & Schubert, 1972; Singer & Harter, 1996) but such knowledge was limited to live parts.

Temporal variation in content of acid detergent fibre and in vitro organic matter digestibility

The weak tendency for ADF in live leaf in samples from non-burnt patches to increase from mid dry season (September) to the end of wet season (May) may be indicative of an accumulation of structural carbohydrates in cells in absence of disturbance such as fire (Figure 5). The significantly higher ADF in samples from non-burnt areas than from burnt areas during March–May suggests that in Serengeti, grasses lay down greater amount of structural carbohydrates in the second part of the wet season. Low concentration of ADF for all vegetative grass components in samples from burnt areas in March (Figure 5) may be caused by fresh growth in burnt areas following the long rains in March to May (Norton-Griffiths *et al.,* 1975), and low ADF concentration in the young biomass. However, it is not clear why the ADF level in all vegetative grass components in samples from non-burnt areas dropped in July (Figure 5). Nutritional value of the fodder was expected to decline with time after fire because more fibrous material would normally build up with maturation stage (Milford & Minson, 1966; Pratt & Gwynne, 1997).

This study also shows that INVOMD in samples of post fire standing dead material increased with an increase in N concentration from two to ten months after fire. This is an indication of positive relationship between N concentration and digestibility following fire, as also described by Crampton & Harris (1969) for live grass parts.

Standing dead plant material may form a significant part of the herbivore diet in the area when the supply of live material is sparse such as in February and July (Hassan *et al.,* 2007). Enhanced N concentration and digestibility and reduced fibre concentration following fire promotes the nutritional value of standing dead, and probably its acceptability to grazing mammals. Reduced ADF and enhanced digestibility enable herbivores grazing in burnt areas to maximize both daily energy and nutrient intake (Fryxell, 1991) because a high overall intake of fibres reduces the extent of digestibility of each food particle (Smith, 1995). With understanding that high quality in forage refers to high N concentration, high digestibility and high mineral level (Hanley *et al.,* 1992; Vázquez-de-Aldana *et al.,* 2000) and low ADF concentration (Kloppenburg *et al.,* 1995), a correct burning regime remains vital for the maintenance of healthy animal populations in Serengeti compared to the consequence of fire exclusion or too frequent burning. A mosaic of burnt and non-burnt patches is essential in western Serengeti since large herbivores appear to shift preferences between burnt and non-burnt areas along the growth season (Hassan *et al.,* 2007).

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Tables

Table I: Concentration of N, K, P, Mg, Ca and Na, and ADF and INVOMD in percent of dry weight of grasses in burnt and non-burnt grassland patches. Values higher in non-burnt area are boldfaced. SE/± = standard error.

Element	Plant component	Treatment				Fire * sampling time interaction
		Burnt	Non-burnt	SE^{B}	P value	P value
N	Live leaf	1.76	1.36	0.04	<0.001**	0.983
K		2.29	2.07	0.09	0.209	0.375
P		0.35	0.31	0.02	0.071	0.820
Mg		0.19	0.18	0.01	0.261	0.514
Ca		0.35	0.32	0.01	0.596	<0.001**
Na		0.46	0.25	0.03	0.003*	0.551
N	live stem	0.75	0.69	0.06	0.632	0.001**
K		1.04	0.94	0.04	0.732	<0.001**
P		0.15	0.15	0.01	0.978	0.207
Mg		0.08	0.06	0.01	0.190	0.370
Ca		0.13	0.08	0.02	0.054	0.780
Na		0.22	0.10	0.01	0.010*	0.003*
N	Flower & Fruit	1.47	0.99	0.13	0.169	0.239
K		1.09	0.94	0.12	0.406	0.612
P		0.23	0.21	0.02	0.630	0.507
Mg		0.11	**0.14**	0.01	0.131	0.573
Ca		0.13	**0.21**	0.01	0.168	0.031*
Na		0.09	0.04	0.02	0.355	0.102
N	Standing dead	0.76	0.59	0.03	0.111	0.006*
K		0.68	0.42	0.04	0.040*	0.024*
P		0.15	0.11	0.01	0.002*	0.905
Mg		0.13	0.11	0.01	0.148	0.116
Ca		0.43	0.35	0.02	0.353	<0.001**
Na		0.22	0.10	0.01	0.010*	0.081
ADF	Live leaf	37.19 (± 0.36)	40.73 (± 0 37)		0.309	<0.001**
INVOMD		56.60 (± 1.52)	46.83 (± 1.55)		0.003*	0.745
ADF	Live stem	47.01 (± 0.59)	51.56 (± 0.59)		0.256	<0.001**
INVOMD		41.47 (± 1.23)	30.45 (± 1.21)		0.014*	0.061
ADF	Standing dead	49.18 (± 0.55)	55.00 (± 0.55)		0.107	<0.001**
INVOMD		36.94 (± 1.10)	30.02 (± 1.10)		0.083	0.009*

* Significant at the 0.05 level; ** significant at $P \leq 0.001$ (Univariate ANOVAs)

^{B}Applies to both treatments

Figure legends

Figure 1: N in percent dry weight in live leaf, live stem and standing dead in burnt (dark bars) and non-burnt (open bars) plots between September 2003 and July 2004. Asterisk indicates significant difference between means (independent sample t-test * $P < 0.05$; ** $P \leq 0.001$). Error bars represent 95 % confidence interval (CI).

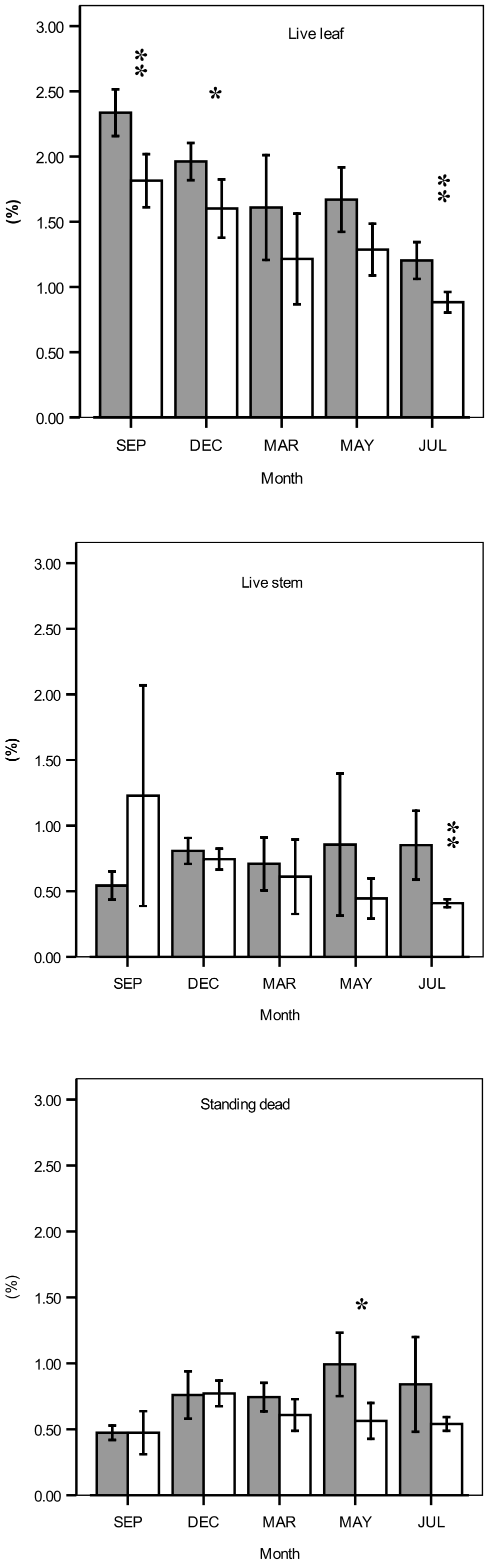
Figure 2: K in percent dry weight in live stem and standing dead material in burnt (dark bars) and non-burnt (open bars) plots between September 2003 and July 2004. Asterisk indicates significant difference between means (independent sample t-test * $P < 0.05$; ** $P \leq 0.001$). Error bars represent 95 % confidence interval (CI).

Figure 3: Ca in percent dry weight in live leaf, flower and fruit and standing dead material in burnt (dark bars) and non-burnt (open bars) plots between September 2003 and July 2004. Asterisk indicates significant difference between means (independent sample t-test * $P < 0.05$; ** $P \leq 0.001$). Error bars represent 95 % confidence interval (CI).

Figure 4: Na in percent dry weight in live stem in burnt (dark bars) and non-burnt (open bars) plots between September 2003 and July 2004. Asterisk indicates significant difference between means (independent sample t-test * $P < 0.05$; ** $P \leq 0.001$). Error bars represent 95 % confidence interval (CI).

Figure 5: Acid detergent fibre in percent of dry weight in live leaf, live stem and standing dead material in burnt and non-burnt plots between September 2003 and July 2004. Asterisk indicates significant difference between means (independent sample t- test ** $P \leq 0.001$). Error bars represent 95 % confidence interval (CI).

Figure 6: *In vitro* organic matter digestibility in percent of dry weight in standing dead in burnt and non-burnt plots between September 2003 and July 2004. Asterisk indicates significant difference between means (independent sample t- test * $P< 0.05$¸**$P \leq 0.001$). Error bars represent 95 % confidence interval (CI).


Live leaf
3.00
2.50
2.00
1.50
1.00
0.50
0.00
(%)
SEP
DEC
MAR
MAY
JUL
Month
Live stem
3.00
2.50
2.00
1.50
1.00
0.50
0.00
(%)
SEP
DEC
MAR
MAY
JUL
Month
Standing dead
3.00
2.50
2.00
1.50
1.00
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(%)
SEP
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JUL
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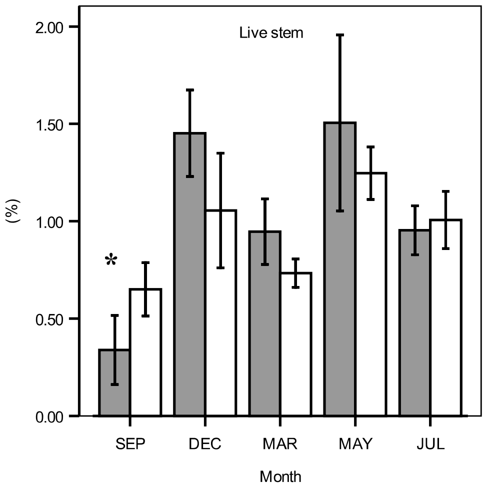
Figure 1


Live stem
2.00
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(%)
*
SEP
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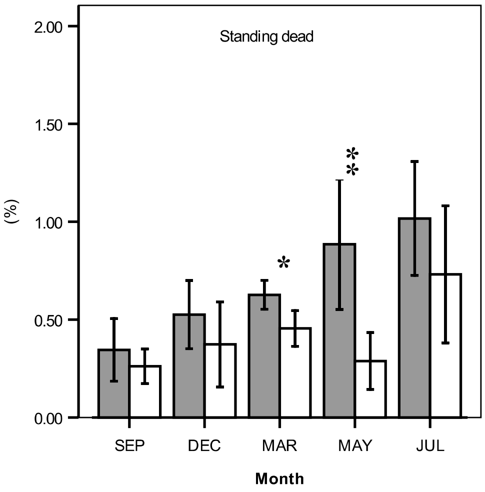
Standing dead
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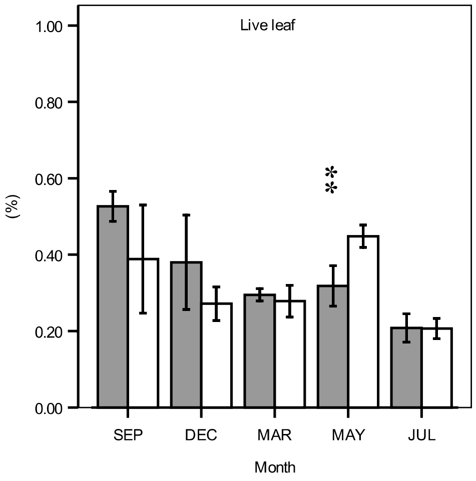
Month

Figure 2


Live leaf
1.00
0.80
0.60
0.40
0.20
0.00
(%)
*
*
SEP
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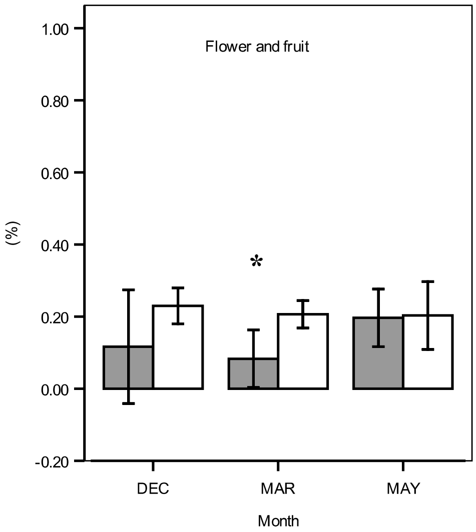
MAR
MAY
JUL
Month


Flower and fruit
1.00
0.80
0.60
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0.20
0.00
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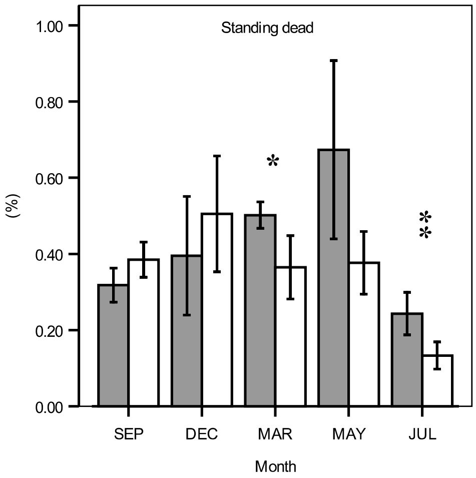
Standing dead
1.00
0.80
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Figure 3

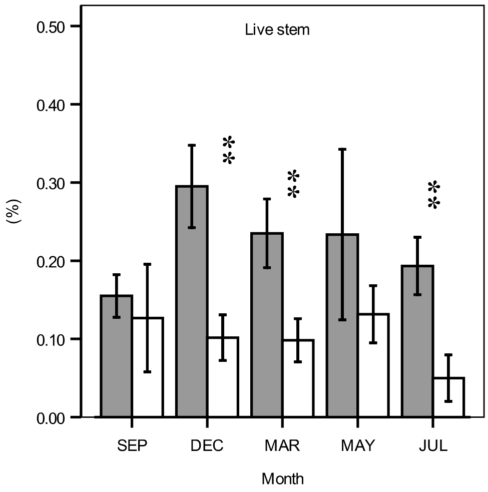
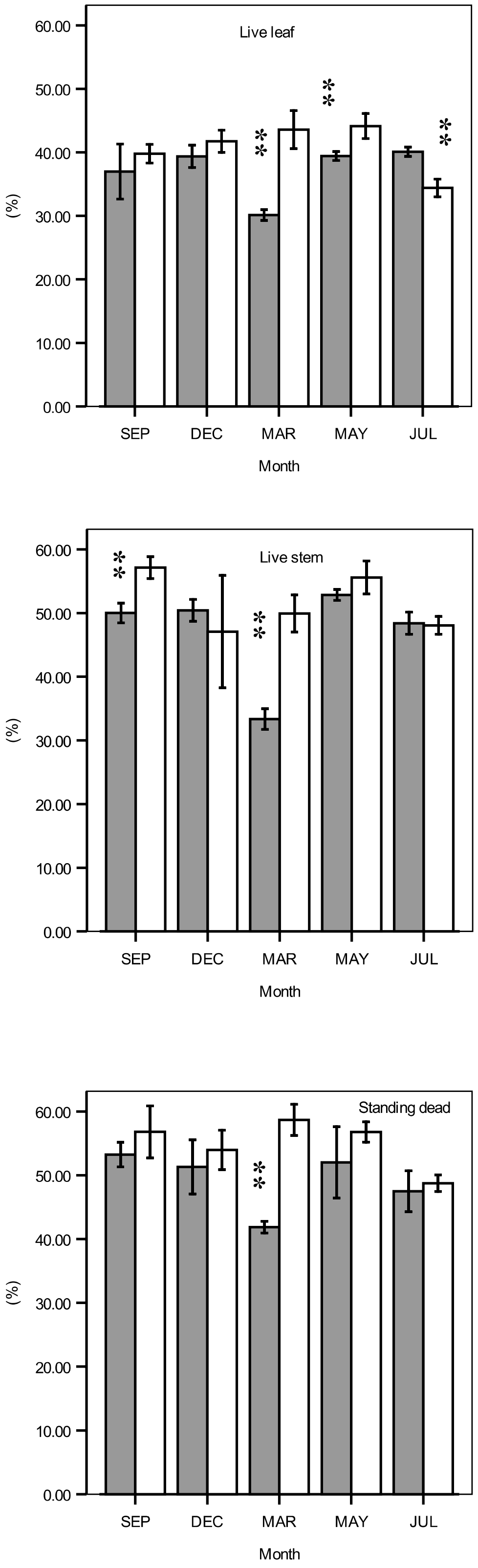


Figure 4


Live leaf
(%)
60.00
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Live stem
(%)
60.00
50.00
40.00
30.00
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SEP
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**
Standing dead
(%)
60.00
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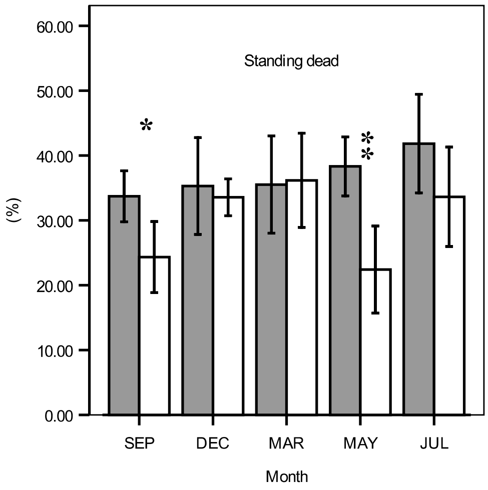
Figure 5


Standing dead
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SEP
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MAR
MAY
JUL
Month

Figure 6

PAPER III

Effects of fire on sward structure and grazing in western Serengeti, Tanzania

Shombe N. Hassan[1,2], Graciela M. Rusch[3], Håkan Hytteborn[1], Christina Skarpe[3,4] and Idris Kikula[5]

Corresponding author: Shombe N. Hassan, Department of Biology, Norwegian University of Science and Technology (NTNU), NO-7491 Trondheim, Norway

Tel: + 47 73550348, FAX: +47 73596100

E-mail:shombe.hassan@bio.ntnu.no and hassanshombe@yahoo.co.uk

[1]Department of Biology, Norwegian University of Science and Technology (NTNU), NO-7491 Trondheim, Norway. Fax:+47 73596100

[2]Department of Wildlife Management, Sokoine University of Agriculture, P.O. Box 3073, Morogoro, Tanzania. Fax: +255 23 2604648

[3]Norwegian Institute for Nature Research, Tungasletta 2, NO-7485, Trondheim, Norway

[4]Faculty of Forestry and Wildlife Management, Hedmark University College, NO-2480 Koppang, Norway

[5]Institute of Resources Assessments, University of Dar-es-Salaam, P.O. Box 35097, Dar -es-Salaam, Tanzania.

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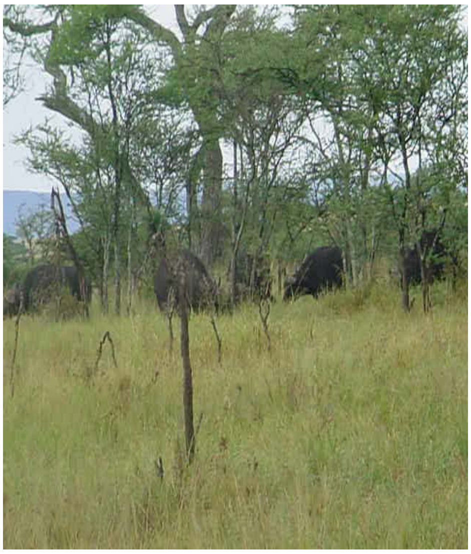
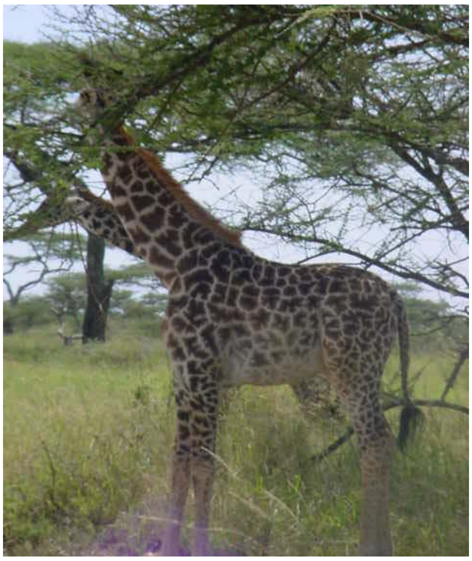
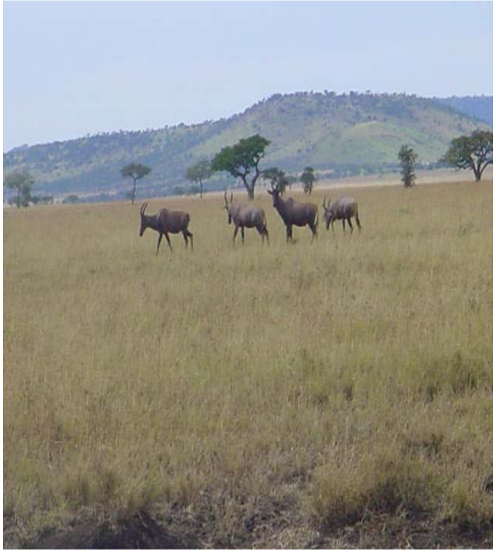
PAPER IV







Fire history and herbivore patch selectivity in Serengeti, Tanzania

Shombe N. Hassan[1,2], Graciela M. Rusch[3], Sigbjørn Stokke[3], Christina Skarpe[3,4], Håkan Hytteborn[1] and Eivin Røskaft[1]

Corresponding author: Shombe N. Hassan, Department of Biology, Norwegian University of Science and Technology (NTNU), NO-7491 Trondheim, Norway

Tel: + 47 73550348, FAX: +47 73596100

E-mail:shombe.hassan@bio.ntnu.no and hassanshombe@yahoo.co.uk

[1]Department of Biology, Norwegian University of Science and Technology (NTNU), NO-7491 Trondheim, Norway. Fax:+47 73596100

[2]Department of Wildlife Management, Sokoine University of Agriculture, P.O. Box 3073, Morogoro, Tanzania. Fax: +255 23 2604648

[3]Norwegian Institute for Nature Research, Tungasletta 2, NO-7485, Trondheim, Norway

[4]Faculty of Forestry and Wildlife Management, Hedmark University College, NO-2480 Koppang, Norway

Abstract

Differences in the use of burnt areas by large herbivore species, the comparative use of burnt and non-burnt areas at the scale of the landscape and how differences in the history of fires affect herbivore patch selection are questions about the role of fires in savannas that are incompletely understood. We examined the degree of herbivore preference to patches differing in three-year fire history by 24 herbivore species in Serengeti. Animal occurrences and their geographical position were recorded at approximately monthly intervals between May 2001 and April 2002 and from May 2003 to April 2006. The areas of burnt and non-burnt patches along transect segments in the period May 2000 to November 2006 were extracted from fire area maps in Dempewolf *et al.* (2007). To test whether herbivore species individually or grouped in diet groups selected patches non-randomly in relation to the availability of the patch, we used chi-square goodness-of-fit tests, and calculated a selection ratio as an index of preference for fire patch types. Both the number of species recorded and the numbers of selective and non-selective species of individual fire patch types varied between years. We found significant differences of selection indices between burnt and non-burnt patch types between years. The shifts could be related to differences among years in the timing of the burns, but also to between-years differences in the accessibility of burnt patches, since in some years a large portion of the burnt areas occurred outside Serengeti National Park. There was a general trend for grazers, except African buffalo (*Syncerus caffer*) to prefer patches burnt in the current year. To some extent, our study reinforces current theories concerning ungulate body weight and the use of burnt and non-burnt patches. Small sized species such as Thompson's gazelle (*Gazella thomsoni*) had significantly higher preference for burnt than non-burnt patch types. Medium sized topi (*Damaliscus lunatus*) and Blue wildebeest (*Connochaetes taurinus*) had higher preference for burnt patch types but with a less clear pattern than in Thomson's gazelle. Of comparable medium size, hartebeest (*Alcelaphus buselaphus*) showed no significant differences between burnt and non-burnt patches. African buffalo, the largest grazer species had higher preference for non-burnt patches. In contrast to grazers, preferential browsers and mixed feeders showed a consistent tendency to occur more frequently in non-burnt patch types. Our results are also indicative that ungulates generally had lower preference for areas that burnt in the current year but that had burnt repetitively in a 3-year period compared to areas that were not burnt for 3 years.

Key words: Fire period, patch type and preference, selection ratio, Serengeti ecosystem

Introduction

Fire frequencies have increased considerably during the past decades in East African savannas (Van de Vijver, Poot & Prins, 1999). Burning is commonly practised in management and conservation of the diverse and rich wildlife without an adequate knowledge about fire-impact on the forage resource and on wildlife utilisation of areas with different fire history.

Burning causes significant changes in the grassland structure (Hassan *et al.,* 2007; Hassan *et al., in prep.*) by removing old plant parts and debris and by stimulating re-sprout of the vegetation (Vesey-Fitzgerald, 1971), thus changing the composition of forage available for herbivores. Since herbivores selectively respond to spatial patterns of forage distribution (Bailey *et al.,* 1996), fire-induced changes in phytomass composition will have consequences for herbivore use. Although several studies in African savannas and elsewhere show that wild large herbivores utilize burnt areas more than non-burnt areas (Moe, Wegge & Kapela, 1990; Wilsey, 1996; Pfeiffer & Hartnett, 1995; Tomor & Owen-Smith, 2002), a couple of studies in Serengeti support that herbivores can shift the preference between burnt and non-burnt vegetation (Wilsey, 1996, Hassan *et al.,* 200). This may result from the fact that foraging ungulates concentrate in areas providing the optimal solution to the trade-off between forage quality and quantity, i. e., the maximum intake of digestible energy and nutrients per bite (Pyke, Pullian & Charnov, 1977; Belovsky, 1984; Wilmshurst, Fryxell & Hudson, 1995).

Although burning in savanna is followed by a rapid increase in phytomass (McNaughton, 1985), the quantity usually remains lower than in non-burnt grassland (Bond-Lamberty, Wang & Gower, 2004, Hassan *et al., in prep.*). Consequently, forage quantity (Spalinger & Hobbs, 1992; Ginnett & Demment, 1995; Hassan *et al., 2007*) may influence selection between burnt and non-burnt patches. Fire can also enhance the quality of the phytomass available to herbivores through higher concentration of nitrogen, particularly in live leaf (Prins & Beekman, 1989; Cook, Hershey & Irwin, 1994; Hassan *et al., in prep.*), and higher ratio of new growth to residual low-quality material from earlier seasons (Everson, 1999).

At the scale of the landscape, fire induced spatial habitat heterogeneity can influence the density and movements of wildlife in the landscape (Weins, 1976) and may also influence individual herbivore species to exploit patches differently. Recently, Hassan *et al.* (2007) found that forage consumption in burnt and non-burnt patches in western Serengeti shifted along the year, likely due to temporal changes in the trade-off between quantity and quality of the forage.

Other factors that, in addition to the quality and the amount of forage available, can affect the preference by herbivores for burnt or non-burnt areas are the size of the patches (Peek, 1986), animal body size, gut type, capacity and ability to crop forage (Senft *et al.,* 1987) and anti-predatory behaviour (Jarman & Jarmann, 1979; Hunter, 1996; Fisher & Linsenmair, 2001; Wolff & van Horn, 2003). The ability of herbivores to detect and efficiently crop resource patches varies (Jiang & Hudson, 1993) and also the size of the patch will affect the ability of a forager to detect finer scales of patchiness (Senft *et al.,* 1987). Wilsey (1996) found that Thomson's gazelle (*Gazella thomsoni*), Grant's gazelle (*G. granti*), impala (*Aepyceros melampus*) and Blue wildebeest (*Connochaetes taurinus*) were more abundant in burnt grassland sites and argued that these species require high forage quality, but can tolerate low food biomass levels (Murray & Illius, 1996; 2000). In contrast, Burchell's zebra (*Equus burchelli*) and topi could balance their intake by grazing in both burnt and non-burnt areas (Wilsey, 1996), due to the ability to utilize high food biomass that is low in quality (Bell, 1971; Jarman, 1974; Demment & Van Soest, 1985).

In the present study we assess the use by different herbivores of areas with different fire history. Previous studies in Serengeti (Wilsey, 1996) and elsewhere (Moe *et al.,* 1990; Tomor & Owen-Smith, 2002) on habitat preference between burnt and non-burnt areas were carried out shortly after burning in a single fire event. However, the effect of multiple fires and of long term response of herbivores to burnt vegetation is less known. This study examines the preference(s) during a full year by different ungulates to patches differently burnt over the proceeding three-year period. This is a comprehensive study in terms of the extent of the area of the ecosystem covered, the length of the time interval, and the intensity of the animal counts. Specifically we examined (1) how herbivore species and diet groups distribute between burnt and non-burnt patches in four different one-year periods with different area and distribution of fires and (2) how the three-year fire history of the patches affects the habitat choice by animal species and diet groups.

Methods

Study system

The core study area is Serengeti National Park (SNP, 14,763 km^2), along with Ngorongoro Conservation Area (NCA, 8,288 km^2), Grumeti Game Reserve (GGR, 416 km^2) and Ikorongo Game Reserve (IGR, 563 km^2), all of which form part of the Serengeti ecosystem. The Serengeti ecosystem extends about 25,000 km^2 (Serneels & Lambin, 2001; Kideghesho *et al.,* 2006) and is located between latitudes 1° and 3° S and longitudes 34° and 36°E (Fig. 1). Annual migrations of wildebeest, Burchell's zebra, Thomson's gazelle, and eland (*Taurotragus oryx*) are important features of the ecosystem (Sinclair, 1975; 1995). There are about 27 species of ungulates in the Serengeti system (Sinclair & Norton-Griffiths, 1982) and wildebeest, Burchell's zebra, Thomson's gazelle, African buffalo (*Syncerus caffer*) and topi (*Damaliscus lunatus*) are the major grazing species (McNaughton, 1985).

Both prescribed and illegal fires are another key ecological feature of the ecosystem (Table 1). Prescribed fires are set by the management authorities of the respective protected areas. For SNP, legal burning commonly occurs from May (end of wet season) to early August (mid dry season). Reasons for burning include control of wildfires originating outside the park, keeping animals in tourist circuit and maintaining green forage for herbivores (Mwangomo, 2003). In GGR and IGR, legal fires occur both during the transition between the short and the long rainy periods (January/February) as well as in May-July. Dry season fires erupt in September/October due to different causes including those associated with illegal hunting activities. Thus, a mosaic of patches burnt at different times or unburnt characterise the landscape (Dempewolf *et al.,* 2007). The mosaic provides a combination of high quality and high quantity food as well as cover for small species (Moe *et al.,* 1990).

Animal counts

Ungulates were counted along transects of varying lengths that were distributed along the existing road-network in the study area, starting from the central region of Serengeti National Park (Seronera). Animals were counted at approximately monthly intervals between May 2001 and April 2002 and from May 2003 to April 2006 (Table 1). Counts were conducted on 1 km long transect segments, spaced at an interval of 2 km. A total of 150 transect segments along 2,050 km were systematically placed and permanently marked in 9 areas as follows:

From Fort Ikoma outside SNP, north-west of GGR, Fort Ikoma/Grumeti road, 14 transect segments

Inside GGR, eastern part, Grumeti/Robanda road, 5 transect segments

Inside SNP, to south-west, Sopa road, 10 transects segments

Inside SNP, to south-east across the Serengeti Plains into NCA Plains

Seronera/Arusha road, 28 transect segments

Inside SNP, to north-west, Seronera/Fort Ikoma road, 25 transect segments

Inside SNP, to the north, Seronera/Lobo road, 20 transect segments

Inside SNP, to the east, Seronera/Barafu kopjes road, 6 transect segments

Inside SNP, to the west (Western 1) of SNP,

Seronera/Ndabaka road, 29 transect segments and

Inside SNP, to the west (Western 2) of SNP, Seronera/Ndabaka road, 13 transect segments

The start and end points of all transect segments together with all other geographical positions were recorded in UTM system, map datum ARC 1960 with a Garmin XL12 GPS. Counting was performed using a Land-rover pickup driven at 15-20 km per hour with one recorder and four experienced observers at the back of the vehicle. Each pair of observers concentrated on one side of the transect (right/left) plus the transect line and scanned for animals in a section of 180 degrees and up to 1000 m. At each observation i. e. a single animal or a group of animals of the same species, the vehicle was stopped and the GPS position of the vehicle, the distance to the animal(s), and the angle of the animal or herd and angle of the road to the magnetic North were recorded using a range finder. For herds the distance was measured to the centre of the cluster. These records were used to calculate the animal/herd geographical location. Counting started no later than 7.00 a.m and ended around 5.00-6.00 p.m depending on the transect length. Transects were driven alternately in both directions to avoid differences in animal activity and visibility as a result of time of day. Species names follow the Mammal Species of the World data base (MSW III).

Fire patch types

The areas of burnt and non-burnt patches along transect segments in the period May 2000 to November 2006 was extracted from the fire maps in Dempewolf *et al.* (2007). Burnt areas were mapped with high accuracy using an automated algorithm based on minimum near infrared composites generated from daily Moderate-Resolution Imaging Spectroradiometer (MODIS) imagery at 250 m resolution. Burned area index thresholds are adjusted dynamically to the spectral characteristics of each composite.

Most fires in Serengeti occur in the early dry season period (May – August), and thus the yearly periods were defined to start in May and to continue to April next year (Table 1). The geographical positions of the transect segments and of the animal counts were collated with the fire maps in Dempewolf *et al.* (2007) using the ArcGIS software version 9. An envelope of 1000 m on both sides of the transect segments of the animal counts was delimited to calculate the available area of the fire patch types in each period.

Eight fire history categories were defined. The definitions of these categories were based on the fire history during the last three consecutive years (Table 3). During the analyses the categories were grouped either in two, three or kept as eight fire types and the analyses of the fire impact on the occurrences of the animals could thus be performed on three different levels of details. The analyses of the animals for each yearly period (May to April, next year) were conducted and analyzed in three independent contrasts (Table 3).

Patch selectivity analysis

Animal counts and the area of the fire history patch types were summed over fire periods extending from May to April the subsequent year (Table 1). The terms 'preference' for a fire patch type (i. e. the likelihood that a patch type will be selected if provided on an equal basis with others) and 'selection ratio' (an index of the probability that a patch type will be selected) are used in accordance to Johnson (1980). To test whether herbivore species selected habitats non-randomly in relation to their availability, we used chi-square goodness-of-fit test (Manly, McDonald & Thomas, 1993; Manly *et al.*, 2002). The same analysis was carried out with "diet groups" i.e. preferential grazers, preferential browsers and mixed feeders. The proportion of each fire patch type available in each fire season was computed relative to the total envelope area (100 %) for each fire season. Species and diet groups that did not meet the Chi-square test requirement of a minimum expected number of counts equal to or larger than 5, were excluded from the analyses.

A preference index for patch types by the individual species, all species and diet groups of large herbivores (Table 2) was calculated based on the selection ratio (Manly *et al.,* 1993; 2002):

$$\hat{w}_i = O_i/p_i$$

where $\hat{w}_i$ is the selection ratio or preference index for the fire patch type *i,* O_i is the proportion of the observations of the species or diet group that is in patch type i, and p_i is the proportion of the available patches that are of type i. This design assumes that all animals have the same access to all patch types (Manly *et al.,* 1993; 2002).

An approximate 100(1-μ) % confidence interval for each selection ratio was computed as:

$\hat{w}i \pm z\mu /2se(\hat{w}_i)$,

where z μ /2 is the critical value of the standard normal distribution corresponding to an upper tail area of μ/2; and se($\hat{w}_i$) is the standard error for the selection ratio (= se O_i/p_i). Comparison between selection ratios was done using the confidence limits with probability of all pair-wise intervals at 0.95 (Manly *et al.,* 1993; 2002). This procedure is a replica of Bonferroni adjustment used to test on proportion of resources selected (Manly *et al.,* 1993; 2002), and it is desirable in avoiding type II error when there are several tests.

Results

Fire distribution

Ideally, the fires should have been equally distributed both along the transects and among the different years. The two periods, May 2003 to April 2004 and May 2004 to April 2005, with most complete observations of ungulates over the whole period, show, however, that during the second of these two years, fires were disproportionably concentrated on one of the game reserves, Grumeti Game Reserve (Fig. 2a, b).

Number of species and species groups

Twenty-four different ungulate species were observed during the four years of animal counts from May 2001 to April 2002, and from May 2003 to April 2006 but the number varied from 18 to 22 between years (Table 2). Six of the species are classified as mainly browsers, ten as mainly grazers and eight as mixed feeders (Table 2). The number of species with different preference for particular fire patch types, i. e. with significantly different likelihood of occurrence in the different fire patch types, and the number of indifferent species, i.e. species with non-significantly different preference for any fire patch type, varied strongly between years (Table 4).

In the analyses with only two fire patch types, burnt the current year vs. not-burnt the current year, the number of species with a preference ranged between 0 and 7 in the different years, and that without a preference ranged between 12 and 19 (Table 4). In the analyses contrasting three fire patch types (Table 3) the number of species with significant differences in preference for individual fire patch types varied among years between 4 and 9, and between 10 and 16 for those without a preference. In the three-patch-types contrast, the number of species with a preference was higher than that of only two types (Table 4). In the eight-patch-types contrast, the number of species with a preference varied between 4 and 11 (Table 4).

Species distributions

In the contrast with two groups there were eleven different species with a significantly different distribution at least one of the years in the study (Table 4). Thirteen species had a significantly different distribution, at least one of the years in the contrast with three groups (Table 4). In the last contrast with eight different patch types the total number of species with a significant distribution at least one year was 12 (Table 4). The two species of duikers (Red-flanked duiker *Cephalophus rufilatus*, bush duiker *Sylvicapra grimmia*), gerenuk (*Litocranius walleri*), klipspringer (*Oreotragus oreotragus*), oribi (*Ourebia ourebi*), spring hare (*Pedetes capensis*) and rock hyrax (*Procavia capensis*) did not have any significant preference in any of the three different contrasts, and Bohor reedbuck (*Redunca redunca*), Defassa waterbuck (*Kobus ellipsiprymnus defassa*), eland and steenbok (*Raphicerus campestris*) only in one year in one of the contrasts (Table 4).

Two-patch-types contrasts, burnt vs. non-burnt in the current year

We compared animal preference for (1) patches burnt the current year regardless of previous fire history (BC) with that of (2) patches not burnt the current year regardless of previous fire history (NBC). Taken all species together, the distribution between these two fire patch types differed between the years. In 2001-2002 and 2004-2005 there was a significantly higher likelihood of occurrences in non-burnt than in burnt patches, but in 2003-2004, the opposite (Table 4, Fig. 3a). The diet group grazers had a similar preference pattern than that of all species together (Table 4, Fig. 3a). Browsers and mixed-feeders consistently preferred non-burnt patches in all years (Table 4, Fig. 3b).

The distributions of individual species within diet groups varied. Giraffe (*Giraffa camelopardalis*), the only browser with significantly different distribution among patch types (Table 4), was found more often in non-burnt patches. Among the grazers, African buffalo was observed consistently more often in non-burnt areas (Fig. 4a), and Burchell's zebra the only year with a significantly different distribution was found more often in burnt areas (Fig. 4b). Thomson's gazelle varied between years with significantly higher likelihood of occurrences in burnt patches in 2003 - 2004 and higher in non-burnt patches in the first year (Fig. 4b). Topi had significantly different distributions between the patches only in the period 2003-2004, with higher likelihood of occurrences in burnt than in non-burnt patches (Table 4, Fig. 4b). Warthog (*Phacochoerus africanus*) had also significantly different distributions only once, namely in the period 2001-2002. During this period Warthog was found more often in non-burnt than in burnt areas (Table 4, Fig. 4b). Wildebeest showed opposite preferences in the two periods with significant different distributions, namely the period 2003-2004 with higher likelihood for occurrences in areas burnt that year and the period 2004-2005 with the opposite distribution.

Among the mixed feeders bushbuck was during one year more often found in non-burnt, and steenbok in burnt patches (Table 4). Grant's gazelle and impala, the two largest mixed feeder populations, consistently (both during 3 years) selected more often non-burnt than burnt patches (Table 4, Fig. 5).

Three-patch-types contrasts

We compared preferences for (1) patches burnt the current year regardless of previous fire history (BC) with (2) patches not burnt the current year but burnt either one or two years ago (NBC, B1 or 2) and patches not burnt during the three years of the study (NB). With all species pooled together, there was a significantly higher occurrence in patches that had not burnt during the three last years (NB) over those that had burnt sometime in the previous two years (NBC, B1 or 2) (Table 4, Fig. 6a). This pattern was consistent in three investigated periods except for the period May 2003- April 2004 and for the three diet groups (Table 4, Fig. 6a, b). The differential preference by the individual diet groups for either patches burnt in the current year (BC) or patches not-burnt in the current year but burnt some time in the previous 2 years (NBC, B1 or 2), varied among years. In the period May 2003-April 2004 all groups preferred patches burnt the current year, but in the two following years the diet groups had different preferences (Fig. 6a, b).

The two browsers, giraffe and Kirk's dik-dik (*Madoqua kirkii*), preferred areas that did not burn for 3 years (except giraffe in one year) (Table 4, Fig. 7a). In contrast, there was no consistent pattern among the individual species of grazers across years. Most grazers preferred patches that had not burnt for 3 years in 2001-2002, but the pattern was not clear in the other years (Table 4, Fig. 7b) and even individual grazer species did not show a consistent preference in these periods (Fig. 7b, c). African buffalo and warthog, both in 2001-2002 seem to have preferred not burnt areas, as well as Bohor reedbuck in 2004-2005, but topi in 2003-2004 preferred areas that burnt the current year. In 2003-2004 Burchell's zebra had significantly higher occurrences on patches burnt the current year than on other patch types (Fig. 7c). Thomson's gazelle (Fig. 7b) and Blue wildebeest (Fig, 7c) had about the same pattern and preferred currently burnt patches in 2003-2004, but preferred not burnt patches in 2004-2005.

The mixed feeders Grant's gazelle and impala had significantly higher occurrence in patches that did not burnt in 3 years in all four years, except impala in 2001-2002 (Table 4, Fig. 7d). There were no observations of bushbuck in areas burnt the current year 2004-2005, but more observations in areas burnt one of the earlier years. African elephant (*Loxodonta africana*), in 2003-2004, the only year with a significantly different distribution, had higher occurrences in not burnt patches.

Eight-patch-types contrasts

In the analysis with all species lumped together and with eight patch types the selection ratio of patches that burnt repeatedly were lower than for those that burnt only once in three years. This pattern was clearer in the first three periods of the study (Table 4 and Fig. 8a). A similar pattern was found for grazers, except in 2003-2004, and also for mixed feeders and browsers (Table 4 & Fig. 8a-b).

The confidence intervals around the selection ratios increased somewhat with the observations divided among eight categories for the individual species. There were significantly fewer occurrences of giraffe in most combinations of repeated burning. Among the grazers, Thomson's gazelle in two of the four years, showed a preference for patches that only burnt in the current year in a period of three years (BC, NB1, NB2). In the period May 2001 – April 2002 Thomson's gazelle preferred non-burnt patches (Table 4 & Fig. 9) but in May 2005 – April 2006 the differences were not clear, i.e. selection indices had high confidence intervals. Confidence intervals (CI) of selection ratios for most of the other grazer and browser species (i.e. in Blue wildebeest, Burchell's zebra and topi) were also considerably high.

The mixed feeders, Grant's gazelle and impala, showed a clear pattern with fewer observations in areas with repeated burning, two years and three years, respectively compared to those in non-burnt and in areas that burnt only once. This pattern was about equally clear for both species.

Discussion

We found clear between-year differences in the likelihood of occurrences of species and diet groups. The patterns found in the period 2003 – 2004 differed from those in other years. In 2003 – 2004 the analysis for all species together, for preferential grazers and for the dominant grazer species except for African buffalo, i.e. Thompson's gazelle, topi, wildebeest, Burchell's zebra had a significant preference for patches burnt in the current year compared to non-burnt patches. In contrast, in the same period, mixed feeders and browsers had a significant preference for non-burnt patch types, but the differential preference was less clear for individual mixed feeder species, e.g. impala.

We associate these differences to three factors. First, the difference between years in the spatial distribution of burnt and non-burnt patches within the ecosystem. Both the goodness-of-fitness test and the selection index are based on the assumption that animals have equal probability of access to all patch types in relation to the patch type availability. However, this may not have been the case in all years. For example, the Eastern Plains are generally less burnt compared to the western and northern sections of the Park (Dempewolf *et al.,* 2007). The distribution of species with a preference for the Eastern Plains habitat, as could be the case for Grant's gazelle, would therefore show a biased distribution for non-burnt patch types. A species-wise analysis beyond the scope of this study, taking the individual species potential distribution patterns into account could give a different result.

Second, other factors than species specific habitat preferences may set constraints to the distribution of the animals. In the period 2003 – 2004 current year burnt patches were largely distributed homogeneously throughout all the animal count transects. In contrast, in other periods, a disproportionately large extent of burnt areas occurred within the Grumeti and Ikorongo game reserves (Dempewolf *et al.,* 2007) where hunting pressure is high, both legal and illegal (Holmern, 2007). In these areas animal observations were generally few (Rusch *et al.,* 2005), and the general use by herbivores is low (Nyahongo *et al.,* 2006). In these areas, there has also been observed significant different behaviour of herbivores compared to the National Park (Setsaas *et al.,* 2007). Consequently, the general preference for non-burnt patches in other periods than in 2003-2004, are likely to be biased due to an avoidance of game reserve areas due to other factors than the food resource.

Third, differences among years on when the fire season took place and the timing of animal counts in relation to fire season could also be important. We think that any of the factors above, either singly or in combination may be responsible at one time or another for the observed differences between years. We lack inference about between-year differences since previous studies in the area and elsewhere (Rowe-Rowe, 1982; Moe *et al.,* 1990; Wilsey, 1996; Tomor & Owen-Smith, 2002) have generally been based on a single fire season. However, this study finds no within-year variation among species, suggesting that timing of the counts may be important. Prolonged dry periods in East Africa may cause herbivores to change diets (Hofmann, 1973), which implies shift among various types of patches to seek of resources. Variability in quantity, time and spatial distribution of rains is characteristic of rainfall pattern in the Serengeti ecosystem (Norton-Griffiths, Herlocker & Pennycuick, 1975). Temporal and spatial differences in rainfall between years may contribute to the change in patterns of forage availability in the landscape, and hence to the differences in selectivity of patches between years.

We associate the tendency of grazers, except African buffalo to prefer patches burnt in the current year during 2003-2004 (Fig. 2a, 5a) to the general notion that herbivores selectively graze on post-fire vegetation. The tendency of grazers to be attracted to recently burnt area has been observed in different parts of African savanna including Serengeti ecosystem (Rowe-Rowe, 1982; Moe *et al.,* 1990; Wilsey, 1996; Tomor & Owen-Smith, 2002; Hassan *et al.,* 2007) but there are few studies that have examined these patterns over spatial scales of the extent of this study and integrated with animal counts over more than 1-year fire periods. Fire changes the amount and quality of the forage and these properties change along the post fire season (Hassan *et al.,* 2007). The reduction of plant dead material and debris and the increased aboveground production a few months after fire (Hassan *et al., in prep.*) causes an increase in leaf/stem ratio (Hassan *et al.,* 2007) which correlates with high crude protein concentration (Prins & Beekman, 1989). Moreover, Hassan *et al.* (*in prep.*) show that in the same ecosystem N, P, K, Mg, and Na concentrations were higher in material from burnt areas than non-burnt areas (live leaf, live stem, flower and fruit and standing grass material). However, forage maturation results in declined nitrogen concentration (Acosta *et al.,* 1991, Mustafa & Seguin, 2003; 2004), increased acid detergent fiber (Pehrson & Faber, 1994) and reduced digestibility (Crampton & Harris, 1969), all of which may deter grazing in patches burnt only in previous years and in patches not burnt in a period of three years.

To some extent, our study reinforces the current theory concerning ungulate body weight and use of burnt and non-burnt patches stating that use of burnt areas is negatively related to ungulate body size (Wilsey, 1996). The pattern for grazers in this study provides three possibilities of grazing strategies in relation to body weight. Considering the period 2003 – 2004, there could be grazers who foraged predominantly in burnt patches, others which forage predominantly in non-burnt patches, and grazers who may switch between the two patch types. Our results for the smallest grazer, Thomson's gazelle conform to a previous study in the area (Wilsey, 1996). Thomson's gazelles are known to make more utilization of areas with sward of low to intermediate biomass (Wilmshurst, Fryxell & Colucci, 1999; Fryxell, Wilmshurst & Sinclair, 2004). In the Serengeti, burnt areas carry low phytomass and have a relatively short sward compared to vegetation in non-burnt patches (Hassan *et al.,* 2007), a situation which favors Thomson's gazelle requirement. Grazing in such patches pays the highest nutritional returns for small grazers (McNaughton, 1984, Fryxell, 1991; WallisdeVries, Laca & Demment, 1996) in combination with the narrow muzzle that facilitates the selective behavior and accessibility to short vegetation. As a small species Thomson's gazelle can afford to feed selectively on nutrient and energy rich sparse food (Bell, 1971) to fulfill the high metabolic demands of a small body (Wilsey, 1996). The theory on energy maximization refutes the previous notion that small ungulates such as Thomson's gazelle occupy areas of short swards as anti-predatory behaviour (Jarman & Jarman, 1979).

Wilsey (1996) reported that grazing ungulates of intermediate body weight switch between burnt and non-burnt patches, a strategy which enable them to balance their nutrient and energy requirements. He hypothesised that topi and Burchell's zebra as relatively large species compared to Thomson's gazelle would tend to maximize energy and nutrient intakes by grazing in burnt areas where forage biomass is low but of high quality, and in non-burnt areas where the forage is low quality but of sufficient quantity. There are some indications in our study in support of this hypothesis, although our study does not enable an assessment of switches of individuals between burnt and non-burnt areas, it provides an estimate of the relative usage by the species of burnt patch types. The medium sized topi and wildebeest had higher preference for burnt patches but the pattern was somewhat less clear than in the case of Thomson's gazelle, with larger confidence intervals of the selection ratios. Also Hartebeest, a species of intermediate size had no significant preference for either currently burnt or non-burnt patches. In contrast, our study shows that Burchell's zebra had a higher likelihood of occurrence in burnt patches, comparable to the preference by Thomson's gazelles. This finding broadens earlier notions about preferences of forage patches based on digestive systems (Bell, 1971) that assume that large cecal herbivores will mainly use low quality forage areas due to their capacity of utilizing low quality forage ('Jarman-Bell principle', Jarman, 1974; Bell, 1971; Van Soest, 1982).

Our results on the preference by the largest grazer species, African buffalo, for currently non-burnt patches agree with hypothesis about body size and with earlier findings in Serengeti (Wilsey, 1996) and in other ecosystems (Field, 1975; Bell & Jachmann, 1984). The preference is attributable to the species bulk feeding behaviour. African buffalo is a heavy grazer that depends largely on perennial forage of higher quantity (Field, 1975). The broad muzzle and a tongue with which to pluck grass is a reward for African buffalo bulk feeding behavior (Beekman & Prins, 1989). Its large size places a high demand of absolute quantity of nutrients per nutrient unit of forge. As a result, the animal can not perform selective feeding to the degree that do small ungulates (Hanley, 1982). Being a bulk feeder, African buffalo would be resource-limited in burnt areas where phytomass is relatively low throughout the year compared to non-burnt areas (Hassan *et al.*, 2007).

In contrast to grazers, preferential browsers and mixed feeders show a consistent tendency to occur more frequently in not burnt patches than in patches burnt in the current year. This response could be attributable to the loss of browse material (leaves, twigs, bark) caused by fire. Wronski (2003) also indicated that burning reduces quality of browse material by scorching. These patterns were consistent for the individual species such as Grant's gazelle and impala. According to Wronski (2003), in dry season mixed feeders browse rather than graze, but burning increases grazing time and reduces browsing time at the same time to nearly zero, and browsing remains low all over the next rainy season. In contrast, Wilsey (1996) reported that Grant's gazelle and impala were more abundant on burnt compared to non-burnt sites. The discrepancy between our results and those by Wilsey (1996) could probably be associated with differences in the extent of study area, the size of data set, as well as method of analysis. Wilsey (1996) performed observations in a 2-months period after the fire (May-June 1993) in grasslands.

Our results are also indicative that ungulates generally had lower preference for areas that burnt in the current year but had burnt repetitively in a 3-year period compared to areas that had not burnt in the previous 3 years, which highlights that the fire history can be an important determinant of forage patch choice and also explain part of the variability found in the preference for currently burnt areas. However, this response may have also been masked by differences in accessibility of the different areas. Game reserve areas appear to have burnt more often than the National Park.

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Tables

Table 1: Fire periods, months during the fire period in which fires were observed, main period during which fires occurred and percentage of the area burnt during the main fire period and total animal counts.

Period	Period of fires	Main fire period	% area burnt	Area burnt, km^2	Total animal counts
May 2000 – Apr 2001	May - Mar	Aug	45 %	2663.70	-
May 2001 – Apr 2002	May - Apr	July	70 %	6032.98	2, 744
May 2003 – Apr 2004	June- Nov	July – Aug	86 %	6610.29	3, 347
May 2004 – Apr 2005	May - Mar	June – July	90 %	6351.80	4, 130
May 2005 – Apr 2006	May - Nov	July – Aug	68 %	3821.29	611

Table 2: The twenty-four mammalian herbivores recorded during animal counts in Serengeti NP and its surroundings along nine transects during four years, May 2001-April 2002, May 2003-April 2004, May 2004-April 2005, May 2005-April 2006. Diet groups: B = browser, G = grazer and MF = mixed feeder. Animal counts: O = observed during the respective year, NO = not observed during the respective year.

Scientific name	**English name**	**Diet group**	**Investigated periods**			
			May 2001-April 2002	**May 2003-April 2003**	**May 2004-April 2005**	**May 2005-April 2006**
Aepyceros melampus	Impala	MF	O	O	O	O
Alcelaphus buselaphus	Coke's hartebeest,	G	O	O	O	O
Cephalophus rufilatus	Red-flanked duiker,	B	NO	NO	O	O
Connochaetes taurinus	Blue wildebeest	G	O	O	O	O
Damaliscus lunatus korrigum	Topi	G	O	O	O	O
Equus burchelli	Burchell’s zebra	G	O	O	O	O
Gazella granti	Grant’s gazelle	MF	O	O	O	O
Gazella thomsoni	Thomson’s gazelle	G	O	O	O	O
Giraffa camelopardalis	Giraffe	B	O	O	O	O
Kobus ellipsiprymnus defassa	Defassa waterbuck	MF	O	O	O	O
Litocranius walleri	Gerenuk	B	NO	NO	O	NO
Loxodonta africana	African elephant	MF	O	O	O	O
Madoqua kirkii	Kirk's dikdik	B	O	O	O	O
Oreotragus oreotragus	Klippspringer	B	O	O	O	O
Ourebia ourebi	Oribi	G	NO	O	NO	NO
Pedetes capensis	Spring hare	G	O	O	O	NO
Phacochoerus aethiopicus	Warthog	G	O	O	O	O
Procavia capensis	Rock hyrax	MF	O	O	O	NO
Rahicerus campestris	Steenbok	MF	NO	O	NO	NO
Redunca redunca	Bohor reedbuck	G	O	O	O	O
Sylvicapra grimmia	Common duiker,	B	NO	O	O	O
Syncerus caffer	African buffalo	G	O	O	O	O
Taurotragus oryx	Eland	MF	NO	O	O	O
Tragelaphus scriptus	Bushbuck	MF	O	NO	O	O
Total (all species)			**18**	**21**	**22**	**19**

Table 3: Fire patch categories and their definitions [or explanations] and patch category contrasts in the Chi square tests.

Fire patch categories	**Patch description**
NB	Not burnt in any year of the three years period
NBC	Not burnt in the current year, regardless of fire history
NBC,B1or2	Not burnt in the current year, but burnt in at least one of the other years
BC	Burnt in the current year, regardless of fire history
BC,NB1,NB2	Burnt only in the current year
NBC,B1,NB2	Burnt only one year ago
NBC,NB1,B2	Burnt only two years ago
BC,B1,NB2	Burnt twice, in the current year and one year ago
BC,NB1,B2	Burnt twice, in the current year and two years ago
NBC,B1,B2	Burnt twice, one year and two years ago
BC,B1,B2	Burnt three times, in the current year, one year and two years ago
Contrasts	
1	BC versus NBC
2	BC versus NB versus NBC,B1or2
3	BC,NB1,NB2 versus NBC,B1,NB2 versus NBC,NB1,B2 versus BC,B1,NB2 versus BC,NB1,B2 versus NBC,B1,B2 versus BC,B1,B2 versus NB

NB=not burnt, B=burnt, C=current year, 1=one year ago, 2

Table 4: Animal distribution related to burnt and non-burnt areas in Serengeti National Park (SNP) and the landscape close to the SNP over a four years' census from May 2001 to April 2006. No result from the period May 2002 – April 2003. Landscape units: BC = burnt the current year irrespective of the other years, NBC = not burnt the current year irrespective of the other years (=NBC, B1 OR 2 +NB), NBC, B1 or 2 = not burnt in current year but burnt sometime in the previous two years, NB = not burnt in any of the investigated years; and for the definition of the eight patch types see the description in Table 3. Chi-squared goodness of fit test. - = no observations. Number of species with significant or non-significant distributions.

Species groups/ species	**Landscape units**	**May 2001- April 2002**		**May 2003- April 2004**		**May 2004- April 2005**		**May 2005- April 2006**	
		Xp^2	**P value**	**Xp^2**	**P value**	**Xp^2**	**P value**	**Xp^2**	**P value**
All species	BC, NBC	64.4	<0.001	13.26	<0.001	64.51	<0.001	3.03	0.082
	BC, NB, NBC,B1OR2	184.71	<0.001	115.59	<0.001	86.85	<0.001	45.31	<0.001
	8 categories	136.72	<0.001	205.63	<0.001	161.85	<0.001	65.21	<0.001
Browsers	BC, NBC	6.92	0.009	0.20	0.652	12.02	0.001	0.01	0.906
	BC, NB, NBC,B1OR2	13.75	0.001	23.65	<0.001	17.00	<0.001	2.00	0.368
	8 categories	7.94	0.338	36.46	<0.001	30.61	<0.001	6.11	0.527
Bush duiker	BC, NBC	-	-	**1.06**	0.304	0.33	0.564	0.07	0.791
	BC, NB, NBC,B1OR2	-	-	**1.34**	0.512	2.76	0.252	0.22	0.895
	8 categories	-	-	**3.63**	0.821	10.24	0.176	1.78	0.971
Giraffe	BC, NBC	5.92	0.015	0.02	0.894	9.56	0.002	0.25	0.614
	BC, NB, NBC,B1OR2	11.82	0.003	17.63	<0.001	11.93	0.003	1.55	0.461
	8 categories	12.16	0.095	29.4	<0.001	22.5	0.002	7.77	0.353
Gerenuk	BC, NBC	-	-	-	-	3.00	0.083	-	-
	BC, NB, NBC,B1OR2	-	-	-	-	3.00	0.223	-	-
	8 categories	-	-	-	-	8.90	0.260	-	-
Kirk's dik-dik	BC, NBC	**0.94**	0.333	**1.48**	0.224	2.14	0.143	0.39	0.533
	BC, NB, NBC,B1OR2	1.81	0.404	10.42	0.005	7.44	0.024	2.12	0.347
	8 categories	**1.97**	0.961	**11.79**	0.108	11.54	0.117	3.99	0.781
Klippspringer	BC, NBC	**0.10**	0.748	**0.52**	0.472	1.33	0.248	0.04	0.851
	BC, NB, NBC,B1OR2	**0.22**	0.898	**0.95**	0.621	4.26	0.119	1.80	0.407
	8 categories	**0.22**	1.000	**1.74**	0.973	4.26	0.749	4.92	0.670
Red-flanked duiker	BC, NBC	-	-	-	-	0.33	0.564	0.04	0.851
	BC, NB, NBC,B1OR2	-	-	-	-	2.76	0.252	0.64	0.725
	8 categories	-	-	-	-	10.24	0.176	0.64	0.999
Grazers	BC, NBC	34.98	<0.001	46.66	<0.001	14.42	<0.001	1.95	0.163
	BC, NB, NBC,B1OR2	129.10	<0.001	92.46	<0.001	20.63	<0.001	22.23	<0.001
	8 categories	100.75	<0.001	132.56	<0.001	73.35	<0.001	41.87	<0.001
African buffalo	BC, NBC	5.11	0.024	1.45	0.228	4.63	0.031	0.92	0.338
	BC, NB, NBC,B1OR2	7.18	0.028	2.67	0.263	4.63	0.099	2.09	0.352
	8 categories	**7.73**	0.357	**10.73**	0.151	11.45	0.120	2.95	0.890
Bohor reedbuck	BC, NBC	**0.41**	0.520	**1.99**	0.159	2.00	0.157	0.07	0.791
	BC, NB, NBC,B1OR2	0.86	0.649	2.04	0.360	12.09	0.002	3.60	0.165
	8 categories	**0.86**	0.997	**3.40**	0.845	13.39	0.063	4.92	0.669
Burchell's zebra	BC, NBC	3.75	0.053	29.89	<0.001	0.97	0.326	0.55	0.457
	BC, NB, NBC,B1OR2	23.28	<0.001	31.55	<0.001	3.88	0.144	11.47	0.003
	8 categories	24.04	0.001	47.8	<0.001	13.63	0.058	15.18	0.034
Coke's hartebeest	BC, NBC	**1.29**	0.256	**0.58**	0.446	0.19	0.665	0.71	0.401
	BC, NB, NBC,B1OR2	**1.57**	0.455	**1.33**	0.513	2.02	0.363	1.28	0.529
	8 categories	2.42	0.933	16.51	0.021	24.32	0.001	10.56	0.159
Oribi	BC, NBC	-	-	**0.26**	0.611	-	-	-	-
	BC, NB, NBC,B1OR2	-	-	**0.82**	0.664	-	-	-	-
	8 categories	-	-	**0.82**	0.997	-	-	-	-
Springhare	BC, NBC	**0.10**	0.748	**0.26**	0.611	0.33	0.564	-	-

	BC, NB, NBC,B1OR2	**0.22**	0.898	**0.82**	0.664	1.07	0.587	-	-
	8 categories	**0.22**	1.000	**0.82**	0.997	1.07	0.994	-	-
Thomson's gazelle	BC, NBC	**28.01**	<0.001	19.3	<0.001	4.88	0.027	0.01	0.926
	BC, NB, NBC,B1OR2	**74.17**	<0.001	54.17	<0.001	27.72	<0.001	10.48	0.005
	8 categories	**75.19**	<0.001	95.88	<0.001	66.96	<0.001	28.11	<0.001
Topi	BC, NBC	**2.13**	0.145	7.23	0.007	0.02	0.878	1.45	0.229
	BC, NB, NBC,B1OR2	**4.94**	0.085	10.39	0.006	4.34	0.114	1.96	0.376
	8 categories	**7.46**	0.383	18.89	0.009	12.33	0.090	3.90	0.792
Warthog	BC, NBC	**10.21**	0.001	0.15	0.694	0.21	0.649	0.20	0.652
	BC, NB, NBC,B1OR2	**24.80**	<0.001	2.31	0.316	0.47	0.791	0.34	0.842
	8 categories	**24.83**	0.001	15.31	0.032	11.33	0.125	19.73	0.006
Wildebeest	BC, NBC	**0.99**	0.319	5.95	0.015	8.13	0.004	0.63	0.426
	BC, NB, NBC,B1OR2	**27.78**	<0.001	22.60	<0.001	13.40	0.001	5.08	0.079
	8 categories	**27.83**	<0.001	58.54	<0.001	26.76	<0.001	8.36	0.302
Mixed feeders	BC, NBC	**32.91**	<0.001	9.24	0.002	62.23	<0.001	1.19	0.276
	BC, NB, NBC,B1OR2	**47.38**	<0.001	47.28	<0.001	80.44	<0.001	23.98	<0.001
	8 categories	**26.48**	<0.001	98.97	<0.001	101.94	<0.001	27.74	<0.001
African elephant	BC, NBC	**0.31**	0.577	**2.25**	0.133	2.25	0.133	0.07	0.791
	BC, NB, NBC,B1OR2	**2.12**	0.347	13.33	0.001	5.62	0.060	0.22	0.895
	8 categories	**2.12**	0.953	15.01	0.036	8.65	0.279	1.78	0.971
Bushbuck	BC, NBC	**0.31**	0.577	-	-	4.67	0.031	0.04	0.851
	BC, NB, NBC,B1OR2	**0.65**	0.723	-	-	6.39	0.041	0.64	0.725
	8 categories	**0.65**	0.999	-	-	9.97	0.190	0.64	0.999
Defassa waterbuck	BC, NBC	**2.48**	0.115	**0.85**	0.356	1.52	0.218	0.18	0.675
	BC, NB, NBC,B1OR2	**5.19**	0.075	**1.13**	0.567	1.53	0.465	0.20	0.906
	8 categories	**5.19**	0.637	16.75	0.019	10.96	0.140	4.30	0.744
Eland	BC, NBC	-	-	**0.30**	0.583	0.16	0.691	0.04	0.851
	BC, NB, NBC,B1OR2	-	-	**0.42**	0.812	2.36	0.307	0.64	0.725
	8 categories	-	-	5.38	0.613	14.59	0.042	0.64	0.999
Grant's gazelle	BC, NBC	**11.07**	0.001	7.09	0.008	15.6	<0.001	1.52	0.218
	BC, NB, NBC,B1OR2	**30.62**	<0.001	15.07	0.001	25.64	<0.001	9.72	0.008
	8 categories	**30.78**	<0.001	41.47	<0.001	44.87	<0.001	11.69	0.111
Impala	BC, NBC	**19.33**	<0.001	4.00	0.046	41.12	<0.001	0.15	0.695
	BC, NB, NBC,B1OR2	**20.37**	<0.001	29.14	<0.001	50.92	<0.001	15.66	<0.001
	8 categories	**32.67**	<0.001	53.11	<0.001	65.59	<0.001	18.91	0.008
Rock hyrax	BC, NBC	**0.21**	0.649	**0.26**	0.611	0.33	0.564	-	-
	BC, NB, NBC,B1OR2	**0.43**	0.806	**0.82**	0.664	1.07	0.587	-	-
	8 categories	**0.43**	1.000	**0.82**	0.997	1.07	0.994	-	-
Steenbok	BC, NBC	-	-	3.86	0.050	-	-	-	-
	BC, NB, NBC,B1OR2	-	-	**3.86**	0.145	-	-	-	-
	8 categories	-	-	**8.43**	0.296	-	-	-	-

DISTRIBUTIONS		**Number of species**			
		May 2001-April 2002	**May 2003-April 2004**	**May 2004-April 2005**	**May 2005-April 2006**
Significant dist.	BC, NBC	6	7	7	0
	BC, NB, NBC,B1OR2	8	9	8	4
	8 categories	6	11	7	4
Non-significant dist.	BC, NBC	12	14	15	19
	BC, NB, NBC,B1OR2	10	12	14	15
	8 categories	12	10	15	15

Figure legends

Figure 1: Map of Serengeti National Park (SNP) and surrounding protected areas that constitute our study area in the Serengeti ecosystem. Protected areas are Ngorongoro Conservation Area under the NCAA Authority (NCAA), Grumeti Game Reserve (GGR), Ikorongo Game Reserve (IGR) and Maswa Game Reserve (MGR). The last area is not a part of study area.

Figure 2a: Map of the fire patches (Dempewolf et al. 2007) and Thomson's gazelle counts along transects segments in the period May 2003 to April 2004.

Figure 2b: Map of the fire patches (Dempewolf et al. 2007) and Thomson's gazelle counts along transects segments in the period May 2004 to April 2005.

Figure 3a: Resource selection of all species pooled together and grazers in the analysis with two fire patch categories, burnt current year and non-burnt current year, in the Serengeti ecosystem in the animal census May 2001-April 2002, and May 2003-April 2005. Error bars represent a probability of about 0.95 for all pair wise intervals.

Figure 3b: Resource selection of browsers and mixed feeders in the analysis with two fire patch categories, burnt current year and non-burnt current year, in the Serengeti ecosystem in the animal census May 2001-April 2002, and May 2003-April 2005. Error bars represent a probability of about 0.95 for all pair wise intervals.

Figure 4a: Resource selection of buffalo in the analysis with two fire patch categories, burnt current year and non-burnt current year, in the Serengeti ecosystem in the animal census May 2001-April 2002, and May 2004-April 2005. Error bars represent a probability of about 0.95 for all pair wise intervals.

Figure 4b: Resource selection of topi, Thomson's gazelle, wildebeest, zebra and warthog in the analysis with two fire patch categories, burnt current year and non-burnt current year, in the Serengeti ecosystem in the animal census from May 2001-April 2002, and May 2003-April 2005. Error bars represent a probability of about 0.95 for all pair wise intervals.

Figure 5: Resource selection of Grant's gazelle and impala in the analysis with two fire patch categories, burnt current year and non-burnt current year, in the Serengeti ecosystem in the animal census May 2001-April 2002, and May 2003-April 2005. Error bars represent a probability of about 0.95 for all pair wise intervals.

Figure 6a: Resource selection of all species together and grazers in the analysis with three patch categories, burnt current year, burnt at least one of the other years and non-burnt current year, in the Serengeti ecosystem in the animal census May 2001-April 2002, and May 2003-April 2006. Error bars represent a probability of about 0.95 for all pair wise intervals.

Figure 6b: Resource selection of browsers and mixed feeders in the analysis with three patch categories, burnt current year, burnt at least one of the other years and non-burnt current year, in the Serengeti ecosystem in the animal census May 2001-April 2002, and May 2003-April 2006. Error bars represent a probability of about 0.95 for all pair wise intervals.

Figure 7a: Resource selection of giraffe and Kirk's dik-dik in the analysis with three patch categories, burnt current year, burnt at least one of the other years and non-burnt current year, in the Serengeti ecosystem in the animal census from May 2001-April 2002, and May 2003-April 2005. Error bars represent a probability of about 0.95 for all pair wise intervals.

Figure 7b: Resource selection of Burchell's zebra, Thomson's gazelle in the analysis with three patch categories, burnt current year, burnt at least one of the other years and non-burnt current year, in the Serengeti ecosystem in the animal census from May 2001-April 2002, and May 2003-April 2006. Error bars represent a probability of about 0.95 for all pair wise intervals.

Figure 7c: Resource selection of wildebeest in the analysis with three patch categories, burnt current year, burnt at least one of the other years and non-burnt current year, in the Serengeti ecosystem in the animal census from May 2001-April 2002, and May 2003-April 2005. Error bars represent a probability of about 0.95 for all pair wise intervals.

Figure 7d: Resource selection of Grant's gazelle and impala in the analysis with three patch categories, burnt current year, burnt at least one of the other years and non-burnt current year, in the Serengeti ecosystem in the animal census from May 2001-April 2002, and May 2003-April 2006. Error bars represent a probability of about 0.95 for all pair wise intervals.

Figure 8a: Resource selection of all species together and grazers in the analysis with eight patch types in the Serengeti ecosystem in different years of the animal census from May 2001 - April 2002, and May 2003-April 2006. Error bars represent a probability of about 0.95 for all pair wise intervals. Data for May 2001 – April 2002 available for only the three patch type.

Figure 8b: Resource selection of mixed feeders and browsers in the analysis with eight patch types in the Serengeti ecosystem in different years of the animal census from May 2001 - April 2002, and May 2003-April 2006. Error bars represent a probability of about 0.95 for all pair wise intervals. Data for May 2001 – April 2002 available for only the three patch type.

Figure 9: Resource selection of Thomson's gazelle in the analysis with eight patch types in the Serengeti ecosystem in different years of the animal census from May 2001 - April 2002, and May 2003-April 2006. Error bars represent a probability of about 0.95 for all pair wise intervals. Data for May 2001 – April 2002 available for only the three patch type.

Figure 10: Resource selection of Grant's gazelle and impala in the analysis with eight patch types in the Serengeti ecosystem in different years of the animal census from May 2001 - April 2002, and May 2003-April 2006. Error bars represent a probability of about 0.95 for all pair wise intervals. Data for May 2001 – April 2002 available for only the three patch type.

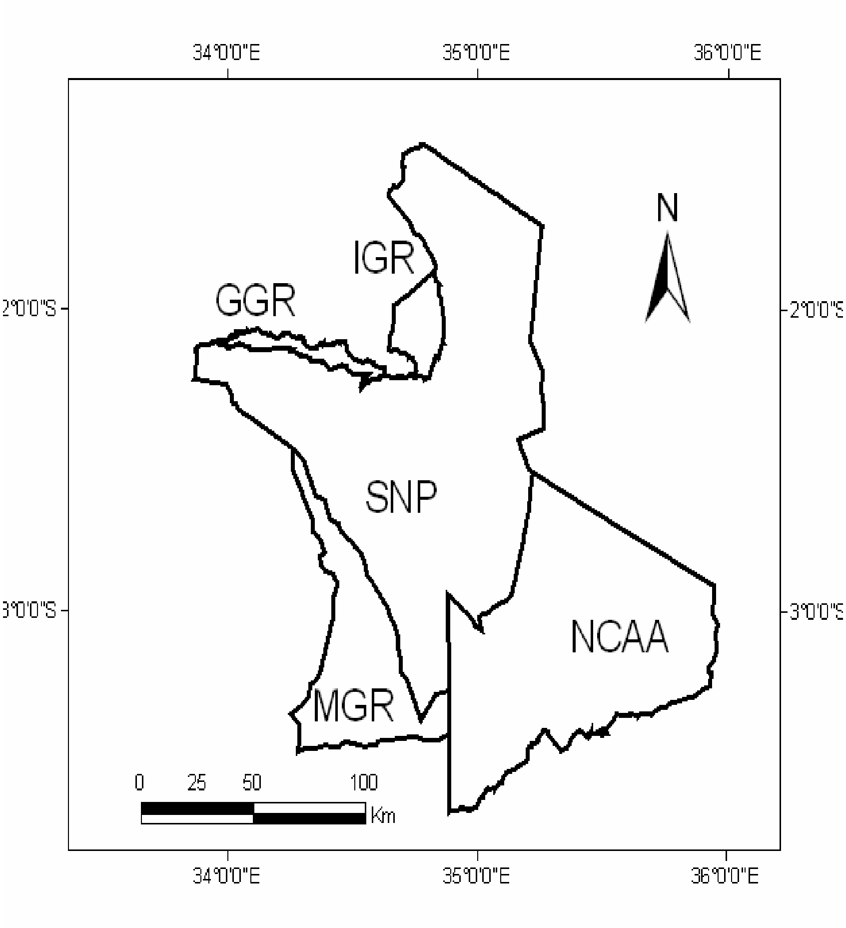
34°0'0"E
35°0'0"E
36°0'0"E
2°0'0"S
3°0'0"S
N
IGR
GGR
SNP
NCAA
MGR
0
25
50
100
Km

Figure 1

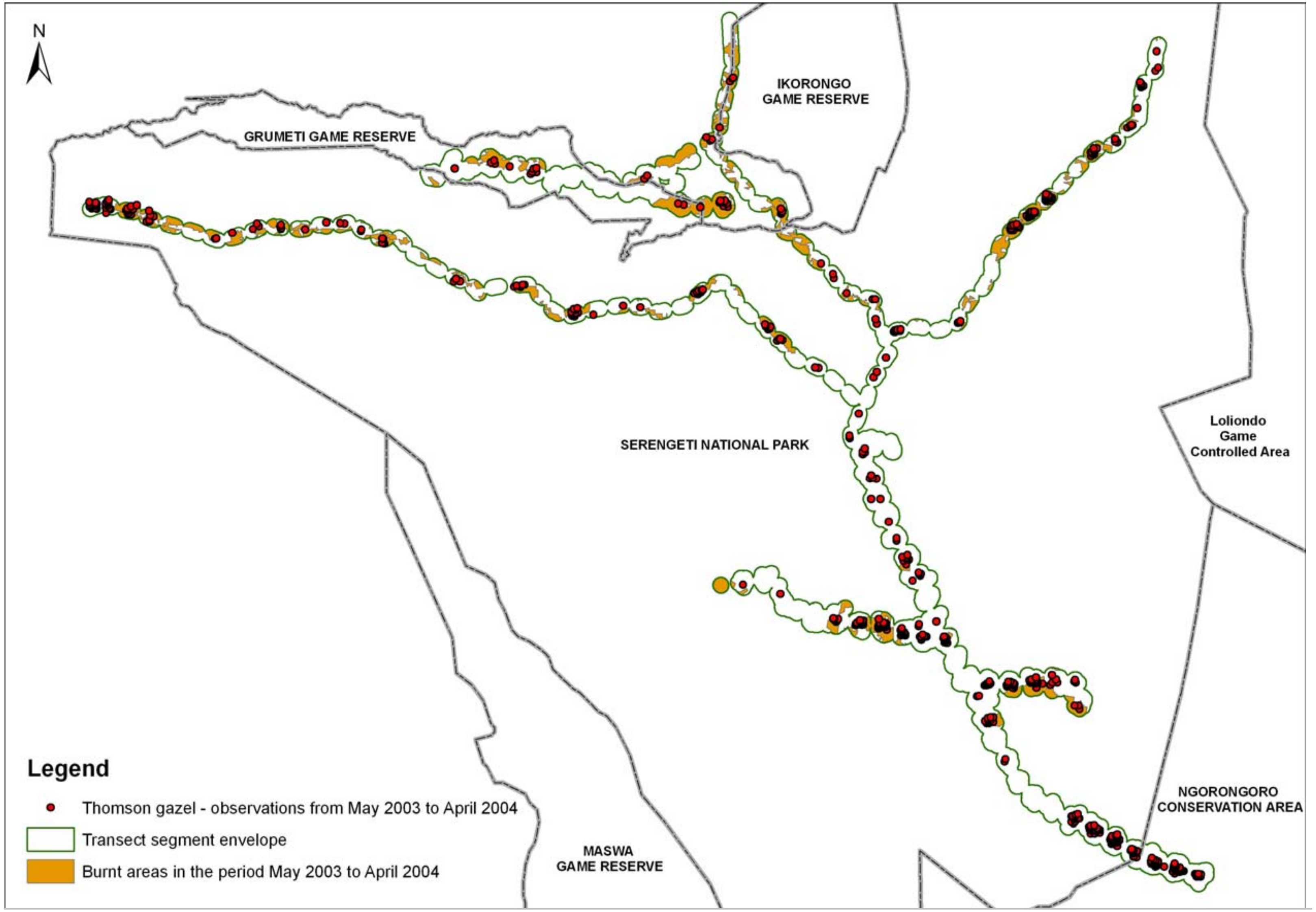
N
GRUMETI GAME RESERVE
IKORONGO
GAME RESERVE
SERENGETI NATIONAL PARK
Loliondo
Game
Controlled Area
NGORONGORO
CONSERVATION AREA
MASWA
GAME RESERVE
Legend
● Thomson gazel - observations from May 2003 to April 2004
☐ Transect segment envelope
■ Burnt areas in the period May 2003 to April 2004

Figure 2a

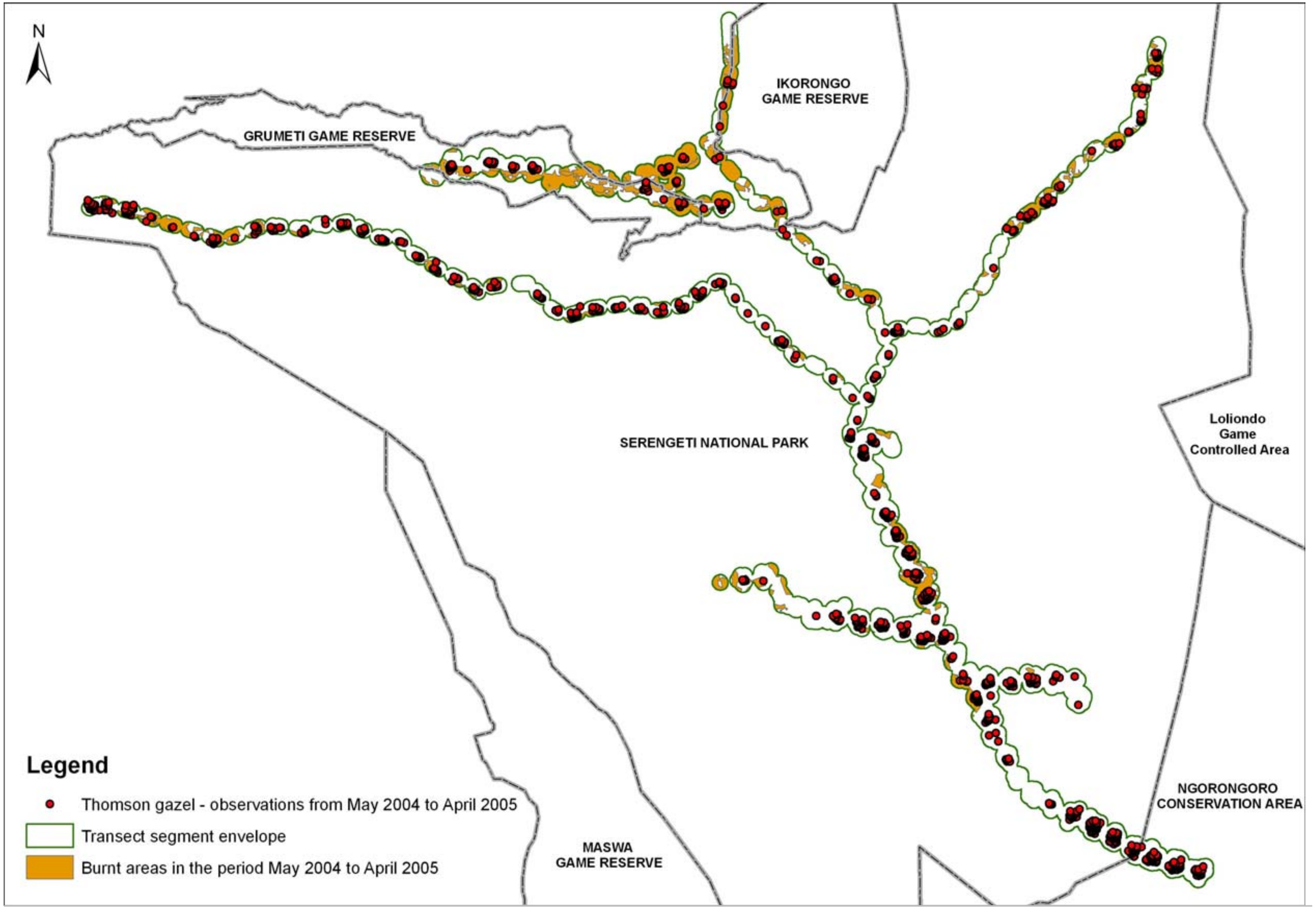
N
IKORONGO
GAME RESERVE
GRUMETI GAME RESERVE
SERENGETI NATIONAL PARK
Loliondo
Game
Controlled Area
NGORONGORO
CONSERVATION AREA
MASWA
GAME RESERVE
Legend
● Thomson gazel - observations from May 2004 to April 2005
☐ Transect segment envelope
▨ Burnt areas in the period May 2004 to April 2005

Figure 2b

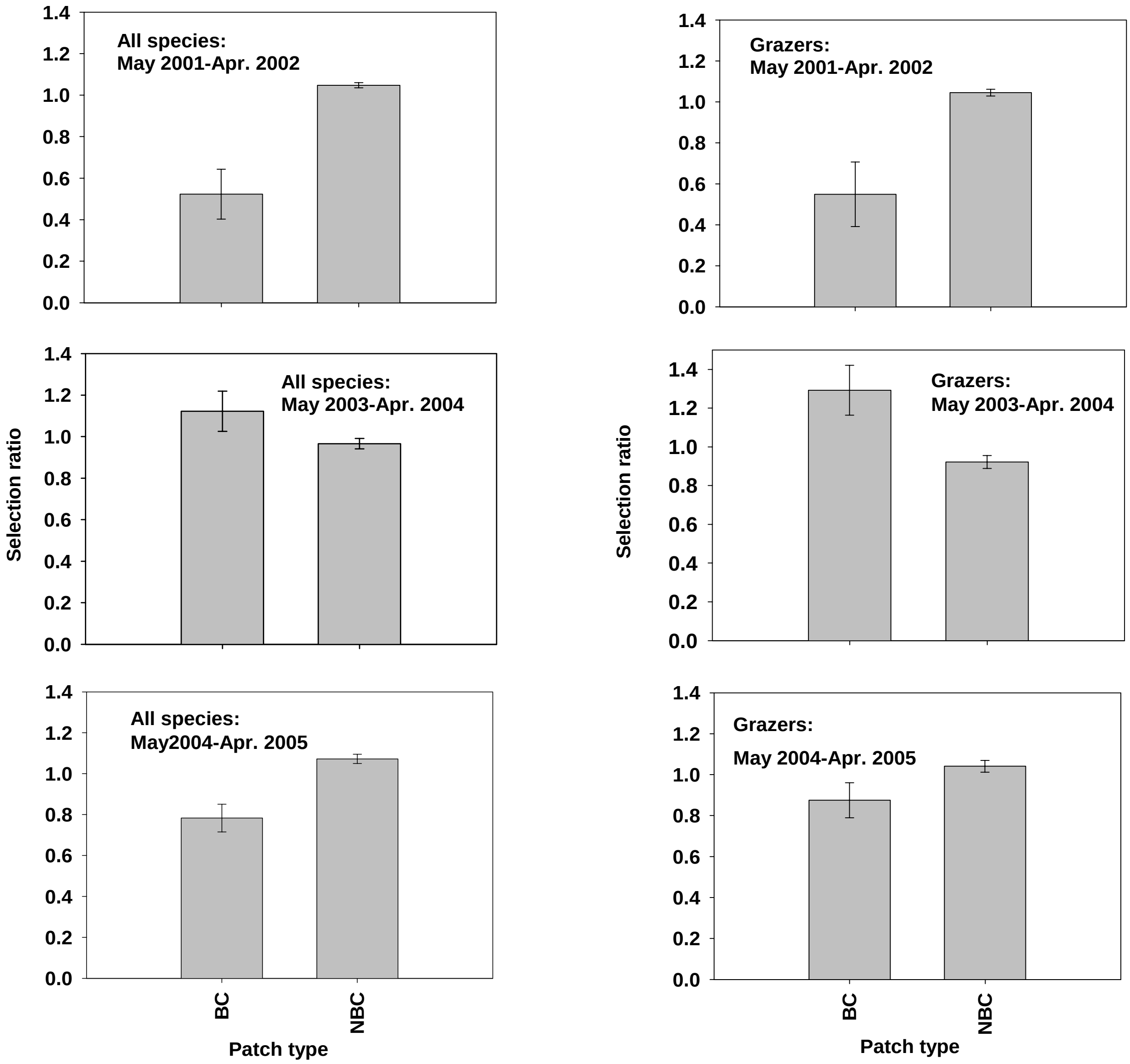
All species:
May 2001-Apr. 2002
Grazers:
May 2001-Apr. 2002
All species:
May 2003-Apr. 2004
Grazers:
May 2003-Apr. 2004
All species:
May2004-Apr. 2005
Grazers:
May 2004-Apr. 2005
Selection ratio
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
BC
NBC
Patch type

Fig 3a

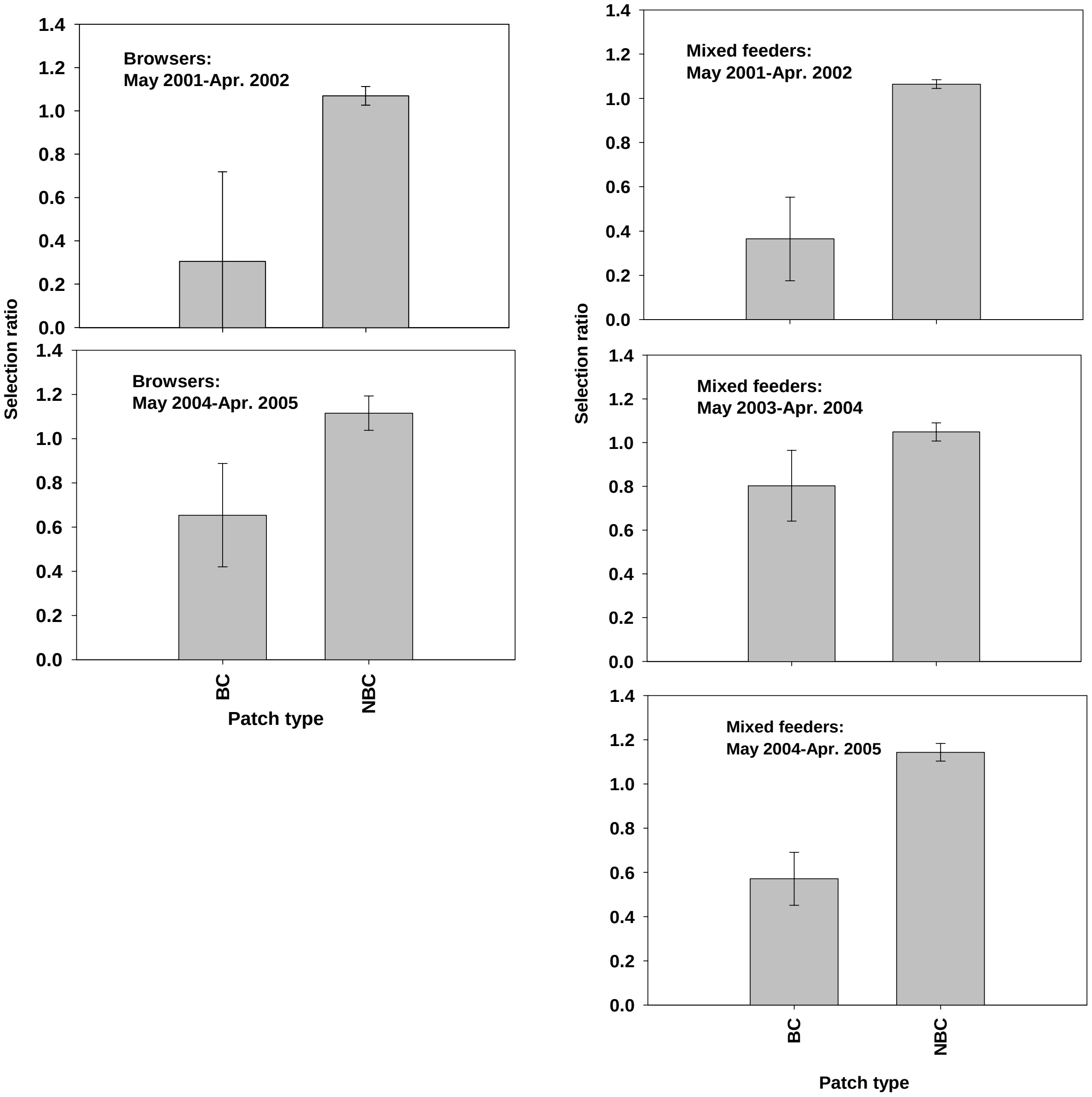
Selection ratio
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Browsers:
May 2001-Apr. 2002
Browsers:
May 2004-Apr. 2005
BC
NBC
Patch type
Mixed feeders:
May 2001-Apr. 2002
Mixed feeders:
May 2003-Apr. 2004
Mixed feeders:
May 2004-Apr. 2005
BC
NBC
Patch type

Figure 3b

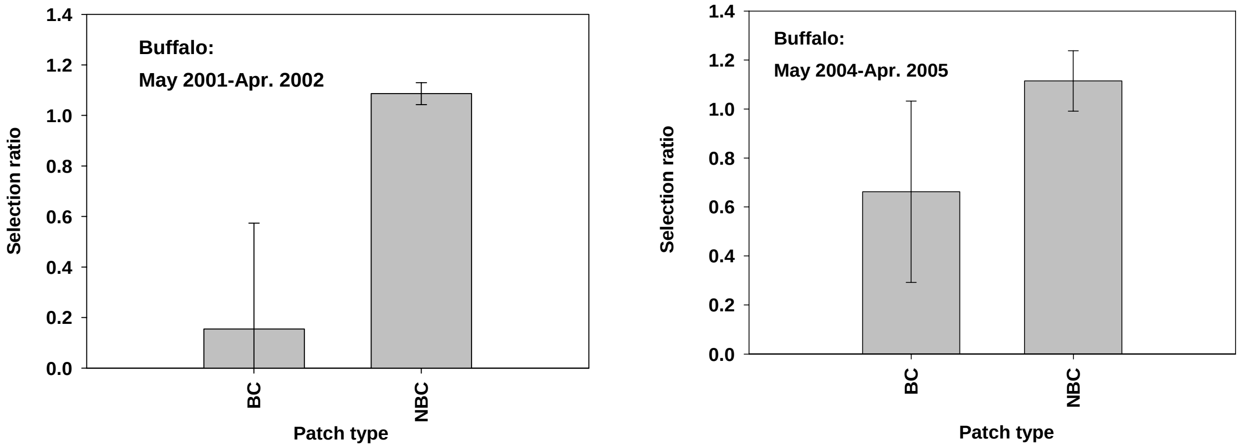
Buffalo:
May 2001-Apr. 2002
Selection ratio
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
BC
NBC
Patch type
Buffalo:
May 2004-Apr. 2005
Selection ratio
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
BC
NBC
Patch type

Figure 4a

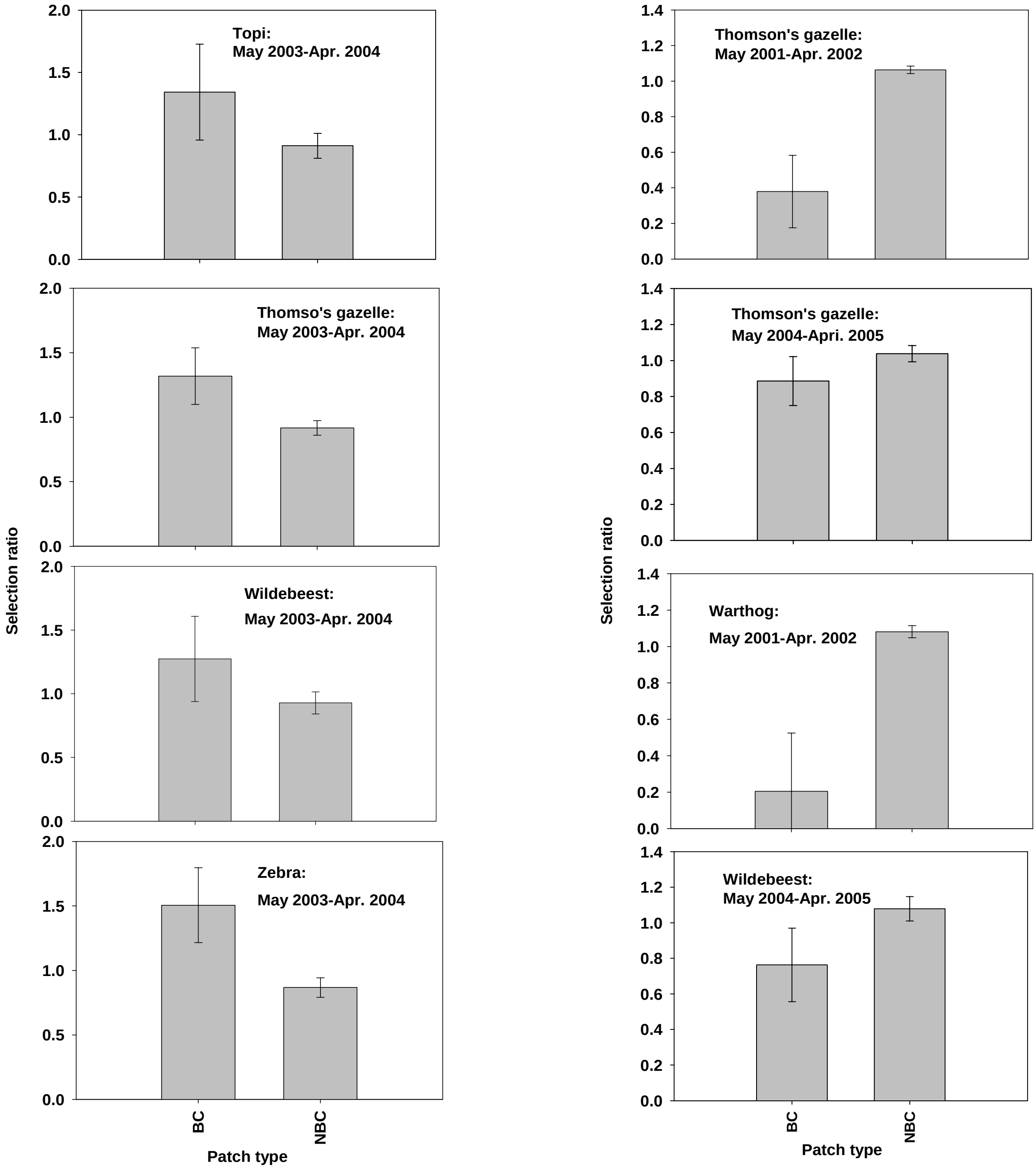
Topi:
May 2003-Apr. 2004
Thomso's gazelle:
May 2003-Apr. 2004
Wildebeest:
May 2003-Apr. 2004
Zebra:
May 2003-Apr. 2004
Thomson's gazelle:
May 2001-Apr. 2002
Thomson's gazelle:
May 2004-Apri. 2005
Warthog:
May 2001-Apr. 2002
Wildebeest:
May 2004-Apr. 2005
Selection ratio
Selection ratio
0.0
0.5
1.0
1.5
2.0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
BC
NBC
BC
NBC
Patch type
Patch type

Figure 4b

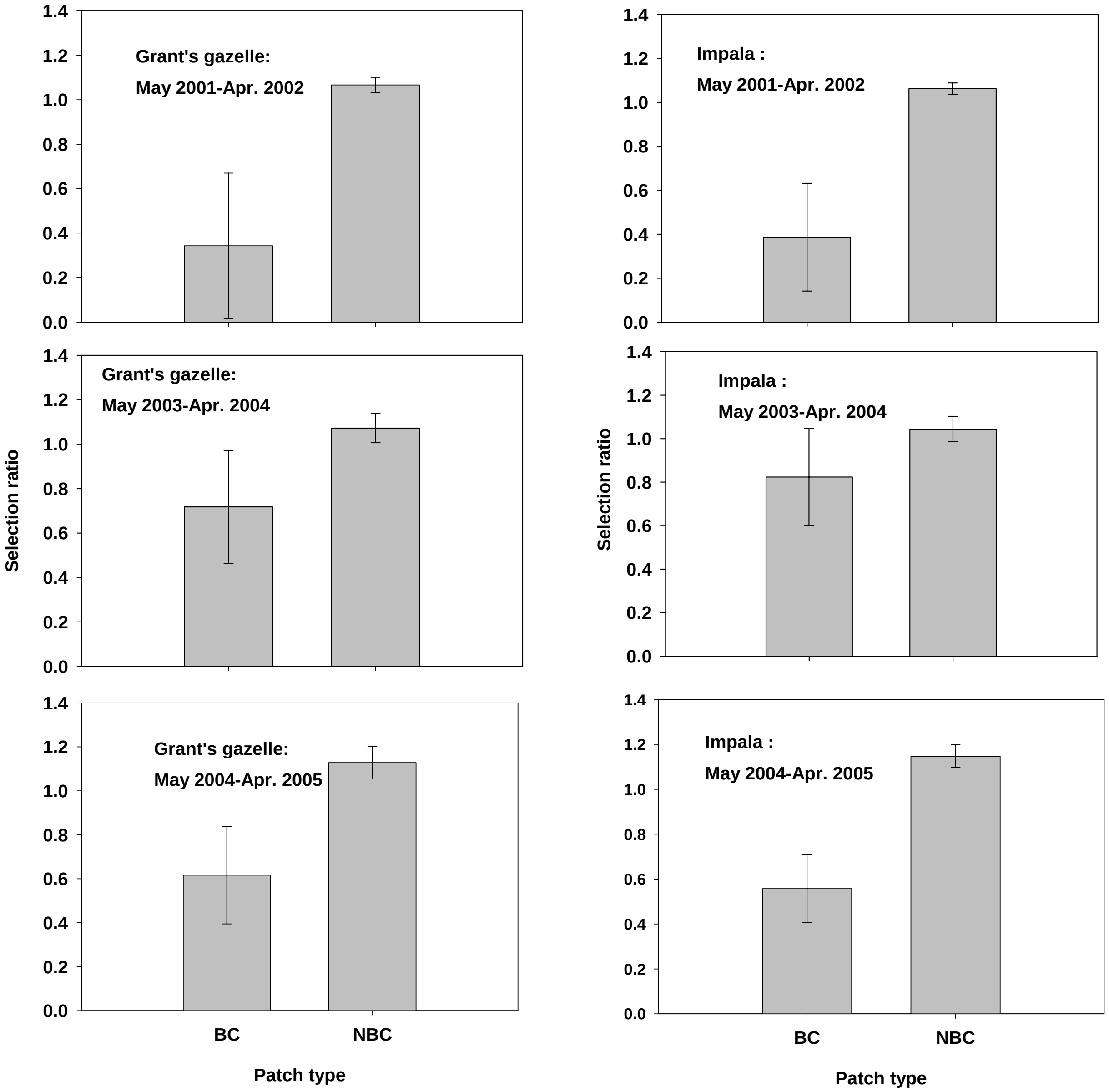
Grant's gazelle:
May 2001-Apr. 2002
Impala :
May 2001-Apr. 2002
Grant's gazelle:
May 2003-Apr. 2004
Impala :
May 2003-Apr. 2004
Grant's gazelle:
May 2004-Apr. 2005
Impala :
May 2004-Apr. 2005
Selection ratio
Selection ratio
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
BC
NBC
BC
NBC
Patch type
Patch type

Figure 5

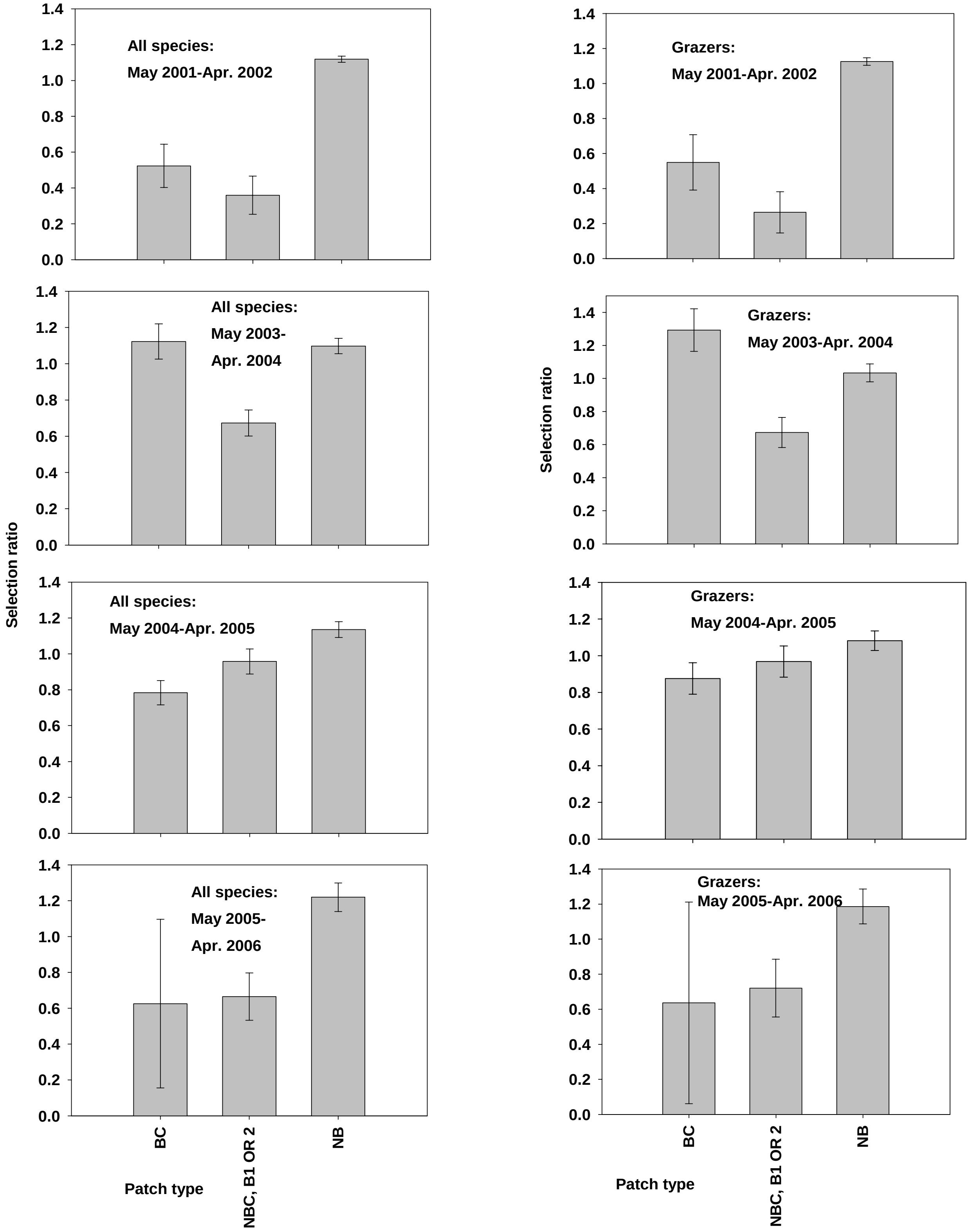
Selection ratio
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
All species:
May 2001-Apr. 2002
Grazers:
May 2001-Apr. 2002
All species:
May 2003-
Apr. 2004
Grazers:
May 2003-Apr. 2004
All species:
May 2004-Apr. 2005
Grazers:
May 2004-Apr. 2005
All species:
May 2005-
Apr. 2006
Grazers:
May 2005-Apr. 2006
BC
NBC, B1 OR 2
NB
Patch type

Figure 6a

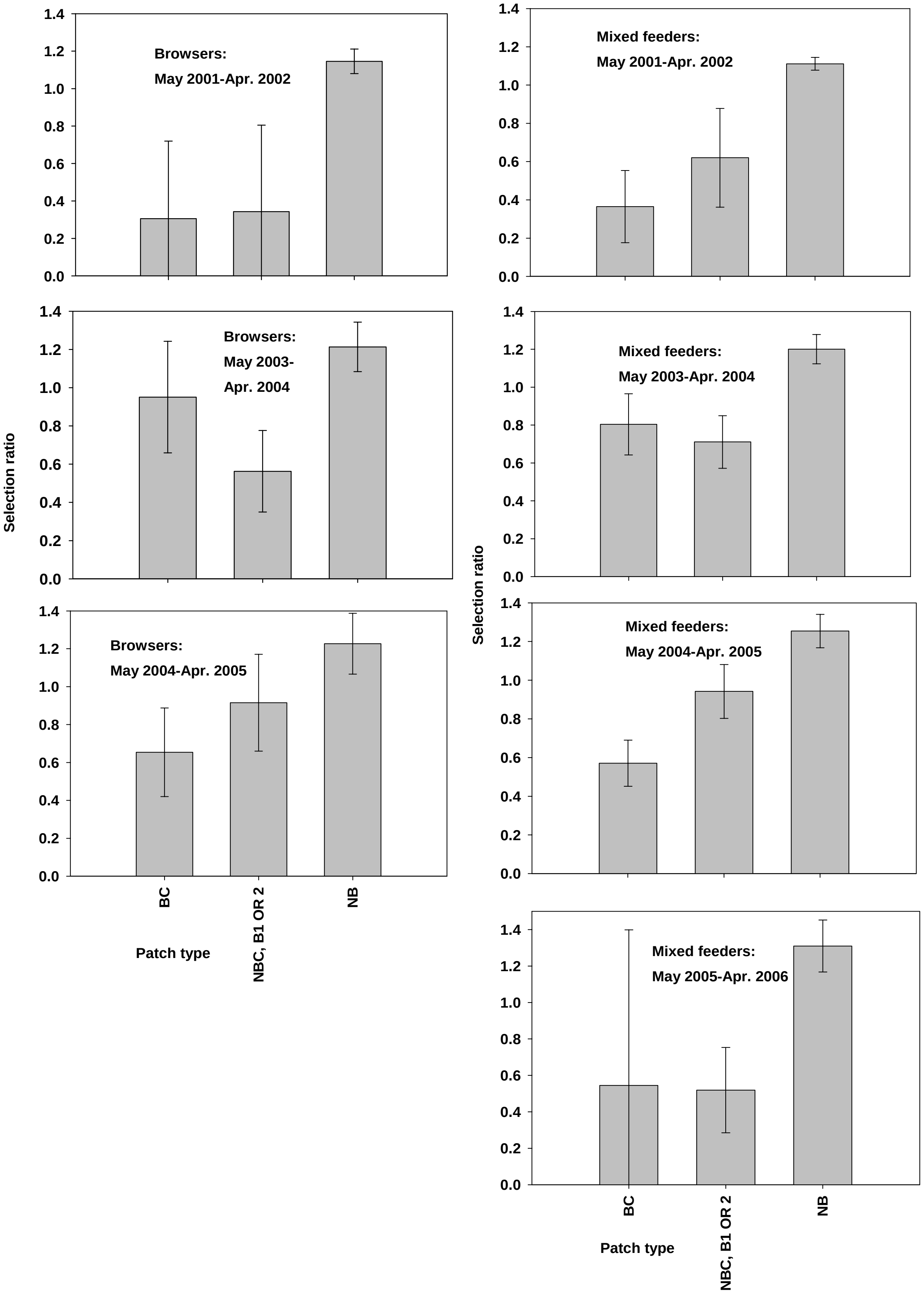
Browsers:
May 2001-Apr. 2002
Browsers:
May 2003-
Apr. 2004
Browsers:
May 2004-Apr. 2005
Mixed feeders:
May 2001-Apr. 2002
Mixed feeders:
May 2003-Apr. 2004
Mixed feeders:
May 2004-Apr. 2005
Mixed feeders:
May 2005-Apr. 2006
Selection ratio
Selection ratio
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
BC
NBC, B1 OR 2
NB
Patch type

Figure 6b

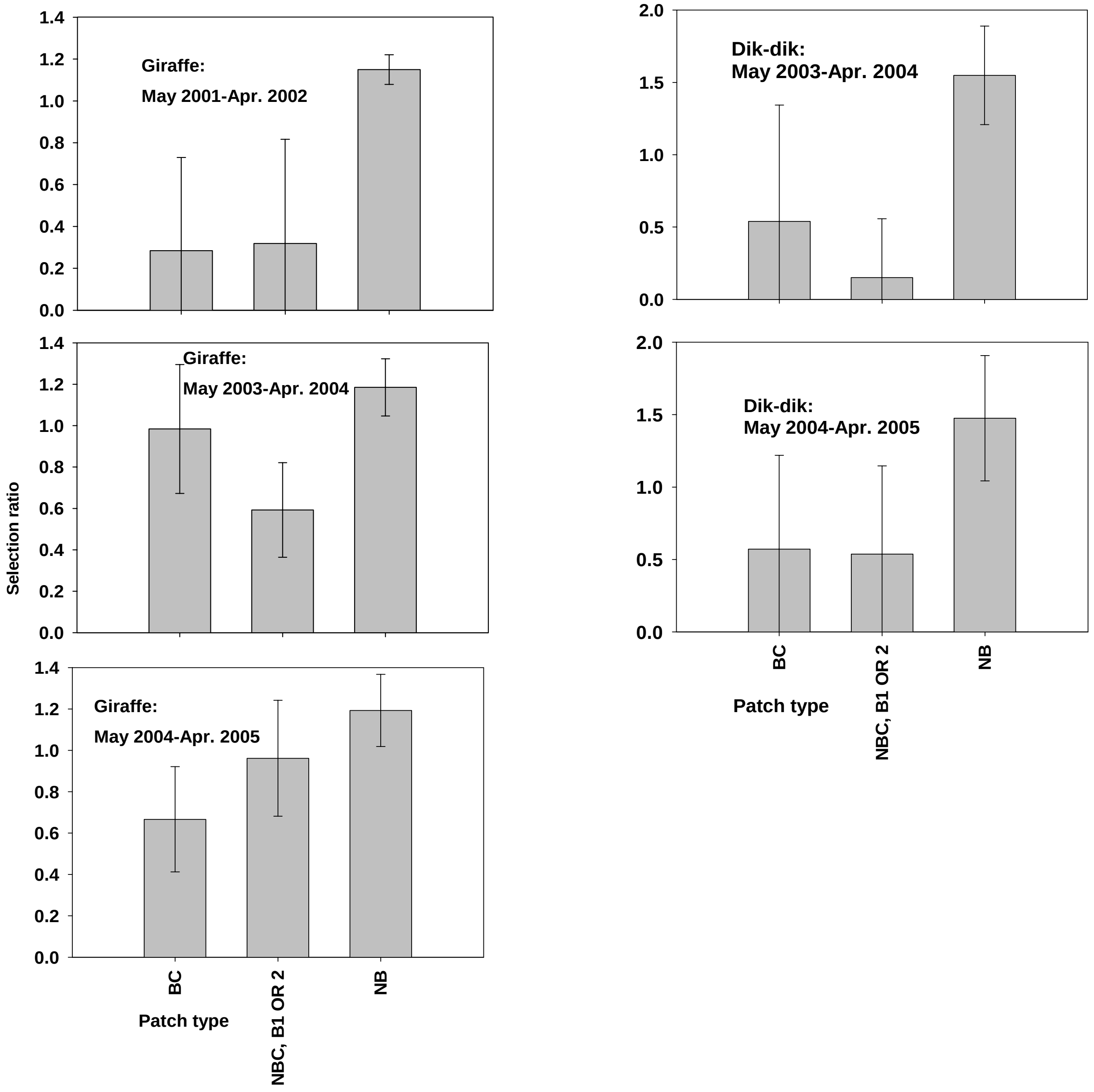
Giraffe:
May 2001-Apr. 2002
Giraffe:
May 2003-Apr. 2004
Giraffe:
May 2004-Apr. 2005
Dik-dik:
May 2003-Apr. 2004
Dik-dik:
May 2004-Apr. 2005
Selection ratio
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
0.0
0.5
1.0
1.5
2.0
BC
NBC, B1 OR 2
NB
Patch type

Figure 7a

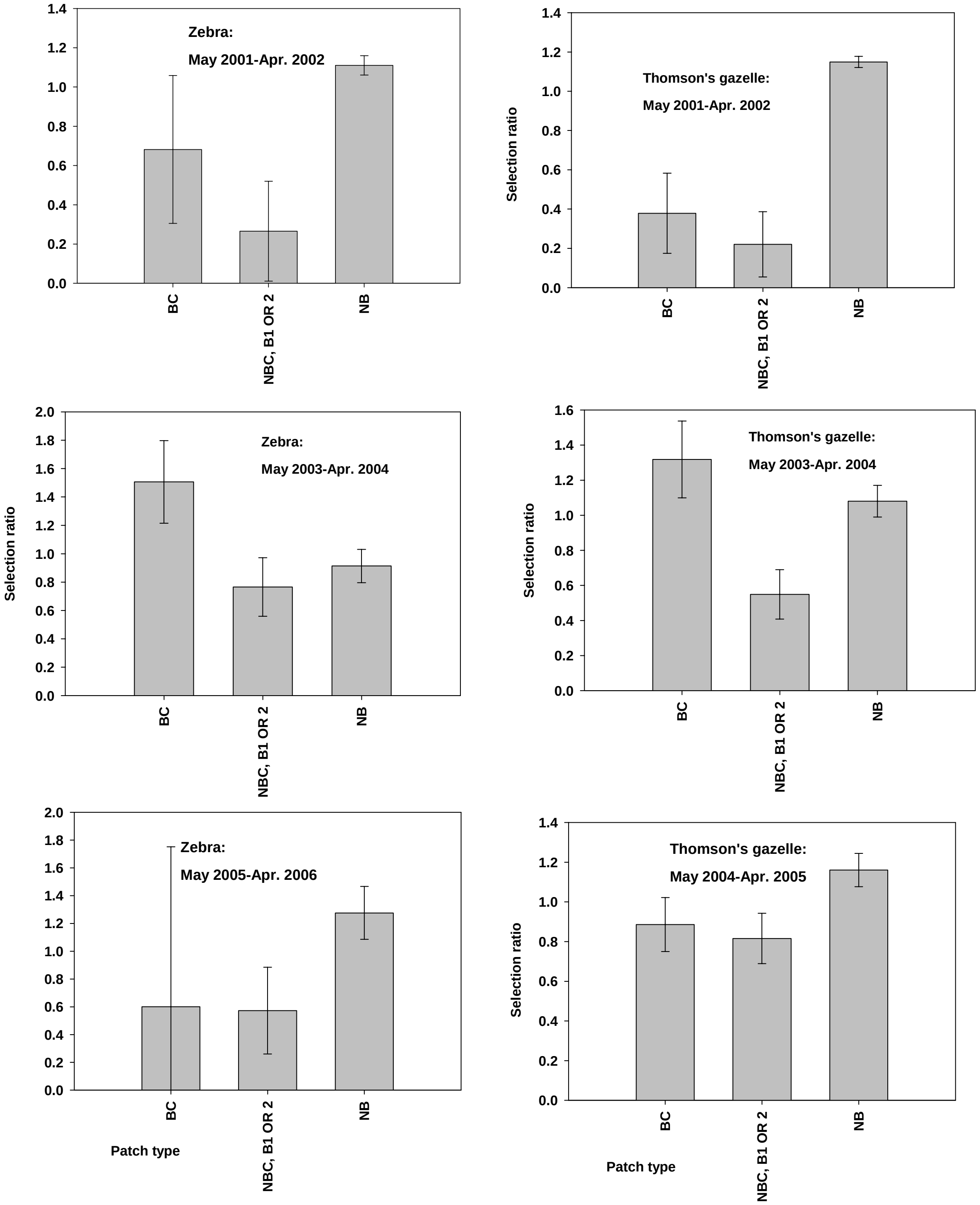
Zebra:
May 2001-Apr. 2002
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
BC
NBC, B1 OR 2
NB
Thomson's gazelle:
May 2001-Apr. 2002
Selection ratio
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
BC
NBC, B1 OR 2
NB
Zebra:
May 2003-Apr. 2004
Selection ratio
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
BC
NBC, B1 OR 2
NB
Thomson's gazelle:
May 2003-Apr. 2004
Selection ratio
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
BC
NBC, B1 OR 2
NB
Zebra:
May 2005-Apr. 2006
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
BC
NBC, B1 OR 2
NB
Patch type
Thomson's gazelle:
May 2004-Apr. 2005
Selection ratio
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
BC
NBC, B1 OR 2
NB
Patch type

Figure 7b

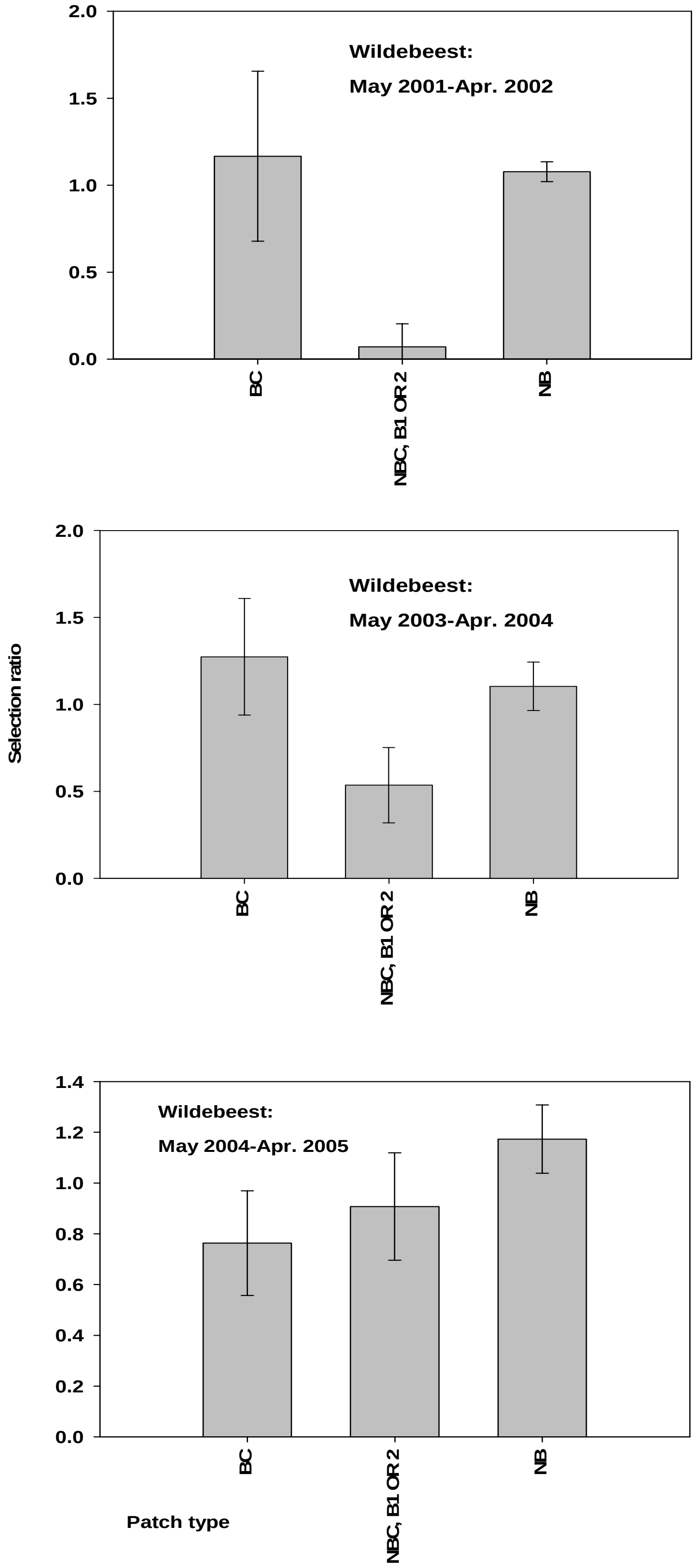
2.0
1.5
1.0
0.5
0.0
Wildebeest:
May 2001-Apr. 2002
BC
NBC, B1 OR 2
NB
2.0
1.5
1.0
0.5
0.0
Selection ratio
Wildebeest:
May 2003-Apr. 2004
BC
NBC, B1 OR 2
NB
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Wildebeest:
May 2004-Apr. 2005
BC
NBC, B1 OR 2
NB
Patch type

Figure 7c

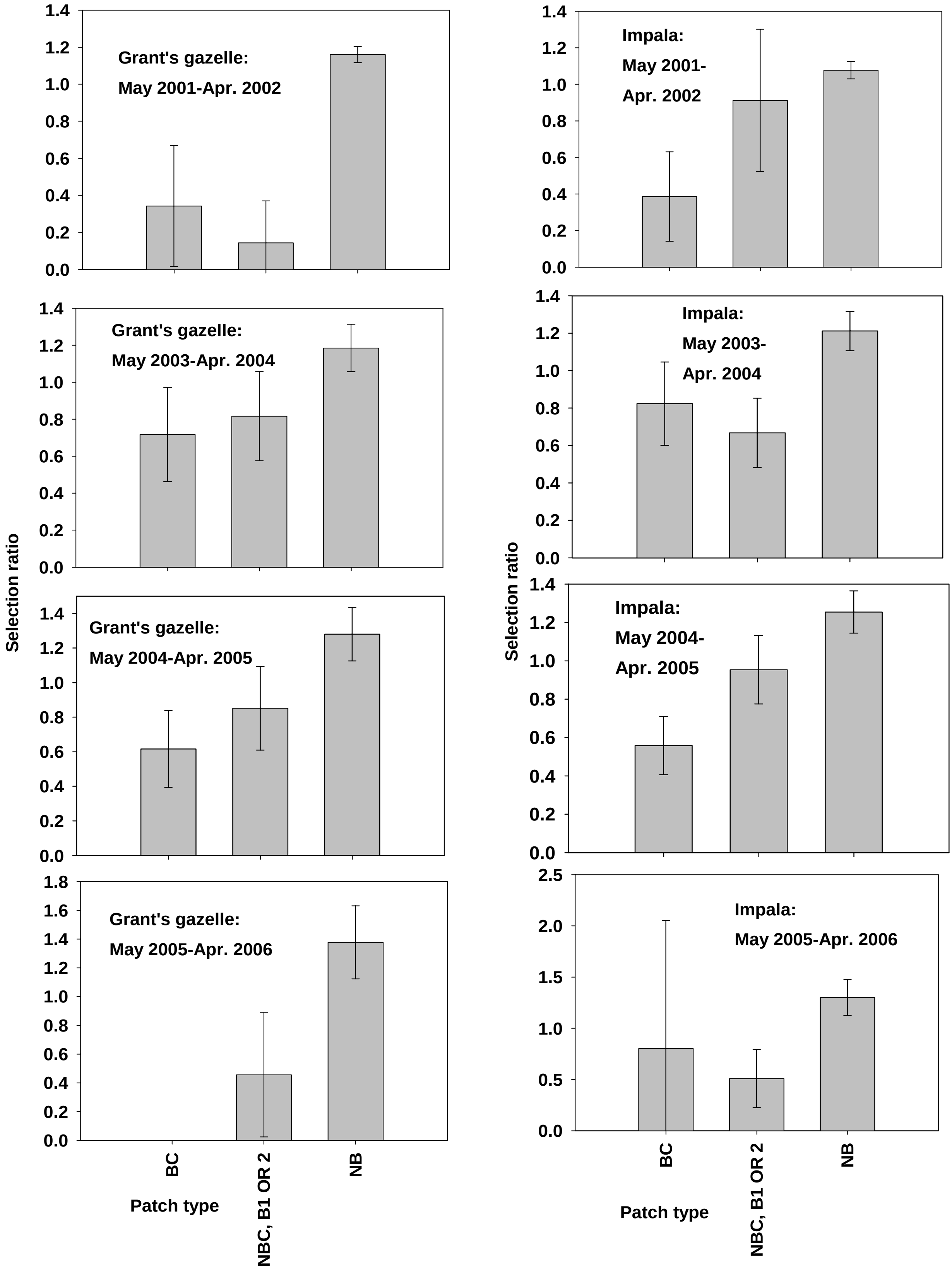
Grant's gazelle:
May 2001-Apr. 2002
Grant's gazelle:
May 2003-Apr. 2004
Grant's gazelle:
May 2004-Apr. 2005
Grant's gazelle:
May 2005-Apr. 2006
Impala:
May 2001-
Apr. 2002
Impala:
May 2003-
Apr. 2004
Impala:
May 2004-
Apr. 2005
Impala:
May 2005-Apr. 2006
Selection ratio
Selection ratio
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
0.5
1.5
2.0
2.5
BC
NBC, B1 OR 2
NB
Patch type
BC
NBC, B1 OR 2
NB
Patch type

Figure 7d

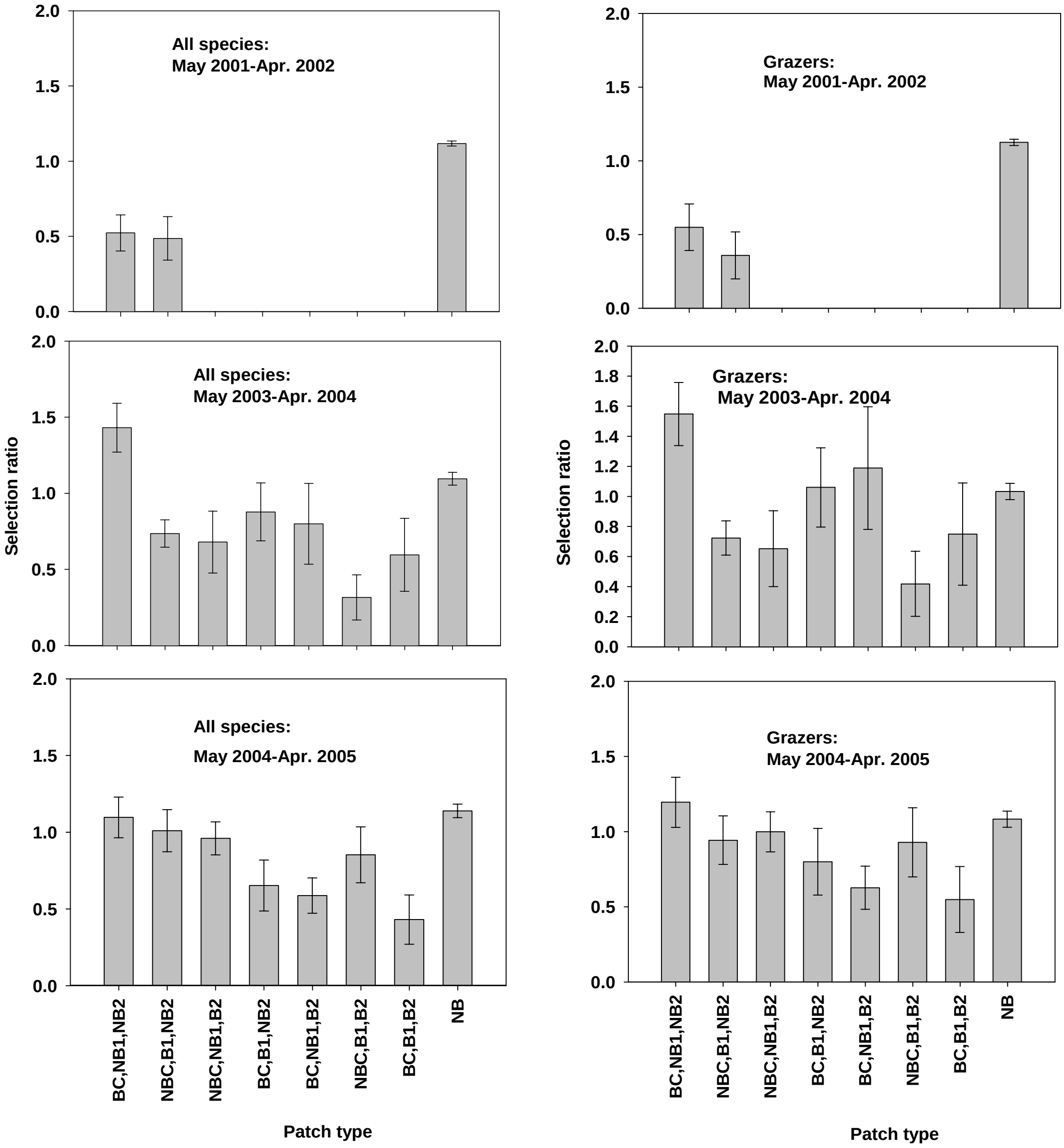
All species:
May 2001-Apr. 2002
Grazers:
May 2001-Apr. 2002
All species:
May 2003-Apr. 2004
Grazers:
May 2003-Apr. 2004
All species:
May 2004-Apr. 2005
Grazers:
May 2004-Apr. 2005
Selection ratio
Selection ratio
0.0
0.2
0.4
0.5
0.6
0.8
1.0
1.2
1.4
1.5
1.6
1.8
2.0
BC,NB1,NB2
NBC,B1,NB2
NBC,NB1,B2
BC,B1,NB2
BC,NB1,B2
NBC,B1,B2
BC,B1,B2
NB
Patch type
Patch type

Figure 8a

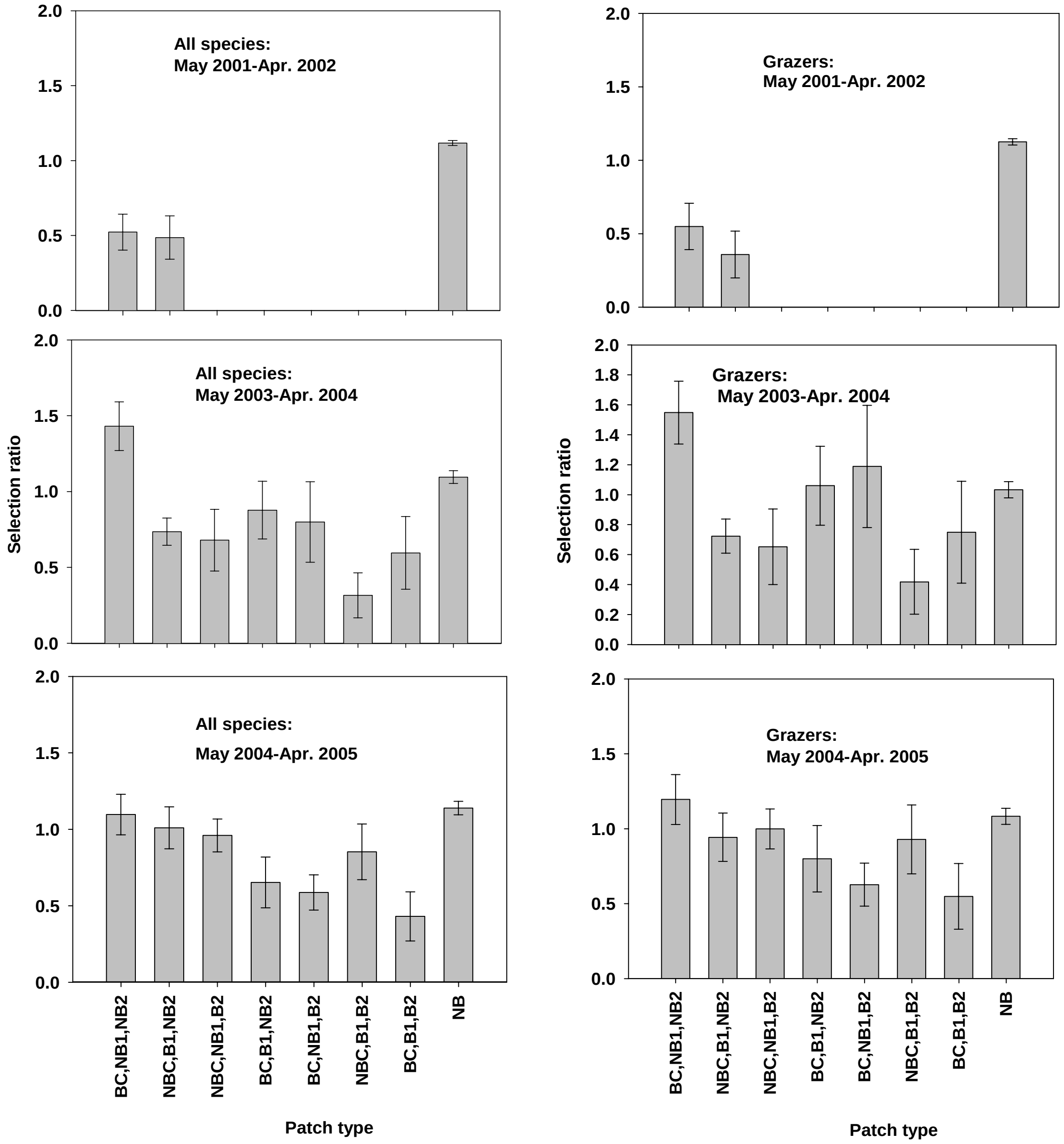
All species:
May 2001-Apr. 2002
Grazers:
May 2001-Apr. 2002
All species:
May 2003-Apr. 2004
Grazers:
May 2003-Apr. 2004
All species:
May 2004-Apr. 2005
Grazers:
May 2004-Apr. 2005
Selection ratio
Selection ratio
0.0
0.5
1.0
1.5
2.0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
BC,NB1,NB2
NBC,B1,NB2
NBC,NB1,B2
BC,B1,NB2
BC,NB1,B2
NBC,B1,B2
BC,B1,B2
NB
Patch type
Patch type

Figure 8a

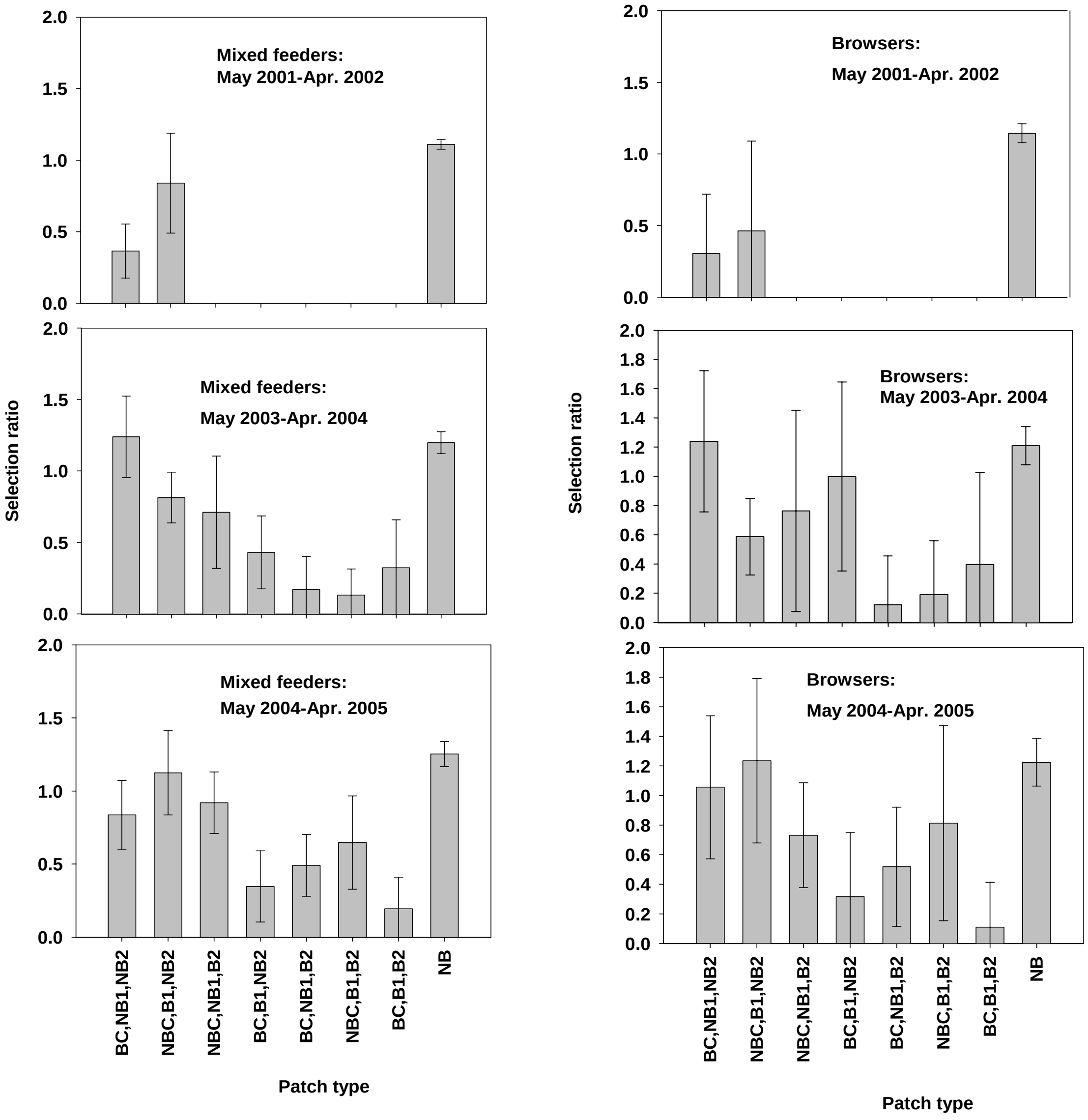
Mixed feeders:
May 2001-Apr. 2002
Mixed feeders:
May 2003-Apr. 2004
Mixed feeders:
May 2004-Apr. 2005
Browsers:
May 2001-Apr. 2002
Browsers:
May 2003-Apr. 2004
Browsers:
May 2004-Apr. 2005
Selection ratio
Selection ratio
0.0
0.5
1.0
1.5
2.0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
BC,NB1,NB2
NBC,B1,NB2
NBC,NB1,B2
BC,B1,NB2
BC,NB1,B2
NBC,B1,B2
BC,B1,B2
NB
Patch type
Patch type

Fig. 8b

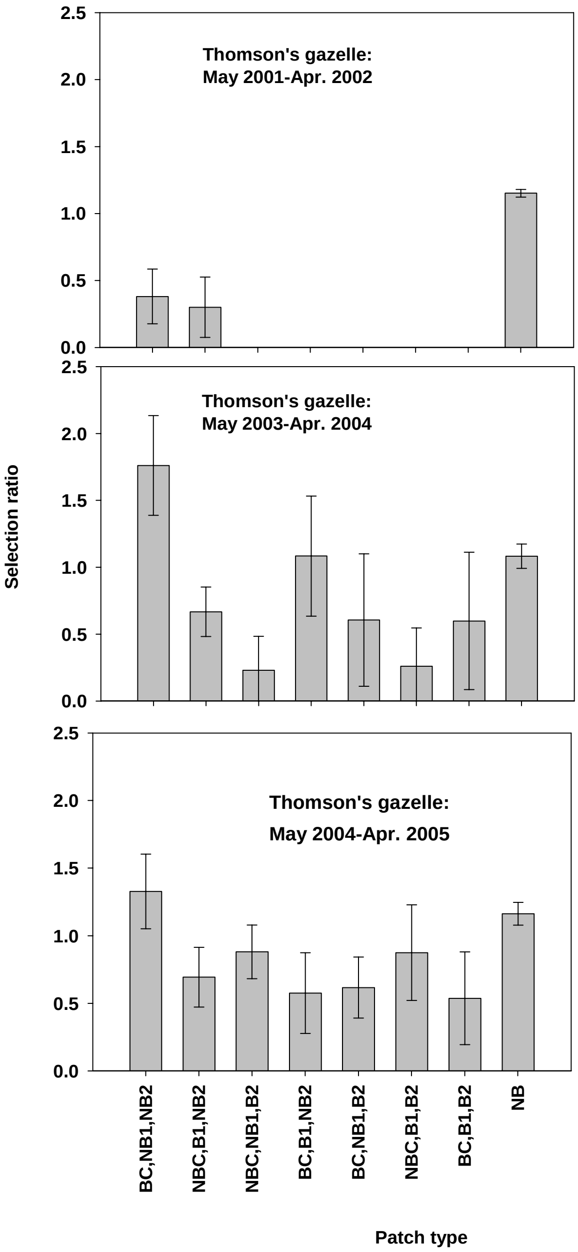
Thomson's gazelle:
May 2001-Apr. 2002
Thomson's gazelle:
May 2003-Apr. 2004
Thomson's gazelle:
May 2004-Apr. 2005
Selection ratio
0.0
0.5
1.0
1.5
2.0
2.5
BC,NB1,NB2
NBC,B1,NB2
NBC,NB1,B2
BC,B1,NB2
BC,NB1,B2
NBC,B1,B2
BC,B1,B2
NB
Patch type

Figure 9

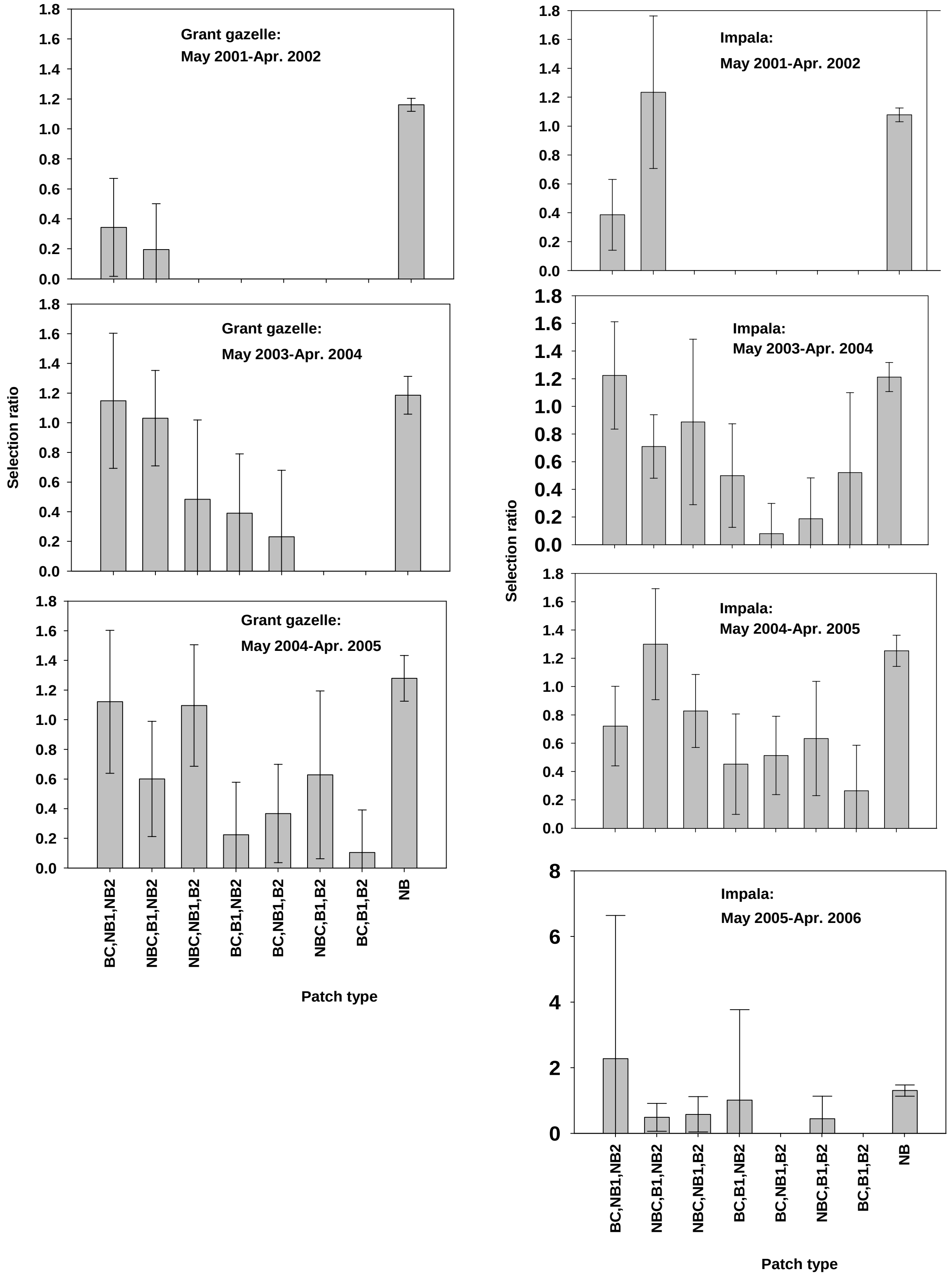
Grant gazelle:
May 2001-Apr. 2002
Grant gazelle:
May 2003-Apr. 2004
Grant gazelle:
May 2004-Apr. 2005
Impala:
May 2001-Apr. 2002
Impala:
May 2003-Apr. 2004
Impala:
May 2004-Apr. 2005
Impala:
May 2005-Apr. 2006
Selection ratio
Selection ratio
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
0
2
4
6
8
BC,NB1,NB2
NBC,B1,NB2
NBC,NB1,B2
BC,B1,NB2
BC,NB1,B2
NBC,B1,B2
BC,B1,B2
NB
Patch type
Patch type

Figure 10

Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos. Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism.
1978	Tore Slagsvold	Dr. philos. Zoology	Breeding events of birds in relation to spring temperature and environmental phenology.
1978	Egil Sakshaug	Dr. philos. Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton".
1980	Arnfinn Langeland	Dr. philos. Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake.
1980	Helge Reinertsen	Dr. philos. Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton.
1982	Gunn Mari Olsen	Dr. scient. Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*.
1982	Dag Dolmen	Dr. philos. Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation.
1984	Eivin Røskaft	Dr. philos. Zoology	Sociobiological studies of the rook *Corvus frugilegus*.
1984	Anne Margrethe Cameron	Dr. scient. Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats.
1984	Asbjørn Magne Nilsen	Dr. scient. Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test.
1985	Jarle Mork	Dr. philos. Zoology	Biochemical genetic studies in fish.
1985	John Solem	Dr. philos. Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains.
1985	Randi E. Reinertsen	Dr. philos. Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds.
1986	Bernt-Erik Sæther	Dr. philos. Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach.
1986	Torleif Holthe	Dr. philos. Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna.
1987	Helene Lampe	Dr. scient. Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires.
1987	Olav Hogstad	Dr. philos. Zoology	Winter survival strategies of the Willow tit *Parus montanus*.
1987	Jarle Inge Holten	Dr. philos. Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway.
1987	Rita Kumar	Dr. scient. Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*.
1987	Bjørn Åge Tømmerås	Dr. scient. Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction.
1988	Hans Christian Pedersen	Dr. philos. Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care.

1988	Tor G. Heggberget	Dr. philos. Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure.
1988	Marianne V. Nielsen	Dr. scient. Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*).
1988	Ole Kristian Berg	Dr. scient. Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.).
1989	John W. Jensen	Dr. philos. Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth.
1989	Helga J. Vivås	Dr. scient. Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*.
1989	Reidar Andersen	Dr. scient. Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation.
1989	Kurt Ingar Draget	Dr. scient. Botany	Alginate gel media for plant tissue culture.
1990	Bengt Finstad	Dr. scient. Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season.
1990	Hege Johannesen	Dr. scient. Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung.
1990	Åse Krøkje	Dr. scient. Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test.
1990	Arne Johan Jensen	Dr. philos. Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams.
1990	Tor Jørgen Almaas	Dr. scient. Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues.
1990	Magne Husby	Dr. scient. Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*.
1991	Tor Kvam	Dr. scient. Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway.
1991	Jan Henning L'Abêe Lund	Dr. philos. Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular.
1991	Asbjørn Moen	Dr. philos. Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands.
1991	Else Marie Løbersli	Dr. scient. Botany	Soil acidification and metal uptake in plants.
1991	Trond Nordtug	Dr. scient. Zoology	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods.
1991	Thyra Solem	Dr. scient. Botany	Age, origin and development of blanket mires in Central Norway.
1991	Odd Terje Sandlund	Dr. philos. Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism.
1991	Nina Jonsson	Dr. philos. Zoology	Aspects of migration and spawning in salmonids.
1991	Atle Bones	Dr. scient. Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase).
1992	Torgrim Breiehagen	Dr. scient. Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher.
1992	Anne Kjersti Bakken	Dr. scient. Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.).

1992	Tycho Anker-Nilssen	Dr. scient. Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*.
1992	Bjørn Munro Jenssen	Dr. philos. Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks.
1992	Arne Vollan Aarset	Dr. philos. Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient. Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells.
1993	Tor Fredrik Næsje	Dr. scient. Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient. Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993	Bård Pedersen	Dr. scient. Botany	Theoretical studies of life history evolution in modular and clonal organisms.
1993	Ole Petter Thangstad	Dr. scient. Botany	Molecular studies of myrosinase in Brassicaceae.
1993	Thrine L. M. Heggberget	Dr. scient. Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient. Botany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2.
1994	Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek.
1994	Kjell Inge Reitan	Dr. scient. Botany	Nutritional effects of algae in first-feeding of marine fish larvae.
1994	Nils Røv	Dr. scient. Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*.
1994	Annette-Susanne Hoepfner	Dr. scient. Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.).
1994	Inga Elise Bruteig	Dr. scient. Botany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers.
1994	Geir Johnsen	Dr. scient. Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses.
1994	Morten Bakken	Dr. scient. Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*.
1994	Arne Moksnes	Dr. philos. Zoology	Host adaptations towards brood parasitism by the Cockoo.
1994	Solveig Bakken	Dr. scient. Botany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply.
1995	Olav Vadstein	Dr. philos. Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions.
1995	Hanne Christensen	Dr. scient. Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*.
1995	Svein Håkon Lorentsen	Dr. scient. Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition.
1995	Chris Jørgen Jensen	Dr. scient. Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity.
1995	Martha Kold Bakkevig	Dr. scient. Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport.

1995	Vidar Moen	Dr. scient. Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations.
1995	Hans Haavardsholm Blom	Dr. philos. Botany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden.
1996	Jorun Skjærmo	Dr. scient. Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae.
1996	Ola Ugedal	Dr. scient. Zoology	Radiocesium turnover in freshwater fishes.
1996	Ingibjørg Einarsdottir	Dr. scient. Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines.
1996	Christina M. S. Pereira	Dr. scient. Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation.
1996	Jan Fredrik Børseth	Dr. scient. Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics.
1996	Gunnar Henriksen	Dr. scient. Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region.
1997	Gunvor Øie	Dr. scient. Botany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae.
1997	Håkon Holien	Dr. scient. Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters.
1997	Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming.
1997	Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture.
1997	Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher.
1997	Torgeir Nygård	Dr. scient. Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors.
1997	Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway.
1997	Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry.
1997	Rolv Lundheim	Dr. scient. Zoology	Adaptive and incidental biological ice nucleators.
1997	Arild Magne Landa	Dr. scient. Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation.
1997	Kåre Magne Nielsen	Dr. scient. Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*.
1997	Jarle Tufto	Dr. scient. Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models.
1997	Trygve Hesthagen	Dr. philos. Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters.
1997	Trygve Sigholt	Dr. philos. Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet.
1997	Jan Østnes	Dr. scient. Zoology	Cold sensation in adult and neonate birds.
1998	Seethaledsumy Visvalingam	Dr. scient. Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins.

1998	Thor Harald Ringsby	Dr. scient. Zoology	Variation in space and time: The biology of a House sparrow metapopulation.
1998	Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment.
1998	Sigurd Mjøen Saastad	Dr. scient. Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity.
1998	Bjarte Mortensen	Dr. scient. Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro.
1998	Gunnar Austrheim	Dr. scient. Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach.
1998	Bente Gunnveig Berg	Dr. scient. Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient. Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach.
1999	Hans Kristen Stenøien	Dr. scient Botany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts).
1999	Trond Arnesen	Dr. scient. Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway.
1999	Ingvar Stenberg	Dr. scient. Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*.
1999	Stein Olle Johansen	Dr. scient. Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis.
1999	Trina Falck Galloway	Dr. scient. Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.).
1999	Torbjørn Forseth	Dr. scient. Zoology	Bioenergetics in ecological and life history studies of fishes.
1999	Marianne Giæver	Dr. scient. Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic.
1999	Hans Martin Hanslin	Dr. scient. Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenioides*, *Ptilium crista-castrensis* and *Rhytidiadelphus loreus*.
1999	Ingrid Bysveen Mjølnerød	Dr. scient. Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques.
1999	Else Berit Skagen	Dr. scient. Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces.
1999	Stein-Are Sæther	Dr. philos. Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe.
1999	Katrine Wangen Rustad	Dr. scient. Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease.
1999	Per Terje Smiseth	Dr. scient. Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*).
1999	Gunnbjørn Bremset	Dr. scient. Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions.
1999	Frode Ødegaard	Dr. scient. Zoology	Host spesificity as parameter in estimates of arhrophod species richness.
1999	Sonja Andersen	Dr. scient. Botany	Expressional and functional analyses of human, secretory phospholipase A2.

2000	Ingrid Salvesen	Dr. scient. Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture.
2000	Ingar Jostein Øien	Dr. scient. Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race.
2000	Pavlos Makridis	Dr. scient. Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae.
2000	Sigbjørn Stokke	Dr. scient. Zoology	Sexual segregation in the African elephant (*Loxodonta africana*).
2000	Odd A. Gulseth	Dr. philos. Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard.
2000	Pål A. Olsvik	Dr. scient. Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway.
2000	Sigurd Einum	Dr. scient. Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size.
2001	Jan Ove Evjemo	Dr. scient. Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species.
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems.
2001	Ingebrigt Uglem	Dr. scient. Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.).
2001	Bård Gunnar Stokke	Dr. scient. Zoology	Coevolutionary adaptations in avian brood parasites and their hosts.
2002	Ronny Aanes	Dr. scient.	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*).
2002	Mariann Sandsund	Dr. scient. Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses.
2002	Dag-Inge Øien	Dr. scient. Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway.
2002	Frank Rosell	Dr. scient. Zoology	The function of scent marking in beaver (*Castor fiber*).
2002	Janne Østvang	Dr. scient. Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development.
2002	Terje Thun	Dr.philos. Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material.
2002	Birgit Hafjeld Borgen	Dr. scient. Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth.
2002	Bård Øyvind Solberg	Dr. scient. Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients.
2002	Per Winge	Dr. scient. Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and
2002	Henrik Jensen	Dr. scient. Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows.
2003	Jens Rohloff	Dr. philos. Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control.
2003	Åsa Maria O. Espmark Wibe	Dr. scient. Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient. Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach.
2003	Bjørn Dahle	Dr. scient. Biology	Reproductive strategies in Scandinavian brown bears.
2003	Cyril Lebogang Taolo	Dr. scient. Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana.
2003	Marit Stranden	Dr. scient. Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*).

2003	Kristian Hassel	Dr.scient. Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*.
2003	David Alexander Rae	Dr. scient. Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments.
2003	Åsa A Borg	Dr. scient. Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective.
2003	Eldar Åsgard Bendiksen	Dr. scient. Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt.
2004	Torkild Bakken	Dr. scient. Biology	A revision of Nereidinae (Polychaeta, Nereididae).
2004	Ingar Pareliussen	Dr. scient. Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar.
2004	Tore Brembu	Dr. scient. Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*.
2004	Liv S. Nilsen	Dr. scient. Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities.
2004	Hanne T. Skiri	Dr. scient. Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*).
2004	Lene Østby	Dr. scient. Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment.
2004	Emmanuel J. Gerreta	Dr. philos. Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania.
2004	Linda Dalen	Dr. scient. Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming.
2004	Lisbeth Mehli	Dr. scient. Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*.
2004	Børge Moe	Dr. scient. Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage.
2005	Matilde Skogen Chauton	Dr. scient. Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples.
2005	Sten Karlsson	Dr. scient. Biology	Dynamics of Genetic Polymorphisms.
2005	Terje Bongard	Dr. scient. Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period.
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths.
2005	Erlend Kristiansen	Dr. scient. Biology	Studies on antifreeze proteins.
2005	Eugen G. Sørmo	Dr. scient. Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations.
2005	Christian Westad	Dr. scient. Biology	Motor control of the upper trapezius.
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments.
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations.
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia.
2005	Ander Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge.

2005	Shimane Washington Makhabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana.
2005	Kjartan Østbye	Dr. scient. Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation.
2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds. Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr. scient. Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates.
2006	Nils Egil Tokle	PhD Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*.
2006	Jan Ove Gjershaug	Dr. philos. Biology	Taxonomy and conservation status of some booted eagles in south-east Asia.
2006	Jon Kristian Skei	Dr. scient. Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway.
2006	Johanna Järnegren	PhD Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity.
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway.
2006	Vidar Grøtan	PhD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates.
2006	Jafari R Kideghesho	PhD Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania.
2006	Anna Maria Billing	PhD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction.
2006	Henrik Pärn	PhD Biology	Female ornaments and reproductive biology in the bluethroat.
2006	Anders J. Fjellheim	PhD Biology	Selection and administration of probiotic bacteria to marine fish larvae.
2006	P. Andreas Svensson	PhD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system.
2007	Sindre A. Pedersen	PhD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine.
2007	Kasper Hancke	PhD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae.
2007	Tomas Holmern	PhD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation.
2007	Kari Jørgensen	PhD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*.
2007	Stig Ulland	PhD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, */Mamestra Brassicae/* L. (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry.
2007	Snorre Henriksen	PhD Biology	Spatial and temporal variation in herbivore resources at northern latitudes.
2007	Roelof Frans May	PhD Biology	Spatial Ecology of Wolverines in Scandinavia.
2007	Vedasto Gabriel Ndibalema	PhD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania.
2007	Julius William Nyahongo	PhD Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania.