

LIVING WITH WILDLIFE

**COEXISTENCE OF WILDLIFE AND LIVESTOCK
IN AN EAST AFRICAN SAVANNA SYSTEM**

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COEXISTENCE OF WILDLIFE AND LIVESTOCK IN AN EAST AFRICAN SAVANNA SYSTEM

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For my mother,

with gratitude for the wisdom of life you showed me,

with sadness that you can't be here,

with solace because of all the precious memories.

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Abstract

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This thesis has as its main theme the coexistence of wildlife and livestock in East African savannas. First however, the group size of native herbivore species was related to their body mass, feeding style, habitat choice and density. Body mass explained most variation in group size because of its relation to food requirements and how different sized animals experience the distribution of food. Differential use of (food)resources by Zebu-cattle, wildebeest and zebra was then investigated. The three species show substantial overlap in resource use by selecting similar feeding sites, foraging on the same grass species and preferring the same habitat types. More overlap was found between cattle and either wildebeest or zebra than between wildebeest and zebra. This overlap in combination with limited resources implicates a strong potential for competition between cattle and the native species. However, wildlife is able to avoid competition with livestock during the dry season by moving to areas where cattle do not have access. This seasonal movement is not because of competition, but is a result of differences in resource availability between areas. This thesis also shows that the animals move to their wet season range because only there they can satisfy all their nutritional needs, which are high at this time of the year since the females are lactating. Their movement back to the dry season range however is related to water requirements. Furthermore, a clipping experiment was performed to investigate if the dry season range of migratory wildebeest and zebra could sustain current populations year-round when access to the wet season range would be restricted. The results indicate that clipping had a positive effect on forage quality, but that the mineral concentrations were still not sufficient to meet herbivore nutrient requirements while clipping also reduced the annual forage production to insufficient levels. The results of this study can be put to use in present land-use issues related to the integration of wildlife conservation and development of pastoral areas.

Key-words: *Ungulates; grazing; Tropics; foraging; wildlife-livestock interactions*

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GENERAL INTRODUCTION

The introduction of an exotic species into a native faunal assemblage can have far reaching negative consequences for natural ecosystems. A notorious example is the change in the native fish fauna after introduction of the Nile perch in Lake Victoria (Goldschmidt 1994, Kitchell et al. 1997). Although not always perceived as such, also livestock can be viewed as exotic species since livestock did not evolve with native herbivore species. In the last decades, it has been recognised that livestock populations are an important factor in the ecological degradation prevailing in many of the arid and semi-arid rangelands of the world (UNEP 1977, Lamprey 1983, Prins 1989, De Haan et al. 1996, Steinfeld et al. 1996, Rietkerk 1998). Because of human influence, livestock is generally less subject to natural regulating mechanisms (Lamprey 1983). As a result livestock numbers can, for prolonged periods, increase to levels which are greater than the safe stocking rates of their habitats, thus negatively affecting habitat conditions. Indeed, high stocking rates of livestock have led to habitat deterioration and displacement of wild herbivores (Werger 1977, leHouérou 1989, De Bie 1991). This has led to the concern that livestock and wild herbivores may compete for the scarce resources in arid and semi-arid rangelands, also because livestock is ecologically similar to several wild herbivore species (Prins 1999, Voeten & Prins 1999). The question thus arises how compatible livestock and wild herbivores are, and if they can coexist.

In East-Africa, with largely rural pastoral economies, this question becomes even more significant as human populations outside protected wildlife areas increase and as demands for land and natural resources grow. Currently, much effort is put into integrating wildlife conservation with development of rural communities. While it might be clear that large-scale agricultural and industrial activities are incompatible with wildlife conservation, there is not yet much consensus on the issue of shared land-use by pastoralism and wildlife. Several authors have stated that pastoralists and their livestock have been able to live side by side with wildlife already for centuries without severely affecting each other (Osemeobo 1988, OleParkipuny 1989, Homewood & Rodgers 1991). Others, however, seriously question this contention (Lamprey 1983, Prins 1992), which is substantiated by the finding that in areas with increased livestock numbers wild herbivore populations are decreasing (Ecosystems LTD 1980, Prins 1992, Happold 1995, De Leeuw et al. 1998). While much attention and research on irreversible changes in semi-arid systems has focussed on livestock-environment interactions, not much effort has been put into studying the animal component, i.e. livestock and wildlife.

This thesis wants to contribute to bridge this gap in knowledge and has as its main theme the coexistence of wildlife and livestock. Besides being a fundamental ecological question namely: if and how livestock fits in a natural system, this question is of cardinal importance for present land-use issues: to find a balance between preservation of natural resources and the development of rural communities in arid and semi-arid regions of the world is a challenge for the next century.

History of pastoralism in East-Africa

Wildlife and livestock in East Africa do not share a long common evolutionary history. While most of the present day wild ungulates have evolved together since the Pliocene approximately 5 million years ago (Estes 1991), domestication of wild ungulates is estimated to have begun in Western Asia about 10,000 years ago (Payne & Hodges 1997, p13). The earliest evidence of pastoralism in East Africa dates from 3500-2500 BP (Homewood & Rodgers 1991, p57, Smith 1992, p80). Before the appearance of herding and farming most inhabitants of East Africa were hunter-gatherers most probably speaking a Khoisan language (Phillipson 1977 but see Schepartz 1988). It is still under debate to what extent local people adopted the pastoral way of life and to what extent livestock keeping was first introduced by Southern-Cushitic language speaking groups immigrating into East Africa from northern Africa (Galaty 1993, Marshall 1994). By 2000 BP, the descendants of these groups dominated Kenya and northern Tanzania (Galaty 1993). According to linguistic and archaeological evidence, the period between 2000 BP and 1000 BP was characterized by the interaction and assimilation of groups with different subsistence practices and languages. The Nilotic linguistic groups from more northern regions further spread into East Africa and split into three different language clusters: the Plains, Highland and River-Lake Nilotes. At the same time Bantu-speaking peoples from the west and south-west entered East-Africa taking along cultivation practices. The period between 2000 and 1000 BP is often referred to as the pastoral iron age and is associated with the development of more intensive and highly specialized forms of pastoralism (Galaty 1993), finally resulting in the present-day distribution of pastoral peoples. This mosaic of social and linguistic groupings shows a variety of life styles: ranging from camel and small stock herding in the more arid areas to

cattle and small stock herding elsewhere and from nomadic pastoralism to more permanent settlements with a combination of husbandry and cultivation (Smith 1992, p168 ff). Description of all these different groups is beyond the scope of this thesis and the remainder of this section will therefore focus on the historic developments in the area where the research described in this thesis was conducted namely the Tanzanian part of what is presently known as Masailand or the Masai-Ecosystem (Prins 1987) (See Fig. 1).

By 1000 BP, the Highland Nilotic linguistic group already covered much of Masailand and they integrated with their Southern Cushitic precursors. From around this period onwards the Plains Nilotes (or Eastern Nilotes) which have developed into the Maa-speaking groups started to expand southward through Kenya (Sommer & Vossen 1993, p25 ff.). Between the sixteenth and eighteenth centuries the Maa-speaking people expanded their influence from Lake Turkana in northern Kenya, southward throughout the Rift Valley area to modern Tanzanian Masailand (Sommer & Vossen 1993), thereby replacing other pastoralist groups such as descendants of the Highland Nilotes and Bantu cultivators (Homewood and Rodgers 1991, p59).

The arrival of European colonists greatly affected pastoralists (and others) during the last two centuries, one of the main events being the rinderpest epidemic at the end of the last century. This non-endemic disease wiped out as much as 90% of domestic stock and wild ungulates such as buffalo and wildebeest (Sinclair 1977, Waller 1985). Besides the loss of livestock, the ensuing famine and outbreaks of diseases such as smallpox affected the human population even more. The decimation of livestock, wildlife and people also had ecological implications. Due to less grazing and less fire, many of the pastoral areas became bush encroached and infected with tsetse (Ford 1971, Van de Vijver 1999). Outbreaks of rinderpest still occur locally (Anderson et al. 1990, Grootenhuis 1999), but both livestock and wildlife populations recovered well from the major epidemic of the 1890s. Buffalo and wildebeest numbers increased exponentially once a cattle vaccination campaign had started in the 1950s but their numbers levelled off in the 1970s in the Serengeti Ecosystem (Sinclair 1979, Plowright 1982). The increase in cattle numbers still continues (see Table 1).

The last decades showed profound changes in many pastoral societies and also in Masailand (Collett 1987, Mwalyosi 1991, Lama 1998). Due to increase in human populations, the expansion of large-scale agriculture and the establishment of protected wildlife areas, pastoralists have become more and more restricted in their movements. Hereby, their

Table 1. Livestock and human populations of Tanzania (source: www.fao.org).

Tanzania (883,590 km ²)	1962	1971	1980	1995
Livestock (x 10⁶)				
Cattle	8.3	10.4	12.6	13.9
Sheep	3.0	2.8	3.8	4.0
Goats	4.5	4.5	5.7	9.7
People (x 10⁶)				
Urban	0.5	0.9	3.8	7.3
Rural	9.7	12.8	17.9	22.7

predominantly nomadic way of life is turning into a more sedentary existence in combination with small-scale agricultural activities. Furthermore, although traditionally pastoralists exercise seasonal rights to grazing lands rather than definitive ownership (Sperling & Galaty 1990), pastoralists are presently forced to secure the tenure of grazing lands by obtaining title deeds (Steinfeld 1996, Lama 1998).

Nowadays, pastoralists occupy the more marginal lands, which are less suitable for agriculture, and at the same time these marginal lands have often been set aside as protected areas for wildlife. Depending on the legal status of these protected areas, limited or no human activities (including cattle grazing) are allowed while wildlife is not bound by fences or regulations. It is particularly in the surroundings of these protected areas that wildlife and livestock still frequently interact.

Interactions between wildlife and livestock

Predation

Predation of livestock by wildlife happens occasionally, but livestock is usually well protected during the day by herdsman and during the night in fenced kraals. Lama (1998) reports that during 1994, 9% of livestock was killed by wildlife (3% cattle and 15% small stock) in Loiborsoit, a village on the Simanjiro Plains in Tanzania with 2500 people using an area of 1200 km². Newmark et al. (1994) conducted a survey among people living close to protected areas in northern Tanzania. Over 71% of local people questioned, reported problems with wildlife over a 2 year period: 10% reported the killing of livestock and poultry while

86% reported crop damage, mainly by elephant, buffalo and hippopotamus. Although direct predation of livestock on wildlife is not possible as such, one could view hunting and poaching by people as the reciprocal of predation of livestock on wildlife. Most pastoralists do not hunt habitually but occasionally kill wildlife to protect their livestock, to supplement their diet with meat, in traditional ceremonies or to recover their wealth (Huntingford 1953, Homewood & Rodgers 1991). The impact on wildlife by hunter/gatherers such as the Wandorobo tribe in Tanzania has possibly never been high, due to their low numbers. The exact impact on wildlife populations however, is difficult to retrieve from the past. Since 1920 trophy hunting occurred at a large scale in East Africa (Delany & Happold 1979) and reduced the populations of some wild species. In the 1970-1980, large-scale poaching by local people either hired by others or on their own initiative, severely diminished the elephant and rhino populations of East Africa. Lately, also meat poaching has become an important factor in the dynamics of wildebeest and buffalo populations (Campbell & Hofer 1995, Mduma et al. 1998). Although the impact on wildlife through hunting by local communities with a pastoral mode of production might increase because of increasing human populations, their impact is still smaller in comparison with recent large scale meat poaching.

Diseases

The main livestock disease in wildlife is the already mentioned rinderpest. Due to extensive vaccination programs in the 1950s, 1960s and 1970s, rinderpest became virtually eradicated. Vaccination has not been kept up in many areas and rinderpest outbreaks have recently become apparent in wildlife, for example in Kenya's Tsavo National Park (Kock et al. 1995), in Nairobi National Park and in Tanzania (pers. com. H.H.T. Prins). Other diseases of domestic animals which can be transmitted to wildlife are tuberculosis, brucellosis and rabies. There are also several indigenous wildlife diseases that can severely affect livestock. Foot and Mouth disease is an important viral disease, which affects several species of livestock. Certain strains of the virus are carried by buffalo but by no other wild animal species. However, cattle maintain most of the strains themselves and the buffalo types will become important when complete control is achieved in domestic livestock (Grootenhuys 1999). Wildebeest carry, but are resistant to, malignant catarrhal fever, a disease fatal to cattle. Pastoralists avoid areas used by wildebeest during the infectious period, namely the calving period (Machange 1997).

Much wildlife is thought to be a major factor in maintenance and spread of so called tickborne diseases such as East Coast Fever. Corridor disease and the so called Ormilo disease, both related to East Coast fever and carried by buffalo, were the main cause of the 52% calf mortality and 18% adult mortality among cattle in 1997/1998 in the Ngorongoro Conservation Area in Tanzania (Rwambo et al. 1999). Trypanosomosis transmitted by tsetse flies limits the distribution of livestock throughout East Africa while their wild hosts can survive infection. However, the large-scale tsetse control programs, involving bushclearing and eradication of game in the 1960s (Homewood & Rodgers 1991) directly affected wildlife populations. Disease transmissions between wildlife and livestock affect their coexistence negatively in a serious but not insurmountable manner. The consequences of disease interactions are mainly dependent on financial resources available for control measurements such as vaccination programs and cattle dips.

Competition for resources

Competition is an interaction in which one organism consumes a resource that would have been available to, and might have been consumed by, another. One organism deprives another, and, as a consequence, the other organism grows more slowly, leaves fewer progeny or is at greater risk of death (Begon et al. 1996). Competition can either lead to exclusion of one (or more) of the species involved or to coexistence depending on the degree of niche differentiation, the initial densities of the competing species and the competitive characteristics of the species involved.

The ecological similarity between wildlife and livestock and the competitive characteristics of livestock (because of protection by herdsman), makes it likely that there is a large potential for competition between wildlife and livestock which eventually may lead to exclusion of wildlife. It has been often emphasized, that too high stocking rates of livestock can change the vegetation structure to such an extent that, over time, the carrying capacity of an area is negatively affected and that therefore livestock indirectly competes with wildlife for resources (Lamprey 1983, Happold 1995, Prins 1999). However, so far, not much effort has been put into studying the conditions necessary for competition to occur, being overlap in diet, in habitat and limited resources (Wiens 1989). Part of this thesis focuses on these conditions and the possible consequences of this.

Study area

The research conducted for this thesis was performed in the Masai Ecosystem (Prins 1987), a savanna ecosystem situated in the eastern part of the Rift Valley in northern Tanzania. Here, large concentrations of wildlife utilise the pastures of the system together with cattle, donkeys, sheep and goats of the herding communities, particularly the Masai and Arusha ethnic groups. The Masai Ecosystem encompasses approximately 35,000 km² and stretches out from Lake Natron in the north to the Simanjiro plain in the south, the Crater highlands in the west and the Monduli Mountains in the east (Fig 1). The boundaries are based on watersheds and the boundaries between populations of migratory large mammals. It contains two National Parks (Lake Manyara NP and Tarangire NP) and large tracts of Game Controlled Areas (GCA). Tarangire NP (2600 km²) was gazetted in 1969, but was already proclaimed a Game Reserve as early as 1958 (Vesey FitzGerald 1972). This area was not often used by the local pastoralists because of the presence of tsetse and the danger of trypanosomosis for their cattle. Also Lake Manyara NP (100 km²) had been set aside as a Game reserve since 1958 but was gazetted a National Park already in 1960. The National Parks have a strictly protected status and no human activities except wildlife viewing by tourists are allowed. The Parks are not fenced and wildlife is free to move in and out. The Mto-wa-Mbu GCA and Simanjiro GCA are mainly used by pastoralists for livestock grazing, small-scale agricultural activities and firewood collection. In addition, tourist hunting is allowed according to the regulations of the Tanzanian Game Department. The Masai-ecosystem as a whole is nowadays confronted with ever increasing human populations, settlements and large-scale commercial farming.

An outstanding feature of the Masai-ecosystem are the seasonal movements of large herbivores. Migratory wildebeest (*Connochaetus taurinus*) and zebra (*Equus burchelli*) concentrate during the dry season in Tarangire NP and to a lesser extent in Lake Manyara NP and disperse into surrounding areas such as the Mto-wa-Mbu GCA and Simanjiro GCA during the wet season. Less abundant and more resident herbivore species are African elephant (*Loxodonta africana*), African buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*), Grant's gazelle (*Gazella granti*), Thomson's gazelle (*Gazella thomsonii*), impala (*Aepyceros melampus*), and eland antelope (*Tragelaphus oryx*). Very infrequently encountered species are oribi, bushbuck, klipspringer, dikdik, duiker, lesser kudu and reedbuck (see Lamprey 1964). Most species occur in larger densities inside the National Parks than outside (TWCW 1995).

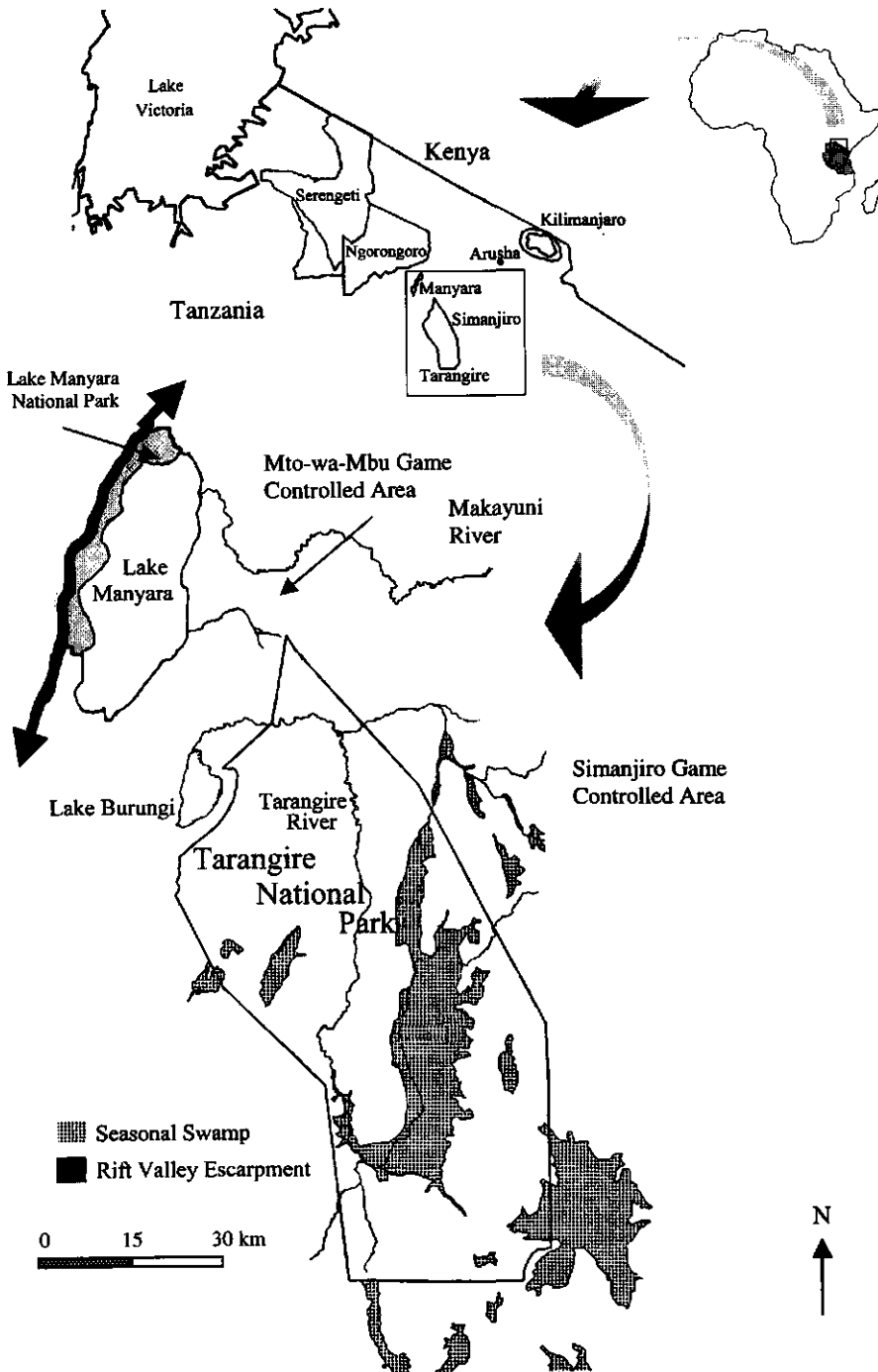


Figure 1: The Masai Ecosystem in northern Tanzania with the different study areas in relation to some important land features.

The Masai-ecosystem lies within the semi-arid climatic region (Pratt & Gwynne 1977). Rainfall is highly erratic and variable and primarily falls between December and May. During the dry season (June-November) rainfall is very rare. A rainfall gradient is observed from West to East. Average annual rainfall is 650 mm in lake Manyara NP (Prins & Loth 1988), 620 mm in Tarangire NP (M.M. Voeten, unpublished data) and 600 mm in the Simanjiro GCA (Kahurananga 1979).

Savanna vegetation is characteristic of this system with extended grasslands and floodplains, acacia woodlands and bush thickets as the main vegetation types (see Kahurananga 1979, Loth & Prins 1986, Chuwa 1996). Geology is based on three types of rock formations: the pre-Cambrium gneiss rock and lacustrine/alluvial deposits of Miocene origin. Vast areas were covered with volcanic ashes during Miocene and Pleistocene volcanic eruptions, which resulted in relatively nutrient rich soils (Medina 1987).

Because of the abundance and diversity of wildlife and the prevalence of pastoral economies, the Masai-ecosystem is an excellent area to study the coexistence of wildlife and livestock.

Outline thesis

This thesis regards several aspects of the coexistence of wildlife and livestock in East Africa. Before focussing on these issues, it is of major interest to investigate some of these aspects within the wild herbivore assemblage itself. Chapter 2 describes the relationship between group size of native ungulate species, their body-mass, feeding style, habitat choice and animal density. Some of these elements can also be considered important for coexistence of wildlife and livestock. Resource partitioning, for example by means of different feeding styles, may explain how species coexist despite extensive overlap in ecological requirements. Chapter 3 describes the resource partitioning between wildebeest, zebra and Zebu-cattle by investigating the overlap in resource use. Feeding sites selected by the different species in different seasons are compared and discussed in the light of the potential for competition between wildlife and livestock. For competition to occur, the species involved should share the same resources. The annual migration of large wild ungulates in the Masai Ecosystem involves a movement from protected National Parks to surrounding unprotected areas, which are inhabited by pastoralists and their cattle. Chapter 4 describes the causes of this seasonal

migration by studying the nutritional requirements of wildebeest and when and where these requirements can be satisfied. Many of these unprotected areas are under great pressure because of increasing human populations and expanding agricultural activities and might therefore become less accessible for wildlife in the future. Chapter 5 explores the consequences of restricted migratory movements by studying the effects of year-round grazing in an area where normally the animals only reside during the dry season. Chapter 6 presents more specific data on overlap in habitat and diet between wildebeest, zebra and cattle in combination with resource availability and food requirements. To study the possible consequences, body condition of a wildebeest population co-occurring with livestock and of one isolated from livestock were compared. Implications are discussed for the migratory system of the Masai ecosystem. Finally, chapter 7 synthesises the conclusions, which could be drawn from the preceding chapters regarding the coexistence of wildlife and livestock and the possible conflicts arising from this. Management strategies of other areas in East Africa where similar situations exist are discussed and suggestions are presented on how to "live with wildlife".

References

- Anderson E.C., Jago M., Mlengeya T., Timms C., Payne A. & Hirji K. (1990). A serological survey of rinderpest antibody in wildlife and sheep and goats in Northern Tanzania. *Epidemiol. Infect.* 105: 203-214.
- Begon M., Harper J.L. & Townsend C.R. (1996). *Ecology: individuals, populations and communities* (3-rd edition). Blackwell Science Ltd, Oxford, 1068p.
- Campbell K. & Hofer H. (1995). People and wildlife: spatial dynamics and zones of interaction. In: Sinclair A.R.E. & Arcese P. (eds.). *Serengeti II: Dynamics, management and conservation of an ecosystem*. The University of Chicago Press, Chicago, pp534-570.
- Chuwa S. (1996). Tarangire National Park, vegetation species composition mapping, General report. New York Zoological Society.

- Collett D. (1987). Pastoralists and wildlife: image and reality in Kenya Maasailand. In: Anderson D. & Grove R. (eds.). Conservation in Africa: people, policies and practice. Cambridge University Press, Cambridge, pp129-148.
- Ecosystems Ltd (1980). Livestock, wildlife and landuse, survey in the Arusha region Tanzania. Final report (3 volumes). Ecosystems Ltd, Nairobi.
- De Bie S. (1991). Wildlife resources of the West African Savanna. PhD-thesis, Agricultural University of Wageningen, the Netherlands.
- De Haan C., Steinfeld H. & Blackburn H. (1996). Livestock and the environment: finding a balance. European Commission Directorate for Development, WRENmedia, Suffolk, UK, 115p.
- Delany M.J. & Happold D.C.D. (1979). Ecology of African Mammals. Longman group limited (London).
- De Leeuw J., Prins H.H.T., Njuguna E.C., Said M.Y. & De By R.A. (1998). Interpretation of DRSRS animal counts (1977-1997) in the rangeland districts of Kenya. International Institute for Aerospace Survey and Earth Science (ITC), Enschede, The Netherlands. Department of Resource Surveys and Remote Sensing (DRSRS), Nairobi, Kenya. 187p.
- Estes R.D. (1991). The behaviour guide to African mammals. The University of California Press, Berkeley.
- Ford J. (1971). The role of trypanosomiasis in African ecology: a study of the tsetse fly problem. Oxford University Press, Oxford.
- Galaty J.G. (1993). Maasai expansion: the new East african pastoralism. In: Spear T. & Waller R.(eds.). Being Maasai: ethnicity & Identity in East Africa. James Currey, London, pp61-86.
- Goldschmidt T. (1994). Darwins hofvijver. Een drama in het Victoriameer. Prometheus, Amsterdam, 286p.
- Grootenhuis J.G. (1999). Wildlife, livestock and animal disease reservoirs. In: Prins H.H.T., Grootenhuis J.G. & Dolan T. (eds.). Conservation of wildlife by sustainable use, Kluwer Academics, Boston, in press.
- Grootenhuis J.G. (1990). Disease research for integration of livestock and wildlife. In: Grootenhuis J.G., Njuguna S.G. & Kat D.W. (eds.). Wildlife research for sustainable

- development. Proceedings of an international conference held in Nairobi, april 22-26 1990, pp97-102.
- Happold D.C.D. (1995). The interactions between humans and mammals in Africa in relation to conservation: a review. *Biodiversity and Conservation* 4: 395-414.
- Huntingford G.W.B. (1953). The southern Nilo-Hamites. *Ethnographic survey of Africa; East Central Africa. part VIII. International African institute, London.*
- Kahurananga J. (1979). The vegetation of the Simanjiro plains, Northern Tanzania. *African Journal of Ecology* 17: 65-83.
- Kitchell J.F., Schindler D.E., Ogutu Ohwayo R. & Reinthal P.N. (1997). The Nile perch in Lake Victoria: Interaction between predation and fisheries. *Ecological Applications* 7: 653-664.
- Lama L. (1998). Conflict and compatibility: An inventory and analysis of land use in a Tanzanian wildlife corridor. Phd-thesis State University of New York, Binghamton.
- Lamprey H.F. (1964). Estimation of the large mammal densities, biomass and energy exchange in the Tarangire Game Reserve and the Masai steppe in Tanganyika. *East African Wildlife Journal* 2: 1-46.
- Lamprey H.F. (1983). Pastoralism yesterday and today: the overgrazing problem. In: Bourliere, F. (ed.). *Ecosystems of the world 13, Tropical savannas*, Elsevier scientific publishing company. (Amsterdam), pp643-666.
- le Houérou H.N. (1989). The grazing land ecosystems of the African Sahel (ecological studies 75). Springer-Verlag.
- Homewood K.M. & Rodgers W.A. (1991). *Maasailand ecology: pastoral development and wildlife conservation in Ngorongoro, Tanzania*. Cambridge University Press, Cambridge, 298p.
- Loth P.E. & Prins H.H.T. (1986). Spatial patterns of the landscape and vegetation of Lake Manyara National Park. *ITC Journal* 1986: 115-130.
- Marshall F. (1994). Archaeological perspectives on east African Pastoralism. In: Fratkin E., Galvin K.A. & Roth E.A. (eds.). *African pastoralist systems, an integrated approach*. Lynne Rienner Publishers, Inc., Boulder, London, 247p.
- Mashange J. (1997). Livestock and wildlife interactions. In: Thompson D.M. (ed.). *Multiple Land-use: the experience of the Ngorongoro Area Tanzania*. IUCN Protected Areas Programme, pp127-141.

- Mduma S., Hilborn R. & Sinclair A.R.E. (1998). Limits to exploitation of Serengeti wildebeest and implications for its management. In: Newberry D.M., Prins H.H.T. & Brown N.D. (eds). Dynamics of tropical communities. British Ecological Society Symposium 37. Blackwell, Oxford, pp243-265.
- Medina E. (1987). Nutrients: requirements, conservation and cycles in the herbaceous layer. In: Walker B.H. (ed.). Determinants of savannas. IUBS Monographs. Series. No. 3 IRL Press, Oxford, pp39-65.
- Mwalyosi R.B.B. (1991). Population growth, Carrying capacity and sustainable development in South-West Masailand. *Journal of Environmental Management* 33: 175-187.
- Mwangi Z.J. & Zulberti C.A. (1985). Optimization Wildlife and livestock production. Wildlife/Livestock interfaces on rangelands. Inter-African bureau of animal resources, Nairobi.
- Newmark W.D., Manyanza D.N., Gamassa D.G.M. & Sariko H.I. (1994). The Conflict Between Wildlife and Local People Living Adjacent to Protected Areas in Tanzania - Human Density as a Predictor. *Conservation Biology* 8: 249-255.
- Osemeobo G.J. (1988). Animal wildlife conservation under multiple land-use systems in Nigeria. *Environmental Conservation* 15: 239-249.
- OleParkipuny M.S. (1989). So that the Serengeti shall never die ? In: Verwey W.D. (ed.). Nature Management and sustainable development, Proceedings of the international congress, IOS, Amsterdam, The Netherlands, pp256-264.
- Payne W.J.A. & Hodges J. (1997). Tropical cattle: origin, breeds and breeding policies. Blackwell Scientific Publications, Oxford.
- Phillipson D.W. (1977). The later prehistory of Eastern and Southern Africa. Heineman, London.
- Plowright W. (1982). The effects of rinderpest and rinderpest control on wildlife in Africa. Symposium Zoological Society London, 50:1-28.
- Pratt D.J. & Gwynne M.E. (1977). Rangelands management and ecology in East Africa. London: Hodder & Stoughton.
- Prins H.H.T. (1987). Nature conservation as an integral part of optimal land use in East Africa: the case of the Masai ecosystem of Northern Tanzania. *Biological conservation* 40: 141-161.
- Prins H.H.T. & Loth P.E. (1988). Rainfall patterns as background to plant phenology in northern Tanzania. *Journal of Biogeography* 15: 451-463.

- Prins H.H.T. (1989). East african grazing lands: overgrazed or stable degraded ?. In: Verwey W.D. (ed.). *Nature Management and sustainable development, Proceedings of the international congress*, IOS, Amsterdam, pp281-307.
- Prins H.H.T. (1992). The pastoral road to extinction: competition between wildlife and traditional pastoralism in East Africa. *Environmental Conservation* 19: 117-123 .
- Prins H.H.T. (1999). Competition between wildlife and livestock in Africa. In: Prins H.H.T., Grootenhuis J.G. & Dolan T. (eds.). *Conservation of wildlife by sustainable use*, Kluwer Academics, Boston, in press.
- Rietkerk M. (1998). Catastrophic vegetation dynamics and soil degradation in semi-arid grazing systems. Phd-thesis, Agricultural University of Wageningen, The Netherlands.
- Rwambo P., Grootenhuis J.G., DeMartini J. & Mkumbo S. (1999). Animal disease risk in the wildlife/livestock interface in the Ngorongor Conservation Area of Tanzania. CSU-CRSP report, p19.
- Schepartz L.A. (1988). Who were the later Pleistocene eastern Africans ? *African Archaeological Review* 6: 57-72.
- Sinclair A.R.E. (1977). *The African Buffalo: a study of resource limitation of populations*. Chigaco, University of Chigaco press.
- Sinclair A.R.E. (1979). The eruption of the ruminants. In: Sinclair A.R.E. & Norton-Griffiths M. (eds.). *Serengeti: dymanics of an ecosystem*. Chicago, University of Chicago press, pp1-10.
- Sommer G. & Vossen R. (1993). Dialects, sectiolects or simply lects ? The Maa language in time perspective. In: Spear T. & Waller R. (eds.). *Being Maasai: ethnicity & Identity in East Africa*. James Currey, London, pp25-37.
- Smith A.B. (1992). *Pastoralism in Africa, origins and development ecology*. Hurst Company, London, 288p.
- Sperling L. & Galaty J.G. (1990). Cattle, culture and economy: dynamics in East African Pastoralism. In: Galaty J.G. & Johnson D.L.(eds.). *The world of pastoralism*, pp69-98.
- Steinfeld H., De Haan C. & Blackburn H. (1996). *Livestock-environment interactions: issues and options*. European Commission Directorate for Development, WRENmedia, Suffolk, UK, 56p.

- TWCM (1995) .Tanzania Wildlife Conservation Monitoring: Aerial Wildlife Census of Tarangire National Park, Wet and Dry Season 1994. Frankfurt Zoological Society, P.O. Box 3134, Arusha, Tanzania.
- UNEP (1977). Ecological change and desertification. UN Conference on Desertification. Background document, Nairobi, 124p.
- Van de Vijver C.A.D.M. (1999). Fire and life in Tarangire: the effects of burning and herbivory on an East African savanna system. PhD Thesis, Wageningen Agricultural University, The Netherlands.
- Vesey FitzGerald D.F.(1972). Fire and animal impact on Vegetation in Tanzania National Parks. Proceedins of the Tall Timbers Fire Ecology Conference 11: 297-317.
- Voeten M.M. & Prins H.H.T. (1999). Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania . *Oecologia* 120: 287-294.
- Waller R.D. (1985). Ecology, migration and expansion in East Africa. *African Affairs* 84: 347-370.
- Wiens J.A. (1989). The ecology of bird communities, vol. 2 processes and variations. Cambridge studies in ecology. Cambridge University Press.
- Werger M.J.A. (1977). Effects of game and domestic livestock on vegetation in East and Southern Africa. In: Krause W. (ed.), Application of vegetation science to grassland husbandry. Handbook of vegetation science, part XIII, Junk (Den Haag).

DIVERSITY IN HERBIVORE GROUP SIZE IN EAST AFRICA

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Abstract

We investigated the relationship between the group size of African ungulates and metabolic mass, feeding style, animal density and habitat type. Unlike other studies, we analysed this relationship by entering all these factors simultaneously in a multiple regression.

The results show that metabolic mass explains most variation in interspecific group size through its effect on food requirements and how different sized animals experience the distribution of food. This relationship was found to be similar for grazers and intermediate feeders although group size of grazers increased more with an increase in metabolic mass than was the case for intermediate feeders. From similar studies we inferred that group size of browsers increased even less with an increase in metabolic mass than intermediate feeders.

Elephant did not comply with the relationship as was found for intermediate feeders. We postulate, that such large intermediate feeders may either conform to the relationship as was found for grazers or to the relationship as inferred for browsers, depending on the amount of grass or browse in the diet.

Animal density and vegetation cover explained very little or no additional variation in group size. The possible effects of predation pressure are also discussed but did not lead to unequivocal conclusions. Besides confirming hypotheses as formulated by earlier researchers, present data show that these hypotheses even apply to a wider range of ungulates.

Keywords: *body mass; ungulates; food availability; browsers; grazers; intermediate feeders*

Introduction

Most mammalian herbivores form groups, either temporarily or permanently. Group size varies widely between species, and also within species marked temporal and spatial variation in grouping patterns occurs. Ultimately, group size reflects in fitness terms the trade-off between costs and benefits of group living. Costs and benefits are primarily related to finding and handling food, to defence against or avoidance of predators and to reproduction (Clutton-Brock 1974, Krebs & Davies 1981, Prins 1996). The trade-off, however, is constrained by factors that have evolved in the past, namely body weight, feeding style and social organization of the species. Jarman (1974) made an inventory how group size and social organization of African antelopes are associated with body mass classes and feeding habits. His investigations resulted in distinguishing five categories of social organization. Classification by Estes (1974, 1992) showed the same patterns as discerned by Jarman (1974), re-emphasizing the relation between body mass and group size.

Factors that influence group size within herbivore species were studied by Leuthold & Leuthold (1975) and Underwood (1982) who presented basic quantitative data for several species. Apart from the factors mentioned already, also other factors appear to determine group size. These are habitat structure, food availability, density of conspecifics and predator density. Also interspecific group size is positively correlated with open habitat (Clutton-Brock et al. 1982, Barrette 1991, Habibi 1997), density of conspecifics (Caughley 1977, Vincent 1995, Toigo 1996, Habibi 1997) and predator density (Prins & Iason 1989, Heard 1992, Caro 1994). In addition, food availability is positively correlated with group size, but this interacts with the spatial distribution of food (Jarman & Jarman 1979, Clutton-Brock et al. 1982, De Boer & Prins 1990). Wirtz & Lörcher (1983) investigated antelopes with lower body mass and found that group size was smaller in more dense habitats but also that interspecifically positive correlations between group size and body mass occurred and between group size and density of herbivores as well. They found that browsers formed smaller groups than grazers and mixed feeders.

The studies mentioned have in common that typically group size was studied in relation to a single causal factor. In this paper we investigate which factors account for most of the variation in herbivore group size in an East African savanna by simultaneously analysing several of the above mentioned factors. Results are presented on differences in group size between

species in relation to body mass, feeding style, animal density and habitat type. Furthermore, intra-annual variation (that is, variation between months) in group size within species all occurring in different localities was studied in relation to animal density.

Study area

Data were collected in three locations in northern Tanzania within the eastern part of the Great Rift Valley, namely Tarangire National Park (NP), Lake Manyara National Park (NP), and the Mto-wa-Mbu Game Controlled Area (GCA). Tarangire NP (lat. 4° S, long. 36° E, 1200 m above sea level) encompasses an area of approximately 2600 km². The park is typified by large migratory herds of wildebeest (*Connochaetes taurinus*) and plains zebra (*Equus burchelli*) that use the area during the dry season. Their wet season ranges are situated to the east and north-west of the park (Chapter 4). Other abundant and more sedentary herbivores are African elephant (*Loxodonta africana*), African buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), Grant's gazelle (*Gazella granti*), Coke's hartebeest (*Alcelaphus buselaphus cokii*) and giraffe (*Giraffa camelopardalis*) (see also Lamprey 1963). Vegetation types based on percentage crown cover of woody plants and species composition have been described by Chuwa (1996). Lake Manyara NP (lat. 3°30' S, long. 35°45' E, 1000 m a.s.l.) consists of a narrow strip of land (100 km²) situated between Lake Manyara and the steeply rising escarpment of the Rift Valley. The herbivore assemblage is similar to that of Tarangire NP (Prins 1996), although some species like Grant's and Thomson's gazelle (*Gazella thomsonii*) do not occur in this Park. The wildebeest and zebra populations here are partly sedentary. The vegetation and landscape ecology of Lake Manyara NP have been described by Loth & Prins (1986). The third locality, the Mto-wa-Mbu GCA (1000 m a.s.l.) is situated between Tarangire NP and Lake Manyara NP. It has limited protection status and is an open access area for pastoralists. The Mto-wa-Mbu GCA is used as a wet season range by wildebeest and zebra from Tarangire NP (Chapter 6). Resident game, like giraffe, Grant's gazelle and Thomson's gazelle, is less abundant than zebra or wildebeest and compared to the National Parks their densities are low. A vegetation description has not been published but a preliminary map with vegetation types based on percentage cover by woody plants has been prepared by the first author.

The average yearly rainfall in the three localities is about 620 mm (unpubl. data) and two seasons can be distinguished (Prins & Loth 1988). During the wet season (November to May) rainfall is highly variable and erratic. During the dry season (June to October) rainfall is very rare.

Methods

Data collection

Animal road counts (Prins et al. 1994) were conducted from November 1994 until August 1995. Each road was driven two to three times per month and all animal groups that were spotted were recorded. Records were made of species, number of animals in the group, vegetation structure type, distance to the road, road name, date and time. In Tarangire NP a total of 3039 km was driven and 3326 observations were made, in Lake Manyara NP 1561 km and 1868 observations and in the Mto-wa-Mbu GCA 2521 km and 1278 observations. Observations were made on all herbivores heavier than about 20 kg, including Thompson's gazelle but excluding hippopotamus (*Hippopotamus amphibius*). For impala a distinction was made between bachelor groups (all males) and harem groups.

Individuals were arbitrarily considered to belong to different groups when the average distance between the individuals was at least about ten times smaller than the distance to another group of individuals with similar nearest neighbour distance. An individual was classified 'solitary' when the distance between this individual and a group was more than about 40 meter (see Leuthold & Leuthold 1975, Underwood 1982). For giraffe and elephant this distance was taken as about 80 meter because these species forage more widely dispersed than the other species. Data on social organization, feeding habits and body mass figures were taken from Estes (1992). All data on group size refer to day light observations only. Vegetation types are defined on basis of vegetation structure (grassland, wooded grassland, wooded bush, forest, etc.) and delineations based on percentage cover by woody species according to Loth and Prins (1986) are followed.

Data analysis

Mean group size and median group size were calculated for each species per year and per month. The median group is the group in which the average individual is found and is calculated as the median value of the cumulative product of group size and frequency (Prins et al. 1994). The median group is an animal-centred parameter as opposed to the arithmetic mean, which is an observer-centred parameter. Data on group size of wildebeest and zebra for Tarangire NP and the Mto-wa-Mbu GCA were pooled because these populations migrate between these two localities. Mean annual group size was taken as the unweighted mean of all group sizes so as to facilitate comparison with other publications.

Visibility in different vegetation structure types and/or spotting distance from the road may influence group size as observed. If so, observed group sizes should be corrected for it. Prins & Van der Jeugd (1993) have related visibility to percentage cover by woody species in Lake Manyara NP and they concluded that correction factors were necessary. In the present study we checked whether the mean and median group sizes for the studied herbivore species were affected by visibility in the different vegetation structure types as taken from the study of Prins & Van der Jeugd (1993). Although the relation between visibility and percentage cover by woody species was developed for Lake Manyara NP, we used it for all three localities because the vegetations are similar. Of the 36 investigated relations (Spearman Rank correlation tests) between group size and visibility, only 2.8 per cent showed a significant relationship after Bonferroni correction. We thus concluded that there was no effect of visibility on observed group size; we concluded this for all species but realise that a Type-II error may have occurred. Also the relationship between median group size or mean group size and spotting distance from the road were tested because there was the possibility that further away large groups were more easily spotted than small ones, while close to the road small groups and large groups would have an equal spotting chance. Again, of the 36 Spearman-rank correlations between group size and distance, only 2.8 per cent were significant after a Bonferroni correction, so we concluded that a correction for distance was not necessary.

Species-specific density was based on the number of animals of each species counted during the road counts (Wirtz & Lörcher 1983). As an index for species-specific density, a relative density parameter, namely, the number of animals/kilometre was calculated for all three localities and for each species. This was calculated per month and for the whole year. Because

not all routes were driven equally frequently, distances driven in all vegetation structure types were not the same for each month and each locality. We thus calculated species-specific density per month as the weighted mean in which we weighed for the proportion of route length per vegetation type only, as:

$$\text{Average density (animals/km)} = \frac{\sum_{i=1}^8 (\text{km driven in } V_i * \frac{\text{sum of animals observed in } V_i}{\text{km driven in } V_i})}{\sum \text{km driven in } V_i}$$

V_i = vegetation structure type 1—8

An analogous formula was applied to calculate species-specific group density (i.e., the number of groups of a herbivore species observed per kilometre).

Stepwise multiple regression analysis was used to explain differences in group sizes of the different herbivore species. We first tested for normality; for some species group size was normally distributed and for others not. Therefore, and because large sample sizes are less sensitive for deviations of normality, we decided not to transform the data. For the regression analysis, a number of functional groups were discerned, namely, (a) all herbivores, (b) species classified as 'grazers' only, (c) species classified as 'intermediate feeders' (Hofmann 1989), (d) intermediate feeders excluding elephant, and (e) all species excluding megaherbivores (that is, giraffe and elephant; see Owen-Smith 1988). In the stepwise multiple regression models for these functional groups five variables were used to explain interspecific group size differences, namely, species-specific density, metabolic mass, feeding-style type (for groups a and e only), vegetation structure and locality. First, two-tailed Spearman rank correlation coefficients were calculated between these 5 variables. Since we found no significant correlations between any of the variables, we considered them as being independent and thus fit for a regression analysis. Further, we considered the observations on group size of the same species in different localities as independent replicates of feeding categories, since only in that way the influence of locality dependent variables such as density and vegetation structure on group size could be analysed. Body mass (W in kg) was transformed to metabolic mass (MW as $W^{0.75}$). Since different vegetation structure types (such as 'wooded bushland' and 'woodland') are characterized by particular cover classes of woody species (see Loth & Prins 1986), the parameters 'percentage

cover by woody species' and 'vegetation structure type' are linked. Effects of locality on the yearly mean group sizes of species were separately tested with an analysis of variance.

Differences within species were also investigated. Two-tailed Spearman rank correlation coefficients were calculated between group size and species-specific animal density, and also between species-specific group density and species-specific animal density by making use of the intra-annual variation in these two parameters. Monthly differences in species-specific group size were analysed with a multiple regression for Thomson's and Grant's gazelle, hartebeest, impala, zebra, wildebeest, and elephant. Not enough data were collected to allow analysis per month for buffalo, waterbuck (*Kobus ellipsiprymnus*), eland antelope (*Tragelaphus oryx*) and warthog (*Phacochoerus aethiopicus*).

Results

Interspecific group size differences

An overview of the average yearly median group size, average yearly mean group size and other descriptive parameters for the different herbivore species are presented in Table 1. Stepwise multiple regression for the different functional groups (Table 2) showed that of the five variables used to explain variation in group size, two variables were frequently selected, namely, metabolic mass and species-specific density. Explained variance was slightly higher in case of median group size than in mean group size (Table 2). Regression models for grazers (group 'b' in Table 2) and for intermediate feeders except elephant (group 'd') were good and explained most variation in median group size differentiation between species (respectively, 83 % and 94 %). The models for all intermediate feeder species (thus including elephant, group 'c' in Table 2) and for all species combined (group 'a') explained little of interspecific group size diversity.

When more variables were included in the model, metabolic body mass always explained most of the variation (see standardized regression coefficients, Table 2). Figure 1 shows the relation between median group size and metabolic mass. The lines describe the linear regressions for different functional groups of herbivore species, namely 'grazers' (group 'b' in Table 2), and 'intermediate feeders-except-elephant' (group 'd') (see the Legend of Fig. 1 for equations). The regressions for grazers only and intermediate feeders-except-elephant were

significantly different (ANCOVA, $F = 4.68$, $P < 0.05$). The analysis displayed in Fig. 1 shows that the two megaherbivores (giraffe and elephant) deviate strongly from the general relation between group size and metabolic mass as established for non-browsers or small to medium-sized herbivores.

Table 1. Average yearly mean (with 95 % confidence limits) and median group size for African herbivores. TAR = Tarangire NP, MAN = Manyara NP, GCA = game controlled area, ^a = pooled data for TAR and GCA. GR = grazer, IF = intermediate feeder and BR = browser. Also body weight, species-specific density (animals/km), most frequently selected vegetation type (based on % cover by woody species) and number of observed groups (n) are given.

Species	Locality	Feeding style	Mean group size	Median group size	Body weight (kg)	Density	Vegetation type	n
Giraffe	TAR	BR	2.54 ± 0.3	3	900	0.14	8 %	170
Giraffe	MAN	BR	3.47 ± 0.5	6	900	0.46	2 %	262
Giraffe	GCA	BR	5.31 ± 0.8	9	900	0.35	10 %	168
Warthog	TAR	GR	2.31 ± 0.2	3	75	0.11	8 %	79
Warthog	MAN	GR	4.24 ± 0.7	5	75	0.21	2 %	96
Hartebeest	TAR	GR	4.83 ± 0.8	8	135	0.20	18 %	132
Waterbuck	TAR	GR	5.03 ± 1.4	8	200	0.10	8 %	63
Wildebeest	TAR ^a	GR	32.80 ± 4.5	115	230	4.87	8 %	838
Wildebeest	MAN	GR	51.00 ± 8.3	150	230	10.96	2 %	393
Zebra	MAN	GR	8.82 ± 1.2	13	240	2.61	2 %	546
Zebra	TAR ^a	GR	10.15 ± 0.9	20	240	3.15	8 %	1760
Buffalo	MAN	GR	44.04 ± 5.8	225	630	2.42	2 %	128
Buffalo	TAR	GR	78.56 ± 34.4	150	630	0.88	8 %	34
Thomson's gazelle	TAR	IF	2.55 ± 2.0	4	20	0.01	8 %	11
Thomson's gazelle	GCA	IF	6.77 ± 1.1	11	20	0.19	2 %	179
Thomson's gazelle	MAN	IF	10.04 ± 2.7	14	20	0.13	2 %	25
Grant's gazelle	GCA	IF	5.20 ± 0.7	7	40	0.22	10 %	105
Grant's gazelle	TAR	IF	7.39 ± 1.1	11	40	0.40	8 %	168
Impala-harem	GCA	IF	16.52 ± 4.0	23	45	0.15	8 %	27
Impala-harem	TAR	IF	23.85 ± 2.3	30	45	1.25	8 %	182
Impala-harem	MAN	IF	23.87 ± 2.7	30	45	1.83	2 %	160
Impala-bachelor	MAN	IF	3.96 ± 0.5	5	60	0.39	18 %	185
Impala-bachelor	GCA	IF	4.50 ± 1.2	5	60	0.03	18 %	16
Impala-bachelor	TAR	IF	4.72 ± 0.6	10	60	0.47	8 %	316
Eland antelope	TAR	IF	32.70 ± 27.2	80	475	0.11	8 %	10
Elephant	MAN	IF	3.56 ± 0.9	5	3500	0.17	55 %	90
Elephant	TAR	IF	10.78 ± 3.2	24	3500	0.76	8 %	272

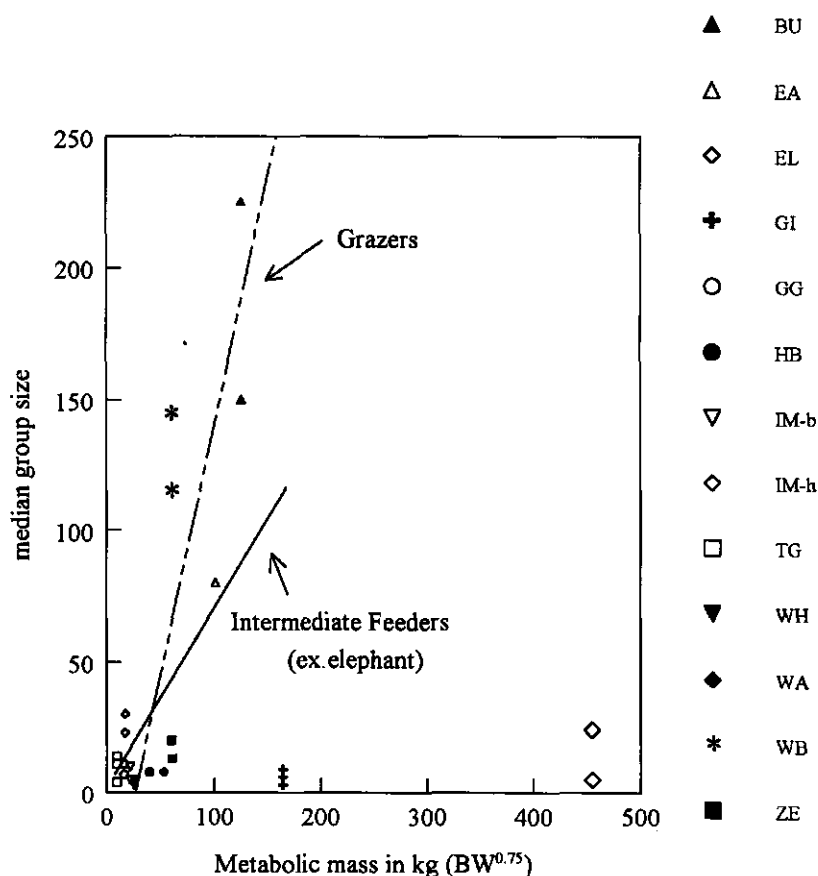


Figure 1. Relation between yearly median group size and metabolic mass for African herbivores. BU = buffalo, EA = Eland antelope, EL = Elephant, GI = Giraffe, GG = Grant's gazelle, HB = Hartebeest, IM-b = Impala-bachelor, IM-h = Impala-harem, TG = Thomson's gazelle, WH = Warthog, WA = Waterbuck, WB = Wildebeest and ZE = Zebra. The fitted lines describe the regressions for grazers ($Y = -50.34 + 1.89X$, $R^2 = 0.67$, $F = 15.91$, $n = 10$, $p < 0.01$) and for intermediate feeders except elephant ($Y = 1.69 + 0.75X$, $R^2 = 0.79$, $F = 37.94$, $n = 12$, $p < 0.001$).

Effect of locality on group size

A number of herbivore species occurred in two or three localities and so the effect of locality on mean group size could be investigated. Mean group sizes are given in Table 1 and the differences between the localities are summarized in Table 3. Even though the three localities are very similar and closely to each other, not all species occur in the three localities. Thomson's and Grant's gazelle do not occur in Lake Manyara NP although Thomson's gazelle can be

observed from that Park just outside the Park along the Simba River. As pointed out in the 'Methods' section, the observations of wildebeest and zebra in the Mto-wa-Mbu GCA and in Tarangire NP were pooled because these populations migrate between these two localities. Hartebeest do not occur in Manyara any more (Prins 1996) and were infrequently observed in the Mto-wa-Mbu GCA. An effect of locality could thus not be studied for this species.

Table 2. Results of stepwise multiple regression analysis. Either mean or median group size was entered as dependent variable. Independent variables were metabolic mass (body weight^{0.75}), species-specific density (animals/km), % cover by woody species, locality and type of feeder (if applicable). Five different functional groups were entered into the model: (a) all species, (b) only grazers (GR), (c) only intermediate feeders (IF), (d) all intermediate feeders except elephant, (e) all species except elephant and giraffe. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Type of feeder	Dependent variable	Selected independent variables	Regression coefficient	Standardized regression coefficient	Sig. level	R ² (%)	F
GR+IF+BR (a)	mean group	density (constant)	4.17 10.14	0.52	**	26.6	9.16**
GR+IF+BR (a)	median group	density (constant)	14.51 18.58	0.58	**	33.5	12.6**
GR (b)	mean group	metabolic mass (constant)	0.60 -13.75	0.81	** ns	65.4	15.1**
GR (b)	median group	metabolic mass density (constant)	1.80 9.98 -70.16	0.78 0.41	** . .	83.1	17.2**
IF (c)	mean group	none					
IF (c)	median group	none					
IF (d)	mean group	metabolic mass density (constant)	0.29 10.47 0.55	0.74 0.58	** ** ns	76.0	14.2**
IF (d)	median group	metabolic mass cover density (constant)	0.80 -1.07 8.43 5.81	0.95 -0.27 0.22	*** . . ns	94.2	43.6***
GR + IF (e)	mean group	metabolic mass density (constant)	0.37 2.34 -1.15	0.68 0.30	*** ** ns	66.0	18.5**
GR + IF (e)	median group	metabolic mass density (constant)	1.21 8.81 -20.60	0.71 0.36	*** ** ns	77.4	32.7***

Table 3. Results of one-way ANOVA in which species-specific annual mean group size was tested between different localities. TAR = Tarangire N.P., GCA = Mto-wa-Mbu game controlled area, MAN = Manyara N.P. Different letters denote significant differences. n.e.d. = not enough data collected to allow analysis. n.o. = not occurring. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Species	Mean group sizes			F-value
	TAR	GCA	MAN	
Giraffe	2.54 ^a	5.31 ^c	3.47 ^b	22.21 ^{***}
Warthog	2.31 ^a	n.e.d.	4.24 ^b	39.39 ^{***}
Wildebeest	32.80 ^a	pooled with TAR	51.01 ^b	18.81 ^{***}
Zebra	10.15 ^a	pooled with TAR	8.82 ^b	1.74 ^{ns}
Buffalo	78.56 ^a	n.o.	44.04 ^a	3.78 ^{ns}
Thomson's gazelle	2.55 ^a	6.77 ^{ab}	10.77 ^b	4.23 ^{**}
Grant's gazelle	7.39 ^a	5.20 ^b	n.o.	8.57 ^{**}
Impala-harem	23.85 ^a	16.52 ^a	23.87 ^a	2.51 ^{ns}
Impala-bachelor	4.72 ^a	4.51 ^a	3.96 ^a	1.37 ^{ns}
Elephant	10.78 ^a	n.e.d.	3.56 ^b	6.57 ^{**}

Table 4. Monthly variation in mean and median group size. The range is the highest and lowest value of the monthly mean and median group size. TAR = Tarangire NP, MAN = Manyara NP, GCA = game controlled area, ^a = pooled data for TAR and GCA. $\text{Coef. Var.} = \frac{S/\bar{X}}{\bar{X}} \times 100\%$

Species	Locality	Range monthly mean group size	Coef. Var. monthly mean group size	Range monthly median group size	Coef. Var. monthly median group size
Thomson's gazelle	GCA	4-12	113 %	6-29	50 %
Grant's gazelle	GCA	4-11	73 %	4-19	57 %
Grant's gazelle	TAR	5-16	95 %	6-20	33 %
Impala-harem	MAN	21-31	61 %	25-35	23 %
Impala-harem	TAR	20-32	67 %	26-40	38 %
Impala-bachelor	MAN	3-8	90 %	4-14	59 %
Impala-bachelor	TAR	2-10	120 %	4-20	55 %
Hartebeest	TAR	3-8	97 %	3-16	44 %
Wildebeest	MAN	22-90	160 %	85-200	25 %
Wildebeest	TAR ^a	12-55	203 %	60-180	40 %
Zebra	MAN	8-15	167 %	6-40	64 %
Zebra	TAR ^a	6-25	217 %	7-80	103 %
Elephant	MAN	2-6	120 %	3-11	46 %
Elephant	TAR	5-50	247 %	8-100	114 %
Giraffe	GCA	3-9	98 %	3-12	43 %
Giraffe	MAN	2-6	114 %	3-9	36 %
Giraffe	TAR	2-4	71 %	2-6	35 %

The stepwise multiple regression analysis (Table 2) did not identify the parameter 'locality' as a significantly contributing factor to explain group size for any of the five discerned functional groups. Table 3 shows that locality (that is, Lake Manyara NP, Tarangire NP and/or the Mto-wa-Mbu GCA) is not consistently associated with larger groups for all individual herbivore species. To the contrary, some species occurred in larger groups in Manyara (four species) and others in Tarangire (two species) while for three species there were no differences.

Effect of woody cover on group size

Most species were predominately observed in rather open vegetation types with less than 10 % cover by woody species (Table 1). Only impala bachelors in Manyara and in the Mto-wa-Mbu GCA, elephant in Manyara and hartebeest were found in more dense vegetation types. Also within the different herbivore species no significant effects of selected vegetation type on group size was found (Spearman rank correlation tests between visibility and group size, see methods).

Intraspecific variation in group size

Table 4 gives an overview of the monthly variation in mean and median group size for those herbivore species for which enough data were collected. Because median group sizes are larger than mean group sizes the coefficients of variation for median group sizes (average 51%) are smaller than those for mean group sizes (average 124%). We were not able to detect any consistent differences in the coefficients of variation for the different species.

Table 5 gives more detailed information because there we show the relation between species-specific density and group size after a multiple regression in which we entered locality as dummy parameter (for Thomson's gazelle and hartebeest only data of one locality could be used: see Methods). The models confirm that locality is of very little consequence because for the seven species tested, locality gives a significant effect only for wildebeest. This may be a spurious correlation. Density explained variation in group size for Grant's gazelle, impala bachelors, elephant and giraffe. Density did not explain variation in group size for Thomson's gazelle, hartebeest, impala females, wildebeest or zebra.

Table 5. Results of multiple regression analysis. Monthly median group size was entered as dependent variable. Independent variables were monthly species-specific density (animals/km) and locality. Independent variables were entered simultaneously. For Thomson's gazelle and hartebeest only data of one locality could be used and for giraffe from three localities. ^{ns} not significant, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Animal species	Independent variables	Regression coefficient	Standardized regression coefficient	Sig.level	R ² (%)	F
Thomson's gazelle	density	0.44	0.03	^{ns}	0.01	0.01 ^{ns}
	(constant)	13.24		*		
Hartebeest	density	21.63	0.62	^{ns}	38.3	4.96 ^{ns}
	(constant)	3.97	1.98	^{ns}		
Grant's gazelle	density	12.80	0.69	**	57.5	11.50***
	locality	1.15	0.13	^{ns}		
	(constant)	4.74		**		
Impala-harem	density	5.83	0.30	^{ns}	17.3	1.67 ^{ns}
	locality	10.52	0.49	^{ns}		
	(constant)	17.78		^{ns}		
Impala-bachelor	density	22.94	0.82	***	75.6	24.91***
	locality	1.70	0.18	^{ns}		
	(constant)	-1.80		^{ns}		
Wildebeest	density	2.62	0.35	^{ns}	45.8	6.77**
	locality	-41.73	-0.45	*		
	(constant)	130.41		***		
Zebra	density	5.49	0.27	^{ns}	13.3	1.23 ^{ns}
	locality	11.45	0.22	^{ns}		
	(constant)	6.27		^{ns}		
Elephant	density	58.81	0.91	***	85.8	48.51***
	locality	2.81	0.03	^{ns}		
	(constant)	-3.79		^{ns}		
Giraffe	density	8.81	0.58	**	56.2	10.71***
	locality 1	2.51	0.38	^{ns}		
	locality 2	-0.87	-0.13	^{ns}		
	(constant)	2.82		**		

Discussion

During the past ten years, multi-species comparisons have come under criticism because of the confounding effect of phylogeny on species phenotypic characteristics (Harvey et al 1995, Westoby et al. 1995, Ricklefs 1996). Since we propose that group size is an adaptation to current forces of natural selection, and because we believe that body size is directly related to physiological processes, the current debate about phylogenetic constraints is of no direct relevance for this paper. Moreover, the families of Bovidae, Equidae, Elephantidae, Suidae and Giraffidae separated already at the beginning of the Miocene (± 30 million year ago). Within the family of Bovidae the separation into tribes took place in the late Miocene and early Pliocene. The concept of phylogenetic constraint would surmise that selective forces of so many years ago still would be of relevance today. We prefer to analyse the present adaptive programme of large mammals.

Jarman (1974) and also Estes (1974) hypothesized that African antelopes with a larger body size form larger groups than smaller ungulates, and that grazers live in larger gatherings than browsers or intermediate feeders. Our results confirm these hypotheses because metabolic mass (Table 2) and feeder-style type (Fig. 1, Table 2) are recurring parameters to predict aggregation size in the animals that we studied. The inferences that body mass or feeder-style is important for predicting group size are based on assumptions regarding food requirements and food availability for different sized animals and for different type of feeders. Firstly, small species need higher quality diets than larger species, and secondly, high quality food items (leaves and fruits) selected by browsers and intermediate feeders are generally more dispersed than low quality food items (grass) selected by grazers. Species that have more difficulty to find their food and to fulfil their daily requirements because of their food's wider dispersion, are likely to experience food competition more readily than those whose food is more equally distributed (Krebs & Davies 1981). Since the potential for competition will be even larger when they live in larger groups, browsers and intermediate feeders are expected to form smaller groups than grazers even though intraspecific competition within groups will set an upper limit to group sizes in grazers too (as was shown for buffalo by Prins 1996). The relation between group size and degree of dispersal or patchiness of food is complicated, as was shown by WallisDeVries (1996): it appears that physical condition of the animals, which is also influenced by competition, plays an important role thus corroborating the central importance of food competition in understanding

group size (see also Fryxell 1991).

Metabolic mass explained more than two-thirds of the variation in group size of African herbivores in our study. The combined relationship for grazers and intermediate feeders explains 66 % of the variance but for each group separately, the coefficient of determination is even higher (Fig. 1). The relationship for browsers only could not be investigated in our area because only giraffe was a strictly browsing ungulate in our study. Wirtz & Lörcher (1982) studied smaller African antelope species (< 60 kg) and found for grazers, browsers and intermediate feeders together a weak significant relationship between body mass and group size (Spearman rank $r_s=0.66$, $P < 0.05$). However, it can be inferred from their data that this relationship is not the same for the group of browsers as it is for grazers and intermediate feeders together: group size for browsers increases much less with an increase in body mass than for grazers and intermediate feeders. Owen-Smith (1988, p163) also did a regression analysis with group size and body mass for a wide range of African herbivores. He found a weak ($R^2 = 0.38$, $N=38$, $P<0.001$) though significant correlation for females (excluding megaherbivores). Also, from the data set he used, it can be inferred that body mass has a less strong effect on group size for browsers (even including megaherbivores) than for grazers and intermediate feeders. It is not clear from the data set if this could also be found, if grazers would be compared with intermediate feeders. However, in our study it appears that grazers show a stronger effect of body mass on group size than intermediate feeders (Fig. 1).

We think that intermediate feeders will conform either to the relation for browsers or to that of grazers depending on whether grass or browse is the dominant component in their diet, which in turn depends on the relative availability and quality of these items in the landscape. As can be seen in Figure 1, elephant form "too small" groups in relation to their body mass as compared to all other species. The finding that elephant group sizes conform more to a browser relationship than to that of the grazers may imply that grass in quantities to satisfy the needs of group-living elephants, is just not readily available in our study areas. This is supported by the observation that extremely large groups of elephants (> 300 , sometimes even some 600, pers. obs.) do occur at times, or did so in the very recent past, on open tall-grass plains and in swamps both in Tarangire and in Manyara but outside our present study areas. Such large groups are also known from Ugandan swampy grasslands (Buss 1990) and may have been typical for the extinct *Elephas recki*, which was much more a grass-eater than the present-day African elephant (Klein 1988).

Species-specific density explained some additional variation in inter- and intra-specific group size although it is not clear why a causal relation between density and group size should be expected, other than that at higher densities the chance of meeting a conspecific increases (Caughley 1977). For species which form stable harem or female groups, like zebra (Klingel 1974) and impala (Jarman & Jarman 1973), no relation between density and group size was found (see table 5), possibly because group size is limited by the physical ability of males to defend their harem group. Impala and zebra groups did not become larger with increasing animal density but more groups were formed (Spearman r_s was respectively 0.75 and 0.73, data not shown). This was also found for elephant group size in Manyara (Spearman r_s was 0.93, data not shown), as can be expected because also elephants form rather stable groups of females with their offspring (Moss & Poole 1983). However, in Tarangire elephants formed larger groups with increasing animal density and not more groups. Tarangire has a much larger area of open wooded grasslands than Manyara and consequently grass availability is higher, which can explain the formation of larger groups (see before).

Because the species we studied selected the same vegetation structure type year-round, we did not find a relation between vegetation structure type ('habitat type') and inter- or intra-specific group size as other studies showed (Leuthold & Leuthold 1975, De Boer & Prins 1990 and Raman 1997).

Besides the positive effect of food availability on group size, herbivores may benefit from living in larger groups because of predator detection (Clutton-Brock 1974, Krebs & Davies 1981). Elephant group size deviated strongly from the found relationship between metabolic mass and group size for intermediate feeders; elephant occurs in much smaller groups than would be expected on basis of the regression of group size on metabolic mass. Perhaps this is also because elephant is a so-called megaherbivore (Owen-Smith 1988) that has escaped natural predation since the extinction of the sabre-tooth cats (Anderson 1984). However, the relation between group size and predation pressure is not straightforward. Wildebeest occurred in larger groups after lions (*Panthera leo*) were introduced into the area in which they lived but group size in impala did not increase (Hunter & Skinner 1998). Also Prins & Iason (1989) found little evidence that buffalo reacted to lion predation pressure. Lake Manyara National Park, where a part of our observations were done, has the highest known lion density (Prins 1996); this density is much higher than in Tarangire National Park (pers. obs.). However, in our study we found no effect of locality on group size in a multiple regression analysis (Table 2). One-way analysis of

variance for the different species on mean group sizes within the different species (Table 3) also showed no effect of locality on buffalo and impala (harem and bachelor groups). Apparently, buffalo do not react to the higher density of lions in Manyara, confirming the deductions in Prins & Iason (1989), and neither do impala, which confirms the conclusion from Hunter & Skinner (1998). Most other species occur in significantly larger groups in Manyara (giraffe, warthog, wildebeest and Thomson's gazelle; Table 3) than in Tarangire, again in line with the results of Hunter & Skinner (1998). However, zebra forms an exception.

We thus conclude that metabolic mass is the main explanatory variable of group size in African ungulates through its relation to food requirements and on how animals experience the distribution of food. The relationship between body mass and group size is similar for grazers and intermediate feeders and possibly different for browsers. Our data largely confirm hypotheses formulated by Jarman (1974) or Estes (1974) although their classifications excluded non-Bovidae like warthog, zebra, giraffe and elephant.

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References

- Anderson E. (1984). Who's who in the Pleistocene: A mammalian bestiary. In: Martin P.S. & Klein R.G. (eds.). *Quaternary Extinction's: A Prehistoric Revolution*. University of Arizona Press, Tucson, pp40-89.
- Buss I.O. (1990). *Elephant Life: Fifteen Years of High Population Density*. Iowa State University Press, Ames.

- Barrette C. (1991). The size of Axis deer fluid groups in Wilpattu National Park, Sri Lanka. *Mammalia* 55: 208-220.
- Caro T.M. (1994). Ungulate antipredator behaviour: Preliminary and comparative data from African bovids. *Behaviour* 128: 189-228.
- Caughley G. (1977). Analysis of vertebrate populations. Wiley, London.
- Chuwa S. (1996). Tarangire National Park, vegetation species composition mapping. General report, New York Zoological Society.
- Clutton-Brock T.T. (1974). Why do animals live in groups? *New Scientist* 7: 72-74.
- Clutton-Brock T.T., Guinness F.E. & Albon S.D. (1982). Red deer, behavior and ecology of two sexes. Edinburgh University Press.
- De Boer W.F. & Prins H.H.T. (1990). Large herbivores that strive mightily but eat and drink as friends. *Oecologia* 82: 264-274.
- Estes R.D. (1974). Social organization of the African Bovidae. In: Geist V. & Walther F. (eds.). *The Behaviour of Ungulates and its Relation to Management*, Vol. I. International Union for the Conservation of Nature and Natural Resources, Morges, pp166-205.
- Estes R.D. (1992). The behavior guide to African Mammals, including Hoofed Mammals, Carnivores, Primates. University of California Press, California.
- Fryxell J.M. (1991). Forage quality and aggregation by large herbivores. *American Naturalist* 138: 478-498.
- Habibi K. (1997). Group dynamics of the Nubian ibex (*Capra ibex nubiana*) in the Tuwayiq canyons, Saudi Arabia. *Journal of Zoology* 241: 791-801.
- Harvey P.H., Read A.F. & Nee S. (1995). Why ecologists need to be phylogenetically challenged. *Journal of Ecology* 83: 535-536.
- Heard D.C. (1992). The effect of wolf predation and snow cover on musk-ox group size. *American Naturalist* 139: 190-204.
- Hunter L.T.B. & Skinner J.D. (1998). Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour* 135: 195-211.
- Jarman P.J. & Jarman M.V. (1973). Social behavior, population structure and reproductive potential in impala. *East African Wildlife Journal* 11: 329-338.
- Jarman P.J. (1974). The social organisation of antelope in relation to their ecology. *Behaviour* 48: 215-267.
- Jarman P.J. & Jarman M.V. (1979). The dynamics of ungulate social organization. In: Sinclair

- A.R.E. & Norton-Griffiths M. (Eds.). *Serengeti, dynamics of an ecosystem*. The University of Chicago Press, Chicago, pp185-220.
- Klein G.R. (1988). The archaeological significance of animal bones from Acheulean sites in southern Africa. *African Archaeological Review* 6: 3-25.
- Klingel H. (1974). A comparison of the social behaviour of Equidae. In: Geist V. & Walther F. (eds.). *The Behaviour of Ungulates and its Relation to Management*, Vol. I. International Union for the Conservation of Nature and Natural Resources, Morges, pp124-132.
- Krebs J.R. & Davies N.B. (1981). *An introduction to behavioural ecology*. Blackwell Science, Oxford.
- Lamprey H.F. (1963). Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika. *East African Wildlife Journal* 1: 63-92.
- Leuthold W. & Leuthold B.M. (1975). Patterns of social grouping in ungulates of Tsavo National Park, Kenya. *Journal of Zoology* 175: 405-420.
- Loth P.E. & Prins H.H.T. (1986). Spatial patterns of the landscape and vegetation of Lake Manyara National Park, Tanzania. *ITC Journal* 1986: 115-130.
- Moss C.J. & Poole J. (1983). Relationships and social structure of African Elephants. In: Hinde R.A. (ed.). *Primate social relationships: an integrated approach*. Blackwell, Oxford, pp315-325.
- Owen-Smith R.N. (1988). *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press, Cambridge.
- Prins H.H.T. & Loth P.E. (1988). Rainfall patterns as background to plant phenology in Northern Tanzania. *Journal of Biogeography* 15: 451-463.
- Prins H.H.T. & Iason G.R. (1989). Dangerous lions and nonchalant buffalo. *Behaviour* 108: 298-324.
- Prins H.H.T. & Van der Jeugd H.P. (1993). Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology* 81: 305-314.
- Prins H.H.T., Van der Jeugd H.P. & Beekman J.H. (1994). Elephant decline in Lake Manyara National Park, Tanzania. *African Journal of Ecology* 32: 185-191.
- Prins H.H.T. (1996). *Behaviour and Ecology of the African Buffalo: Social Inequality and Decision Making*. Chapman & Hall, London.
- Raman T.R.S. (1997). Factors influencing seasonal and monthly changes in the group size of Chital or Axis deer in southern India. *Journal of Bioscience* 22: 203-218.

- Ricklefs R.E. (1996). Phylogeny and ecology. *Trends in Ecology and Evolution* 11: 229-230.
- Toigo C., Gaillard J.M. & Michallet J. (1996). Group size: a biological indicator of population size in Alpin ibex (*Capra ibex ibex*). *Mammalia* 60: 463-472.
- Underwood R. (1982). Seasonal changes in African ungulate groups. *Journal of Zoology* 196: 191-205.
- Vincent J.P., Bideau E., Hewison A.J.M. & Angibault J.M. (1995). The influence of increasing density on body weight, kid production, home range and winter grouping in roe deer (*Capreolus capreolus*). *Journal of Zoology* 236: 371-382.
- WallisDeVries M.F. (1996). Effects of resource distribution patterns on ungulate foraging behaviour: a modelling approach. *Forest Ecology Management* 88: 167-177.
- Westoby M., Leishman M.R. & Lord J.M. (1995). On misinterpreting the "phylogenetic correction". *Journal of Ecology* 83: 531-534.
- Wirtz P. & Lörcher J. (1983). Group sizes of antelopes in an East African National Park. *Behaviour* 84: 135-156.

**RESOURCE PARTITIONING BETWEEN SYMPATRIC
WILD AND DOMESTIC HERBIVORES IN THE
TARANGIRE REGION OF TANZANIA**

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Abstract

The effect of the introduction of an exotic species (cattle) into a native African herbivore assemblage was investigated by studying resource partitioning between Zebu-cattle, wildebeest and zebra. Resource partitioning was investigated by analysing grass sward characteristics (such as sward height and percentage nitrogen in leaves) of feeding sites selected by the different herbivore species. Linear discriminant analysis was used to determine whether a distinction could be made between feeding sites selected by the different animal species or whether the animal species showed overlap in resource use by selecting similar feeding sites.

Wildebeest and zebra did not show overlap in resource use except in the wet season when resources were ample. Cattle showed overlap in resource use with zebra in the early wet season and with wildebeest in the early dry season, seasons when food limitation is likely. In the wet season, cattle showed overlap in resource use with both zebra and wildebeest.

Implications of these results for competitive relationships between livestock and wildlife are discussed. We suggest that the occurrence and consequences of overlap in resource use may be different for an assemblage of long-term coexisting native species as compared to an assemblage of native and exotic species. Among native herbivores, complete overlap in resource use is not expected when resources are limited. In a native assemblage to which an exotic species has been introduced however, overlap in resource use can occur between exotic and native species under food-limited conditions and consequently implies competition.

Keywords: *Niche; Competition; Ungulates; Savanna; Grazers.*

Introduction

East-African savannas are renowned for their abundant and diverse assemblages of wild herbivores. Species-richness of grazers (larger than two kg) in the savannas of Eastern Africa amounts to more than 31 species (Prins and Olff 1998). Herbivore biomass in Lake Manyara National Park in Tanzania is estimated as $18,000 \text{ kg km}^{-2}$ (Drent and Prins 1987) and biomass in the Serengeti/Masai Mara on the border of Tanzania and Kenya is estimated as $68,000 \text{ kg km}^{-2}$ during the seasonal migration (Norton-Griffiths 1979). This diversity and abundance of species can be explained to a large extent by resource partitioning in combination with high primary production and evolutionary history (Jarman and Sinclair 1979; Murray and Illius 1996; Prins and Olff 1998).

Resource partitioning is defined as the differential use by organisms of resources such as food and space (Schoener 1974, Begon et al. 1990). Resource partitioning may explain how species coexist despite similar ecological requirements (Hutchinson 1959; MacArthur and Wilson 1967; MacArthur 1972; May 1973). Competition is considered to be the major selective force causing this differential use of resources, although processes like predation or different responses of species to environmental gradients may also lead to resource partitioning (Schoener 1974; 1986).

The wild herbivore species presently found in East-Africa have evolved together since the Pliocene approximately 5 million years ago (Estes 1991). Over this evolutionary time, natural selection would have effected separation in resource use between regularly interacting sets of species because fitness is reduced by competition. Indeed, patterns of resource partitioning have been well described for different assemblages of native African herbivores (Lamprey 1963; Bell 1970; Leuthold 1978; Jarman and Sinclair 1979) and also for herbivores in temperate areas (Gordon and Illius 1989; Putman 1996). In this paper, the question is raised as to how an exotic species fits into a natural system where niche compartmentalisation has been established by resident local species over time and where because of niche saturation only a finite number of species can coexist.

The effects of introducing a new species should be apparent if the new species is ecologically similar to the species already occurring. In East-Africa, livestock can be viewed as such new species. The common Zebu-cattle (*Bos indicus*) are similar in feeding habits and

body weight to other abundant native species, namely wildebeest (*Connochaetes taurinus*) and plains zebra (*Equus burchelli*). In addition, livestock and wild herbivores have not shared a long common evolutionary history. The earliest evidence of pastoralism in East-Africa dates from 3000-2500 BP and large-scale expansion has been occurring since approximately 1000-500 BP (Homewood and Rodgers 1991; Smith 1992; Payne and Hodges 1997, Prins 1999). The aim of this study was to investigate resource partitioning between cattle, wildebeest and zebra, and to discuss the results in relation to the coexistence of wild and domestic herbivores and the implications for possible competition.

When food resources occur as discrete items such as seeds and fruits, resource partitioning can be accomplished by selecting different size classes. For large grazers such as wildebeest, zebra and cattle, the grass layer does not consist of easily distinguishable items and selection for individual grass leaves is difficult. However, grass has several characteristics related to quantity (such as biomass and grass height) and quality (such as mineral concentrations and digestibility) for which large grazers can select (Chacon and Stobbs 1976; Distel et al. 1995; Prins 1996; Heitkönig and Owen-Smith 1998). Selection for these specific characteristics can lead to differential use of grass as a resource (see Prins and Olff 1998). Bell (1970) and Jarman & Sinclair (1979) have described how African ungulates select for different vegetation types, plant parts or species which resulted in ecological separation. Murray and Brown (1993) suggested that the growth stage of grass swards is an important determinant of resource partitioning between three species of alcelaphine antelopes (which include wildebeest). Very few studies have actually measured resource partitioning between wildlife and livestock in East-Africa and these studies either concentrated on dietary overlap at the plant species level (Casebeer and Koss 1970; Hoppe et al. 1977) or overlap in habitat (Fritz et al. 1996; Machange 1997). The present study, however, investigated resource partitioning by analysing the similarities and differences in grass sward characteristics of feeding sites selected by cattle, wildebeest and zebra respectively, during seasons with different food availability.

Cattle are ruminants and have been classified as non-selective roughage grazers (Hofmann 1989, Van Soest 1994). The body weight of Zebu-cattle ranges from 200 kg for females to 250 kg for males (Homewood and Rodgers 1991). Wildebeest are also ruminants and they are classified as more selective grazers (Hofmann 1989, Van Soest 1994). Body weight ranges from 141-186 kg for females to 171-242 kg for males (Estes 1991). Plains zebra

are hindgut fermenters and are classified as non-selective roughage grazers (Van Soest 1994). Body weight ranges from 175-250 kg for females to 220-322 kg for males (Estes 1991).

Both the differences in digestive systems and forage selection and differences in the morphology of the animal's mouth will affect feeding site selection. The body weights of these three species are similar, and therefore differences in feeding site selection related to allometric relationships are not expected. Detailed hypotheses about feeding site selection were not formulated for the present study because the goal was not to predict differences in specific grass sward characteristics between the feeding sites. Rather, from an evolutionary point of view it was hypothesised that wildebeest and zebra would show resource partitioning and therefore these species would select different feeding sites. In contrast, because cattle are exotic, resource partitioning with either wild species would not be expected and it was hypothesised that cattle would select feeding sites similar to wildebeest and/or zebra feeding sites.

Study area

Data were collected in the Mto-wa-Mbu Game Controlled Area (GCA) and Tarangire National Park (NP) both located in Northern Tanzania within the eastern part of the Great Rift Valley. The Mto-wa-Mbu GCA (lat. 3°35' S, long. 35°55' E, 1000 m above sea level) is used by traditional Masai and Warusha pastoralists for cattle grazing, small scale agricultural activities and firewood collection. The area is used as a wet season range by wildebeest and plains zebra from the nearby Tarangire NP (Chapter 6). Resident game such as giraffe (*Giraffa camelopardalis*), Grant's gazelle (*Gazella granti*) and Thomson's gazelle (*Gazella thomsonii*) are the next most abundant species (Chapter 2). Most large herbivores are found on the extensive grasslands and flood plains, which are dominated by grass species such as *Brachiaria xantholeuca*, *Cenchrus ciliaris*, *Chloris* spp., *Dactyloctenium aegyptium*, *Odysea jaegeri*, *Panicum* spp., *Pennisetum mezianum* and *Sporobolus* spp. (M.M. Voeten, unpublished results).

Tarangire National Park (lat. 4° S, long. 36° E, 1200 m above sea level) is situated east of and adjacent to the Mto-wa-Mbu GCA and encompasses an area of approximately 2600

km². Large migratory herds of wildebeest and plains zebra are present during the dry season but leave the Park during the wet season (Chapter 4 and Chapter 5). Their wet season range includes the Mto-wa-Mbu GCA. Other abundant and more sedentary herbivores in Tarangire NP are African elephant (*Loxodonta africana*), African buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), Coke's hartebeest (*Alcelaphus buselaphus cokii*), Grant's gazelle and giraffe. The vegetation has been described by Chuwa (1996). The extensive grasslands and flood plains are dominated by grass species such as *Bothriochloa insculpta*, *Brachiaria xantholeuca*, *Cenchrus ciliaris*, *Dactyloctenium aegyptium*, *Digitaria* spp., *Panicum* spp., *Pennisetum mezianum* and *Sporobolus* spp..

The average yearly rainfall in the research area is 620 mm. Two seasons can be distinguished (Prins and Loth 1988): during the wet season (December-May) rainfall is highly variable and erratic, while during the dry season (June-November) rainfall is very rare.

Methods

Data collection

A feeding site was defined as a location where a herd of either wildebeest (> 40 individuals), cattle (> 40 individuals) or zebra (>20 individuals) were observed to graze. At least 90 % of the herd had to be actively grazing before a location was identified as a feeding site. Once a site met these criteria the animals were driven away; in this way it was ensured that sampling took place when the site still contained the main characteristics for which the animals selected. For each animal species 5-8 feeding sites were sampled in January, April, July and October 1995. These months are representative of the beginning of the wet season (hereafter called the early wet season), the middle of the wet season, the beginning of the dry season (hereafter called the early dry season) and the middle of the dry season. Data for the early wet, wet and early dry season were collected in the Mto-wa-Mbu GCA for all three animal species. Data for the dry season were collected in Mto-wa-Mbu GCA for cattle and in Tarangire NP for wildebeest and zebra. Within each season all feeding sites for all species (15-24) were sampled within one day and within an area of approximately 20 km². The selected feeding sites were all

on open grasslands. At each site five randomly placed frames of 1.0m x 0.5m were sampled. Within each frame sward height was measured at leaf table level. Within-frame variability in sward height was accounted for by using the average of five measurements. Subsequently, vegetation was harvested to ground level. The grasses were hand-sorted into green leaf, green stem and dead material, air-dried and weighed. Total nitrogen, phosphorus and calcium concentration in leaves, stem and dead material were determined after a modified Kjeldahl analysis (Novozamsky et al. 1983). Nitrogen and phosphorus concentrations were measured colorimetrically using a continuous-flow analyser (Skalar SA-4000). Calcium concentration was measured by atomic emission spectrophotometry using a flame-photospectrometer (Varian SpectraAA-600). Neutral detergent fibre (NDF) was determined according to Goering and Van Soest (1970).

Data analysis

Grass sward characteristics analysed were: green leaf standing crop (g/m^2), green stem standing crop (g/m^2), dead standing crop (g/m^2), total standing crop (g/m^2), sward height (cm), live/total biomass ratio ((green leaf + green stem standing crop) / (green leaf + green stem + dead standing crop), no dimension), leaf bulk density (green leaf standing crop / sward height, g/m^3), leaf weight ratio (green leaf standing crop / (green leaf + green stem standing crop), no dimension), as well as nitrogen, phosphorus, calcium and fibre content (percentage) of green leaf. In the dry season, no green plant material was available, so data presented for that season only relate to dead biomass. For each grass sward characteristic, the average of the five measurements per site was used for analysis. Prior to statistical analysis, data were either log-transformed (biomass-data) or arcsine-transformed (ratios and percentages minerals) to adjust for deviations from normality and to improve homogeneity of variance.

Linear discriminant analysis (Tatsuoka 1971) was used to determine whether feeding sites, selected by the different animal species, could be discriminated based on grass sward characteristics. Discriminant analysis proceeds by forming linear combinations of predictor variables serving as the basis for classifying cases (each case is a feeding site) into one of the groups based on animal species. The coefficients for each predictor variable (the previously listed grass sward characteristics) were chosen so that the different groups (animal species)

were maximally separated along an axis. A stepwise procedure was followed to identify the grass sward features most important for group characterisation. The scores of the discriminant functions were tested in a one-way ANOVA and Tukey HSD was used to test which groups differed significantly. Species-specific differences between grass sward characteristics were tested with the same procedures. All statistical procedures were performed with SPSS 6.0 for Windows.

Results

Early wet season

Feeding sites selected by the different animal species in the early wet season were separated by one discriminant function (Table 1). This function discriminated between feeding sites selected by wildebeest and feeding sites selected by cattle and zebra (Table 2 and Fig. 1a). Cattle and zebra thus selected similar feeding sites. Sward height was the most important variable for discrimination between the feeding sites (Table 3), with wildebeest selecting sites with a significantly lower sward height than cattle and zebra (Fig. 2a).

Wet season

Feeding sites selected by wildebeest, cattle and zebra in the wet season could not be discriminated from one another (Table 1) and all three species therefore showed overlap in resource use.

Early dry season

Feeding sites selected by wildebeest, cattle and zebra in the early dry season could be discriminated by two functions (Table 1). The first function separated feeding sites selected by zebra from sites selected by wildebeest and cattle (Table 2 and Fig. 1b). Wildebeest and cattle selected similar feeding sites. Because the second function was not significant (Table 1), no further discrimination between the feeding sites of the different animal species could be made.

Table 1. Results of stepwise linear discriminant analysis per season to test whether groups (i.e. feeding sites selected by wildebeest, zebra and cattle) could be distinguished based on different characteristics of the grass sward. The eigenvalue is the ratio of between-groups to within-groups sum of squares. % of var. is the percentage of the total between groups variability attributable to each function. The squared canonical correlation (can.cor)² is the proportion of total variability explained by differences between groups. ** $P \leq 0.01$, *** $P \leq 0.001$.

Season	Function	Eigenvalue	% of var.	can.cor.	χ^2
Early wet	1	1.67	100	0.79	11.75**
Wet	none	-	-	-	-
Early dry	1	6.86	99.68	0.93	38.55***
	2	0.02	0.32	0.15	0.40 ^{ns}
Dry	1	42.25	84.85	0.99	35.48***
	2	7.55	15.15	0.94	12.87**

Table 2. Results of one-way ANOVA with discriminant scores of the different discriminant function(s) (see Table 1) as the dependent variable and the different animal species as the independent variables. Different letters denote significant differences between species. ** $P \leq 0.01$, *** $P \leq 0.001$.

Season	Function	F-value	Wildebeest	Cattle	Zebra
Early wet	1	9.97**	a	b	b
Early dry	1	65.21***	a	a	b
	2	0.21 ^{ns}			
Dry	1	147.89***	a	b	c
	2	26.42***	a	b	b

Table 3. The standardised canonical discriminant function coefficients for the analysis in Table 1. The absolute value indicates the relevance of each variable per function. SC is standing crop and NDF is neutral detergent fibre.

Season	Variables selected for each function	Standardised canonical discriminant function coefficients	
		Function 1	Function 2
Early wet	Sward height	1.00	-
Early dry	% NDF in green leaf	1.12	0.16
	Sward height	-0.67	0.91
Dry	Sward height	0.96	-0.56
	% NDF in dead SC	1.03	1.09
	% Phosphorus in dead SC	0.40	1.23

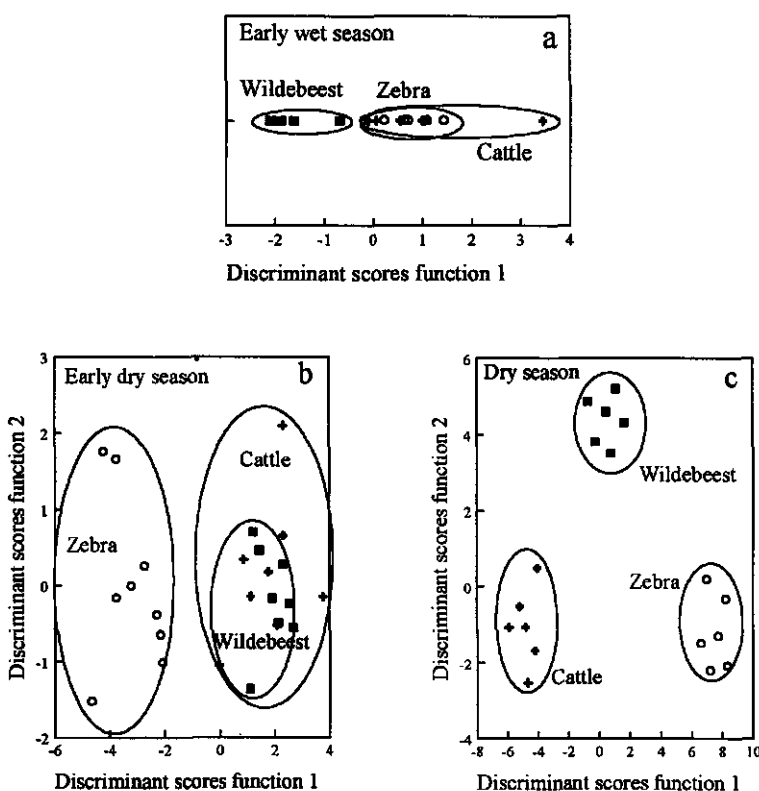


Figure 1. Results of discriminant analysis, which show whether feeding sites selected by wildebeest, zebra and cattle could be discriminated in different seasons. Plotted are the values of the discriminant scores for each feeding site. a) In the early wet season, one function discriminated between feeding sites selected by wildebeest and feeding sites selected by zebra and cattle. b) In the early dry season, two functions discriminated feeding sites selected by zebra and feeding sites selected by wildebeest and cattle. c) In the dry season, two functions discriminated feeding sites selected by wildebeest, zebra and cattle.

Percentage fibre in green leaves (% NDF) was the most important variable for discrimination between feeding sites in the first function (see the canonical discriminant function coefficients in Table 3). Zebra selected sites with a significantly lower level of fibre than wildebeest and cattle in the early dry season (Fig 1b). Sward height was the most important variable in the second function, but as mentioned above, this function did not significantly discriminate between the different feeding sites (Table 1). This is also illustrated by the finding that sward height did not differ significantly between the selected feeding sites in the early dry season (Table 4).

Table 4. Mean (\pm 95 % confidence limits) of grass sward characteristics measured in the feeding sites selected by wildebeest, zebra and cattle in the different seasons. Data for the three animal species are averaged unless a significant difference was found between species (one-way ANOVA, $P < 0.05$ see Table 5 and Fig. 2). Leaf bulk density and leaf weight ratios are based on green leaves. In the dry season no green biomass (leaves or stems) was available; so live / (live+dead) ratio, leaf bulk density and leaf / (leaf + stem) ratio could not be calculated. Percentages of minerals for the dry season were determined in dead standing crop and for all other seasons in green leaf. SC is standing crop, N is nitrogen, P is phosphorus, Ca is calcium and NDF is neutral detergent fibre.

Sward characteristics	Season			
	Early wet	Wet	Early dry	Dry
Green leaf SC (g/m ²)	35.78 \pm 10.76	48.75 \pm 22.02	39.44 \pm 14.39	0.00
Green stem SC (g/m ²)	31.31 \pm 8.21	97.62 \pm 33.03	74.47 \pm 29.90	0.00
Dead SC (g/m ²)	2.23 \pm 1.15	29.92 \pm 24.74	55.20 \pm 22.8	203.44 \pm 26.54
Total SC (g/m ²)	69.32 \pm 17.23	176.3 \pm 75.24	168.11 \pm 54.43	203.44 \pm 26.54
Sward height (cm)	see Figure 2a	14.03 \pm 4.99	16.69 \pm 3.51	see Figure 2a
Live / (live + dead)	0.95 \pm 0.02	0.88 \pm 0.05	0.71 \pm 0.05	-
Leaf bulk density	see Table 5	3.57 \pm 1.19	2.73 \pm 1.17	-
Leaf weight ratio	0.54 \pm 0.06	0.32 \pm 0.07	0.37 \pm 0.11	-
% N in leaf	see Table 5	2.05 \pm 0.39	1.45 \pm 0.18	0.53 \pm 0.10
% P in leaf	0.27 \pm 0.05	0.22 \pm 0.03	0.33 \pm 0.08	0.09 \pm 0.02
% Ca in leaf	0.45 \pm 0.03	0.58 \pm 0.07	0.59 \pm 0.09	see Table 5
% NDF in leaf	66.29 \pm 2.72	75.91 \pm 2.63	see Figure 2b	see Figure 2b

Dry season

In the dry season, the feeding sites selected by wildebeest, cattle and zebra could be clearly discriminated using two functions (Table 1). The first function separated the feeding sites of all three species, while the second function additionally separated wildebeest from cattle and zebra (Table 2 and Fig 1c). Percentage fibre (% NDF) in dead standing crop and sward height were the most important variables for group separation in the first function (see the canonical discriminant function coefficients in Table 3). Percentage fibre was important for separating feeding sites selected by cattle and those selected by wildebeest and zebra; cattle selected sites with a significantly lower percentage of fibre than wildebeest or zebra (Fig. 2b). Sward height was important for separation between wildebeest feeding sites and zebra feeding sites; wildebeest selected sites with a significantly lower sward height than zebra (Fig. 2a). Cattle selected sites with a sward height that did not differ from feeding sites selected by wildebeest or zebra (Fig 2a).

energy and nutrient assimilation obtained by hindgut fermenters on low-quality diets is higher than that obtained by ruminants (Bell 1971; Rittenhouse 1986; Beekman and Prins 1989; Duncan et al. 1990; Van Soest 1994). However, when digestibility of the food becomes very low, as was found in this study in the early dry season (namely when % NDF > 75 %), the higher food intake of hindgut fermenters no longer compensates for their lower digestive efficiency (Van Wieren 1996). Van Wieren found that, even while intake on such low quality food was still higher in hindgut fermenters than in ruminants, the extraction of digestible energy was less than that by ruminants. Apparently, zebra can only fulfil their energy requirements by selecting feeding sites with a low percentage of fibre. Feeding sites selected by wildebeest and cattle in the early dry season could not be discriminated and thus these two ruminants showed overlap in resource use during this time of the year (Fig. 1b).

During the dry season, the feeding sites of all three species were strongly differentiated (Fig 1c). During this season however, wildebeest and zebra are inside Tarangire NP and cattle occur outside the National Park in the Mto-wa-Mbu GCA. Therefore, it is difficult to determine whether the differences between feeding sites of wildebeest and zebra, and the feeding sites of cattle are related to species-specific selectivity or whether they merely reflect the park's prohibition of cattle grazing inside the National Park. Wildebeest and zebra did occur in the same area in the dry season and their feeding sites differed in sward height, as they did in the early wet season.

Thus, it can be concluded, that wildebeest and zebra showed resource partitioning by selecting different feeding sites (except in the wet season but see further discussion). Cattle selected feeding sites that were similar to those of either wildebeest or zebra. These findings are clearly illustrated by figure 1 and agree with the broad hypotheses formulated in the Introduction.

What do the observed patterns in resource partitioning and overlap in resource use imply for potential competitive relationships between wildebeest, zebra and cattle ? Prins (1992) analysed stocking rates and energy requirements of livestock and wildlife and concluded that livestock competes with wildlife (see also Chapter 6). To the contrary, Homewood and Rodgers (1991) stated that wildlife populations in the Ngorongoro Conservation Area in Tanzania have not suffered from shared land use with pastoralists and their livestock. However, since the eviction of cattle from the Ngorongoro crater floor, buffalo

numbers have increased and wildebeest numbers decreased (Perkin 1995, Runyoro et al 1995); this observation suggests that competitive relationships between these species do exist.

Experiments usually provide the most unambiguous evidence of competition but very often, as in this study, experiments are not feasible. An overlap in resource use in combination with limited resources are prerequisites for competition to occur (Wiens 1989). Table 6 summarises the possible outcomes for the different seasons based on these conditions. If there is no overlap in resource use between species, potential for competition is absent. This is the case for wildebeest and zebra in the early wet season, early dry season and dry season. If there is overlap in resource use between species, these species can only compete when resources are limited (but see Connell 1980, de Boer and Prins 1990, Putman 1996). In this study no exact measurements of total food availability and requirements by the different animal species were made. However, during the wet season, savanna systems produce abundant grasses of high quality (Prins 1996) and it is not likely that grasses are a limited resource in this particular season. Therefore, competition for food between wildebeest, zebra and cattle is not likely during the wet season, although all three species selected similar feeding sites and thus showed overlap in resource use. Also, increase in overlap in resource use is very often associated with an increase in resource abundance (Schoener 1982, Gordon and Illius 1989).

Table 6. The potential for competition as it follows from the overlap and non-overlap in resource use. Overlap and non-overlap in resource use was based on the finding that feeding sites selected by different animal species could be discriminated or could not be discriminated on the basis of different grass sward characteristics. WB is wildebeest, ZE is zebra and CA is cattle.

Season	Overlap in resource use	Potential for competition
Early wet	no overlap WB and ZE	absent
	no overlap WB and CA	absent
	overlap ZE and CA	only if resources are limited
Wet	overlap WB, ZE, CA	only if resources are limited
Early dry	no overlap ZE and WB	absent
	no overlap ZE and CA	absent
	overlap WB and CA	only if resources are limited
Dry	no overlap WB, ZE	absent
	CA separated in space from WB and ZE	-

Cattle showed overlap in resource use with zebra and with wildebeest in the early wet and early dry season respectively. Therefore competition may occur but only when resources are limited. Limited resources do not necessarily solely occur in the most unfavourable season which is the dry season in tropical savanna systems: for instance, it could be possible that at the beginning of the growing season (early wet season) the quantity of food is limited while at the end of the growing season (early dry season), the quality of food becomes limited. Under these conditions, competition may occur between cattle and zebra in the early wet season and between cattle and wildebeest in the early dry season.

When species have evolved together like wildebeest and zebra, the observation of overlap in resource use is likely to be indicative of the absence of food limitation and thus of the absence of competition. Moreover, complete overlap in resource use under food-limited conditions is not expected among native species, as this study also has shown. However, when individuals of an exotic species like cattle are introduced into an array of coexisting species, overlap in resource use under food limited conditions between the native and introduced species can occur and may be indicative of competition. Indeed, results presented in this paper on the resource partitioning between wildebeest, zebra and cattle suggest that there is a strong potential for competition between the native wild species and cattle, which consequently will have a negative effect on their coexistence.

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References

- Beekman J.H. & Prins H.H.T. (1989). Feeding strategies of sedentary large herbivores in East Africa, with emphasis on the African buffalo, *Syncerus caffer*. *African Journal of Ecology* 27: 129-147.
- Begon M., Harper J.L. & Townsend C.R. (1990). *Ecology: Individuals, Populations and Communities*. Blackwell Scientific Publications, Oxford.
- Bell R.H.V. (1970). The use of the herb layer by grazing ungulates in the Serengeti. In: Watson A. (ed.). *Animal populations in relation to their food resources*. Symposium of the British Ecological Society, Aberdeen 1969. Blackwell Scientific Publications, Oxford, pp111-124.
- Bell R.H.V. (1971). A grazing ecosystem in the Serengeti. *Scientific American* 225: 86-93.
- Casebeer R.L. & Koss G.G. (1970). Food habits of wildebeest, zebra, hartebeest and cattle in Kenya Masailand. *East African Wildlife Journal* 8: 25-36.
- Chacon E. & Stobbs T.H. (1976). Influence of progressive defoliation of a grass sward on the eating behaviour of cattle. *Australian Journal of Agricultural Research* 27: 709-727.
- Chuwa S. (1996). Tarangire National Park, vegetation species composition mapping, General report. New York Zoological Society.
- Connell J.H. (1980). Diversity and the coevolution of competitors, or the ghost of the past. *Oikos* 35: 131-138.
- De Boer W.F. & Prins H.H.T. (1990). Large herbivores that strive mightily but eat and drink as friends. *Oecologia* 82:264-274.
- Distel R.A., Laca E.A., Griggs T.C. & Demment M.W. (1995). Patch selection by cattle: maximization of intake rate in horizontally heterogeneous pastures. *Applied Animal Behavior Science* 45: 11-21.
- Drent R.H. & Prins H.H.T. (1987). The herbivore as prisoner of its food supply. In: Van Andel J., Bakker J.P. & Snaydon R.W. (eds.). *Disturbance in grasslands: species and population responses*. Dr W Junk Publishers Co. Dordrecht, pp131-147.
- Duncan P., Foote T.J., Gakahu C.G. & Lloyd M. (1990). Comparative nutrient extraction from forages by grazing bovids and equids: a test of the nutritional model of equid/bovid competition and coexistence. *Oecologia* 84: 411-418.

- Duncan P. (1992). *Horses and grasses; the nutritional ecology of equids and their impact on the Camargue*. Ecological studies 87, Springer-Verlag, New York.
- Estes R.D. (1991). *The behavior guide to African mammals*. The University of California Press, Berkeley.
- Fritz H., De Garine-Wichatitsky M. & Letessier G. (1996). Habitat use by sympatric wild and domestic herbivores in an African savanna woodland: the influence of cattle spatial behaviour. *Journal of Applied Ecology* 33: 589-598.
- Goering H.K. & Van Soest R.J. (1970). Forage fiber analyses (apparatus, reagents, procedures and some applications). USDA-ARS Agricultural Handbook 379. US Government Printing Office, Washington.
- Gordon I.J. & Illius A.W. (1988). Incisor arcade structure and diet selection in ruminants. *Functional Ecology* 2: 15-22.
- Gordon I.J. & Illius A.W. (1989). Resource partitioning by ungulates on the Isle of Rhum. *Oecologia* 79: 383-389.
- Heitkönig I.M.A. & Owen-Smith N. (1998). Seasonal selection of soil types and grass swards by roan antelope in a South African savanna. *African Journal of Ecology* 36: 57-70.
- Hofmann R.R. (1973). *The ruminant stomach vol. 2*. East African Literature Bureau, Nairobi Kenya.
- Hofmann R.R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78: 443-457.
- Homewood K.M. & Rodgers W.A. (1991). *Maasailand ecology: pastoral development and wildlife conservation in Ngorongoro, Tanzania*. Cambridge University Press, Cambridge.
- Hoppe P.P., Qvortrup S.A. & Woodford M.H. (1977). Rumen fermentation and food selection in East African Zebu cattle, wildebeest, Coke's hartebeest and topi. *Journal of Zoology* 181: 1-9.
- Hutchinson G.E. (1959). Homage to Santa Rosalia or why are there so many kinds of animals? *American Naturalist* 93: 145-159.
- Illius A.W. & Gordon I.J. (1987). The allometry of food intake in grazing ruminants. *Journal of Animal Ecology* 56: 989-999.

- Jarman P.J. & Sinclair A.R.E. (1979). Feeding strategy and the pattern of resource partitioning in ungulates. In: Sinclair A.R.E. & Norton-Griffiths N. (eds.). *Serengeti: dynamics of an ecosystem*. Chicago University press, Chicago, pp130-163.
- Lamprey H.F. (1963). Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika. *East African Wildlife Journal* 1: 63-92.
- Leuthold E. (1978). Ecological separation among browsing ungulates in Tsavo East National Park, Kenya. *Oecologia* 35: 241-252.
- MacArthur R.H. & Wilson E.O. (1967). *The theory of island biogeography*. Princeton University Press, Princeton.
- MacArthur R.H. (1972). *Geographical ecology: patterns in the distribution of species*. Harper Row Publishers, New York.
- Machange J. (1997). Livestock and wildlife interactions. In: Thompson D.M. (ed.). *Multiple landuse, the experience of the Ngorongoro Conservation Area Tanzania*. IUCN, Gland Switzerland and Cambridge, pp27-141.
- May M.R. (1973). *Stability and complexity in model ecosystems*. Princeton University Press, Princeton.
- Murray M.G. & Brown D. (1993). Niche separation of grazing ungulates in the Serengeti - an experimental test. *Journal of Animal Ecology* 62: 380-389.
- Murray M.G. & Illius A.W. (1996). Multispecies grazing in the Serengeti. In: Hodgson J. & Illius A.W. (eds.). *The ecology and management of grazing systems*. CAB international Wallingford, UK, pp247-272.
- Norton-Griffiths M. (1979). The influence of grazing, browsing and fire on the vegetation dynamics of the Serengeti. In: Sinclair A.R.E. & Norton-Griffiths N. (eds.). *Serengeti: dynamics of an ecosystem*. Chicago University press, Chicago, pp310-352.
- Novozamsky I., Houba V.J.G., Van Eck R. & Van Vark W. (1983). A novel digestion technique for multi-elemental plant analysis. *Communications in Soil Science and Plant Analyses* 14: 239-249.
- Payne W.J.A. & Hodges J. (1997). *Tropical cattle: origin, breeds and breeding policies*. Blackwell Scientific Publications, Oxford.

- Perkin S. (1995). Multiple land use in the Serengeti region. In : Sinclair A.R.E. & Arcese P. (eds.). *Serengeti II: Dynamics, management and conservation of an ecosystem*. The University of Chicago Press, Chicago, pp571-587.
- Prins H.H.T. & Loth P.E. (1988). Rainfall patterns as background to plant phenology in northern Tanzania. *Journal of Biogeography* 15: 451-463.
- Prins H.H.T. (1992). The pastoral road to extinction: competition between wildlife and traditional pastoralism in East Africa. *Environmental Conservation* 19: 117-123.
- Prins H.H.T. (1996). Ecology and behaviour of the African buffalo: social inequality and decision making. Chapman Hall, London UK.
- Prins H.H.T. & Olff H. (1998). Species-richness of African grazer assemblages: towards a functional explanation. In: Newberry D.M., Prins H.H.T. & Brown N.D. (eds.). *Dynamics of tropical communities*. British Ecological Society Symposium 37. Blackwell, Oxford., pp449-490.
- Prins H.H.T. (1999). Competition between wildlife and livestock in Africa. In: Prins H.H.T., Grootenhuis J.G. & Dolan T. (eds.). *Conservation of wildlife by sustainable use*. Kluwer Academics, Boston. In press.
- Putman R.J. (1996). Competition and resource partitioning in temperate ungulate assemblages. Chapman Hall, London.
- Rittenhouse L.R. (1986). The relative efficiency of rangeland use by ruminant and non-ruminant herbivores. In : Gudmundson O. (ed.). *Grazing research at Northern latitudes*. Plenum Press, New York, pp179-191.
- Runyoro V.A., Hofer H., Chausi E.B. & Moehlman P.D. (1995). Long-term trends in the herbivore populations of the Ngorongoro crater, Tanzania. In: Sinclair A.R.E. & Arcese P. (eds.). *Serengeti II: Dynamics, management and conservation of an ecosystem*. The University of Chicago Press, Chicago, pp146-168.
- Schoener T.W. (1974). Competition and the form of habitat shift. *Theoretical Population Biology* 6: 265-307.
- Schoener T.W. (1982). The controversy over interspecific competition. *American Scientist* 70: 586-595.

- Schoener T.W. (1986). Resource partitioning. In: Kikkawa J. & Anderson D.J. (eds.). Community ecology, pattern and process. Blackwell Scientific publications, Oxford, pp91-126.
- Smith A.B. (1992). Pastoralism in Africa, origins and development ecology. Hurst Company, London, 288p.
- Tatsuoka M.M. (1971). Multivariate analyses. John Wiley and Sons, New York.
- Van Soest P.J. (1994). Nutritional ecology of the ruminant, second edition. Cornell University Press, Ithaca, New York.
- Van Wieren S.E. (1996). Digestive strategies in ruminants and non-ruminants. PhD-thesis Agricultural University of Wageningen, The Netherlands.
- Wiens J.A. (1989). The ecology of bird communities. Vol 2 processes and variations. Cambridge University press, Cambridge.

MIGRATORY UNGULATES:
Is the grass really greener at the other side ?

Margje M. Voeten and Herbert H.T. Prins

Abstract

We used linear programming to predict in which area, the wet season range or the dry season range, migratory wildebeest should forage to satisfy all their nutritional requirements while at the same time maximizing their energy or protein intake. The model correctly predicted the seasonal movements to the wet season range. In this period of the year phosphorus and fibre intake constraints determine the possible outcomes of the model. High phosphorus requirements of lactating females prevent the animals to satisfy their requirements in the dry season range. In the early dry season, the animals can satisfy their requirements in the wet as well as in the dry season range. We show that the movement back to the dry season range is related to water requirements. In the dry season, fibre content of the vegetation severely restricts intake and the animals are not able to fulfil their nutritional requirements in any of the ranges. Finally, we discuss why male wildebeest should migrate with the females.

Keywords: *grazing; nutritional requirements; linear programming; East Africa.*

Introduction

Large-scale seasonal migrations by ungulates were once a widespread phenomenon in many tropical and temperate grassland ecosystems (Fryxell et al. 1988). Nowadays, East Africa is one of the few places where this impressive spectacle can still be observed. In the Serengeti-Mara system, over a million wildebeest (*Connochaetes taurinus*) and plains zebra (*Equus burchelli*) migrate each year at the beginning of the wet season to their wet season range in the south-east of the Serengeti National Park. Four to six months later, when the rains stop, the animals slowly move back up north to their dry season range where they spend the final months of the dry season (Maddock 1979).

Wild grazing ungulates generally encounter food resources, which temporally as well as spatially vary in quantity and quality. Hence, most hypotheses which have been put forward to explain the seasonal migration are related to differences in food quality between wet and dry season ranges. Kreulen (1975), McNaughton (1990) and Murray (1995) found evidence that the grasslands of the wet season range in the Serengeti-Mara ecosystem have higher concentrations of most minerals, notably N, P, Ca, Mg and Na. They suggested that cyclic requirements of female wildebeest for one or more mineral elements could account for their seasonal migration in the Serengeti and that the migration was related to an avoidance of mineral deficiencies, notably of phosphorus. Also Fryxell & Sinclair (1988) related the seasonal migration of white-eared kob in the Sudan to nutritional differences between the wet and dry season range. In addition, Fryxell (1995) pointed out that migratory patterns might be related to predator avoidance (but see Hofer & East 1995).

The above-mentioned studies in the Serengeti system regarded the requirements and concentrations of each mineral separately without taking into account mineral balances or protein and energy requirements. In this paper, we use a linear programming model (Westoby 1974, Belovsky 1978) to try to understand the causation of the seasonal migration by ungulates. Linear programming permits simultaneous treatment of energy and nutrient requirements in explaining diet choice. In diet studies, linear programming is usually used to predict the optimal combination of two or more diet components which satisfies certain nutritional requirements and at the same time maximizes (or minimizes) a certain goal. Linear programming also gives the array of possible diets with which an animal can satisfy all its

requirements without necessarily foraging optimally. These models have been applied to several mammalian herbivores (Belovsky 1978, Seagle & McNaughton 1992, Forchhammer & Boomsma 1995, Nolet et al. 1995, but see Hobbs 1990 and Owen-Smith 1993, 1996). In this paper, linear programming is used to predict in which area (namely the wet season range or the dry season range) migratory ungulates should forage to satisfy all their nutritional requirements.

The linear programming model is applied to data collected in the Masai-ecosystem (Prins 1987), located in Northern Tanzania and situated about 500 km east of the Serengeti-Mara ecosystem. Here some 40,000 wildebeest and zebra show a seasonal migration pattern similar to the one described in the Serengeti (Lamprey 1964, Kahurananga 1997). At the beginning of the wet season, all wildebeest and most zebra leave their dry season ranges and disperse into the surrounding areas. A few weeks after arrival the females of both species give birth. About six months later when the rains have stopped, the animals migrate back into their dry season ranges where they spend the remaining months of the dry season.

This paper focuses on two questions: 1) Are the observed migratory movements in correspondence with the predicted migratory movements if the animals were foraging in an area (i.e. wet or dry season range) where they can satisfy all their nutritional requirements ? 2) Which are the nutritional characteristics of the vegetation that determine the array of possible outcomes of the linear programming model ? Nutritional requirements of wildebeest for two scenarios were studied, namely those during lactation and those for maintenance only. These correspond with the two main seasons: in the early wet and wet season females are lactating, and during the early dry and dry season the animals basically have to satisfy their maintenance requirements only. The linear programming model was solved for different foraging goals, namely, maximization of energy and of nutrients (protein).

Methods

Study area

Data were collected in Tarangire National Park (NP) and in the Simanjiro Game Controlled Area (GCA) both located in northern Tanzania. Tarangire NP (lat. 4° S, long. 36° E, 1200 m above sea level) is situated in the eastern part of the Great Rift Valley and encompasses an area of approximately 2600 km². The Park is used as a dry season range by most of the large migratory herds of wildebeest and plains zebra of the 35,000 km² Masai Ecosystem (Prins 1987). The animals concentrate during the dry season along the Tarangire River, which is one of the few permanent water sources in the area. Other abundant and more sedentary herbivores in Tarangire NP are African elephant (*Loxodonta africana*), African buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), Grant's gazelle (*Gazella granti*), Coke's hartebeest (*Alcelaphus buselaphus cokii*) and giraffe (*Giraffa camelopardalis*), (Chapter 2). The vegetation of the northern part of the Park, where animal density is highest, is characterised by wooded grasslands, with *Acacia tortilis* intermixed with *Adansonia digitata*, and by seasonal flood plains with various perennial grass species (Chuwa 1996). Soils are of lacustrine and alluvial origin underlain by pre-Cambrian gneiss rock.

The Simanjiro GCA is situated c. 50 km east of Tarangire NP and is used by Masai and Warusha pastoralists for cattle grazing, small-scale agricultural activities and firewood collection. It is used as a wet season range by the migratory herds from Tarangire NP. The most abundant resident species are Grant's gazelle, giraffe and Thomson's gazelle (*Gazella thomsonii*). The vegetation mainly consists of *Digitaria macroblephera* - *Panicum coloratum* short grasslands surrounded by smaller areas of *Acacia tortilis* - *Commiphora schimperi* woodland (Kahurananga 1979). Soils are of volcanic origin and underlain by pre-Cambrian gneiss rock.

The average yearly rainfall is 620 mm in Tarangire NP (M.M. Voeten, unpublished data) and 600 mm in the Simanjiro GCA (Kahurananga 1979). During the wet season (December-May) rainfall is highly variable and erratic. During the dry season (June-November) rainfall is very rare.

Data collection and analysis

In 1995 and 1996, vegetation samples were collected in the wet season range and in the dry season range. Sampling took place in the early wet season (January), in the middle of the wet season (April), in the early dry season (July) and in the middle of the dry season (October). The animals migrate in the early wet season to their wet season range and in the early dry season back to the dry season range. Vegetation was collected on sites where large mixed herds of wildebeest and zebra were observed grazing during the different seasons. A total of 90 different sites were sampled. In the early wet season, 14 sites were sampled in the dry season range and 15 in the wet season range. In the wet season, 12 sites were sampled in the dry season range and 9 in the wet season range. In the early dry season, this was respectively 16 sites for the dry season range and 14 for the wet season range. In the dry season, 5 sites were sampled in the dry season range and 5 sites in the wet season range. At each site, all vegetation within 5 randomly placed frames of 1.0 m x 0.5 m was harvested. All sampling sites were on open grasslands and we removed the odd herb that was encountered in the sampling frame. Of each of the 5 vegetation samples harvested per site, a sub-samples was hand-sorted into green leaf, green stem, dead leaf and dead stem fractions, thereupon air-dried, weighed and stored for chemical analysis. Total nitrogen, phosphorus, sodium and calcium concentrations in leaves were determined after a modified Kjeldahl destruction (Novozamsky et al. 1983). Total nitrogen and phosphorus concentrations were measured colorimetrically using a continuous-flow analyser (Skalar SA-4000). Total calcium and sodium concentrations were measured using a flame-photospectrometer (Varian SpectraAA-600). Crude protein was calculated as $6.25 \times \% \text{ nitrogen}$. Neutral detergent fibre (% NDF) was determined according to Goering & van Soest (1970). Digestibility of organic matter (% DOM) was determined according to Tilley & Terry (1963). The results of the chemical analysis were averaged per site and used for further statistical analysis.

Before statistical analysis, data were arcsines-transformed to adjust for deviations of normality and to improve homogeneity of variance. Differences in forage quality parameters between years were first tested with a two-way ANOVA per season. Year and range (dry and wet season range) were used as independent factors. Data for the two years were pooled because neither significant year x range interactions nor significant differences between years

were found. Subsequently, differences in forage quality parameters between the dry and wet season range were tested with a one-way ANOVA per season. All statistical procedures were performed with SPSS 7.0 for Windows.

Linear programming

The general problem, having to comply simultaneously with an array of requirements can be analysed with a linear programming model (Westoby 1974, Belovsky 1978). Linear programming models are optimisation models whereby a goal is maximized (or minimized), subject to constraints. These constraints can be formulated as linear equations of the form:

$$C \geq \text{or} \leq \sum c_i \times I_i \quad (1)$$

where C is a constraint value that cannot be exceeded or must be surpassed. I_i is the amount of food of class i consumed (in this study, i is not a food type but a foraging area, so here I_i is the amount of food consumed in area i), c_i is a parameter that converts I_i into the same units as C and is based on the measured mineral or energy contents of the food from the different areas. The Solver module of Excel 97 was used to model the optimal foraging area choice in the different seasons under different foraging goals: maximization of metabolizable energy intake or maximization of protein intake. The following limits (constraints which cannot be exceeded) and requirements (constraints which should be surpassed) were formulated:

Energy constraints: Energy requirements are usually expressed as metabolisable energy (ME), and is that part of the digestible energy which is available for metabolism after subtraction of losses through urine and methane (Van Soest 1994). From feeding trials, conducted with wildebeest in the Serengeti National Park, Murray (1993) found that the animals maintained constant body weight with an average daily metabolizable energy intake of $0.512 \text{ MJ/kg } W^{0.75}$. Extrapolating from these results and including an extra energy expenditure for daily movement related to foraging (Kreulen 1975), Murray (1995) calculated that the intake of metabolizable energy for maintenance would be 22.32 MJ/day . This is based on a wildebeest with a body weight of 143 kg , which is the average weight for adult females in the Serengeti migratory wildebeest population (Watson 1967). For lactating females the daily metabolizable energy intake would be 32.69 MJ/day (Murray 1995).

The metabolic energy content of the food in the wet and dry season range was calculated using the following relationships: metabolisable energy is $0.82 \times$ digestible energy (DE) (Van Soest 1994). Digestible energy depends on the digestibility of the food and can be calculated as $\%$ digestibility of organic matter ($\%$ DOM) \times the gross energy (GE) of the food. The gross energy content of grasses is fairly constant and averages 19 MJ/kg dry weight (DW) (Crampton & Harris 1969). Hence the constraint equation for daily metabolisable energy intake for maintenance is:

$$22.32 \text{ (MJ/day)} \leq \sum 19 \text{ (MJ/kg DW)} \times \% \text{ DOM}_i \times 0.82 \times I_i \quad (2a)$$

and during lactation:

$$32.69 \text{ (MJ/day)} \leq \sum 19 \text{ (MJ/kg DW)} \times \% \text{ DOM}_i \times 0.82 \times I_i \quad (2b)$$

Whereby $\%$ DOM is the percentage digestibility of organic matter as measured in the vegetation. I is daily intake (kg DW/day) and subscript i denotes a foraging area.

Nutrient constraints: Nutrient requirements used here for phosphorus, sodium and calcium were taken from Murray (1995) who applied the ARC (1980) and AFRC (1991) requirements for cattle to wildebeest. The constraint equations for daily intake of the different minerals for maintenance thus used were:

$$5.76 \text{ g P/day} \leq \sum P_i \times I_i \quad (3a)$$

$$1.07 \text{ g Na/day} \leq \sum \text{Na}_i \times I_i \quad (3b)$$

$$3.59 \text{ g Ca/day} \leq \sum \text{Ca}_i \times I_i \quad (3c)$$

and during lactation

$$17.61 \text{ g P/day} \leq \sum P_i \times I_i \quad (4a)$$

$$2.35 \text{ g Na/day} \leq \sum \text{Na}_i \times I_i \quad (4b)$$

$$15.51 \text{ g Ca/day} \leq \sum \text{Ca}_i \times I_i \quad (4c)$$

Crude protein (CP) constraints used in the linear programming model were based on ARC (1980, table 10.3 and 10.5) requirements and adjusted for a 143 kg wildebeest. The constraint equation for daily intake of the crude protein for maintenance thus used was:

$$152 \text{ g CP/day} \leq \sum \text{CP}_i \times I_i \quad (5a)$$

and during lactation

$$441 \text{ g CP/day} \leq \sum \text{CP}_i \times I_i \quad (5b)$$

Whereby P_i , Na_i , Ca_i and CP_i are the respective mean concentrations (expressed as g/kg DW) as measured in the vegetation.

Digestibility constraints: For ruminants, daily intake rates are often constrained by rate of digestion and passage of ingesta through the rumen. Digestibility of food is very well correlated with the cell wall content, measured as percentage neutral detergent fibre (% NDF) in the van Soest system (Van Soest 1994). Reid et al. (1988) report of feeding trials with cattle and sheep on three forage classes: C_3 grasses, C_3 legumes and C_4 grasses (most tropical lowland grasses belong to the C_4 class). They found significant negative correlations between NDF intake and % NDF in all three forage classes. For cattle on a diet with C_4 grasses, mean daily NDF intake was not higher than on average 66.7 g/kg $W^{0.75}$ ($n=78$, $se \pm 1.1$). In the linear programming model here this is set as a maximum during maintenance as well as during lactation. Hence the constraint equation for a 143-kg wildebeest becomes:

$$2.76 \text{ kg NDF/day} \geq \sum NDF_i \times I_i \quad (6)$$

Whereby NDF is the mean fibre concentration (expressed as g/kg DW) as measured in the vegetation.

Results

Nutritional properties of the vegetation in the wet and dry season range

Most of the nutritional quality parameters of the vegetation did not differ much between the wet and dry season ranges (Fig. 1). Most striking differences between feeding areas were found in phosphorus and in sodium concentrations: the vegetation in the wet season range contained twice as much phosphorus but a much lower content of sodium than the vegetation in the dry season range. We also found these differences in the mineral concentrations in the soil. The average total phosphorus in soil of the wet season range was $0.04 \% \pm 0.01$ (95% confidence limits) and in the dry season range average total phosphorus was $0.10 \% \pm 0.01$ (95% confidence limits) (M.M. Voeten, unpub. data, see also Chapter 5). Also crude protein in the vegetation differed significantly between the two areas for most of the year while total nitrogen

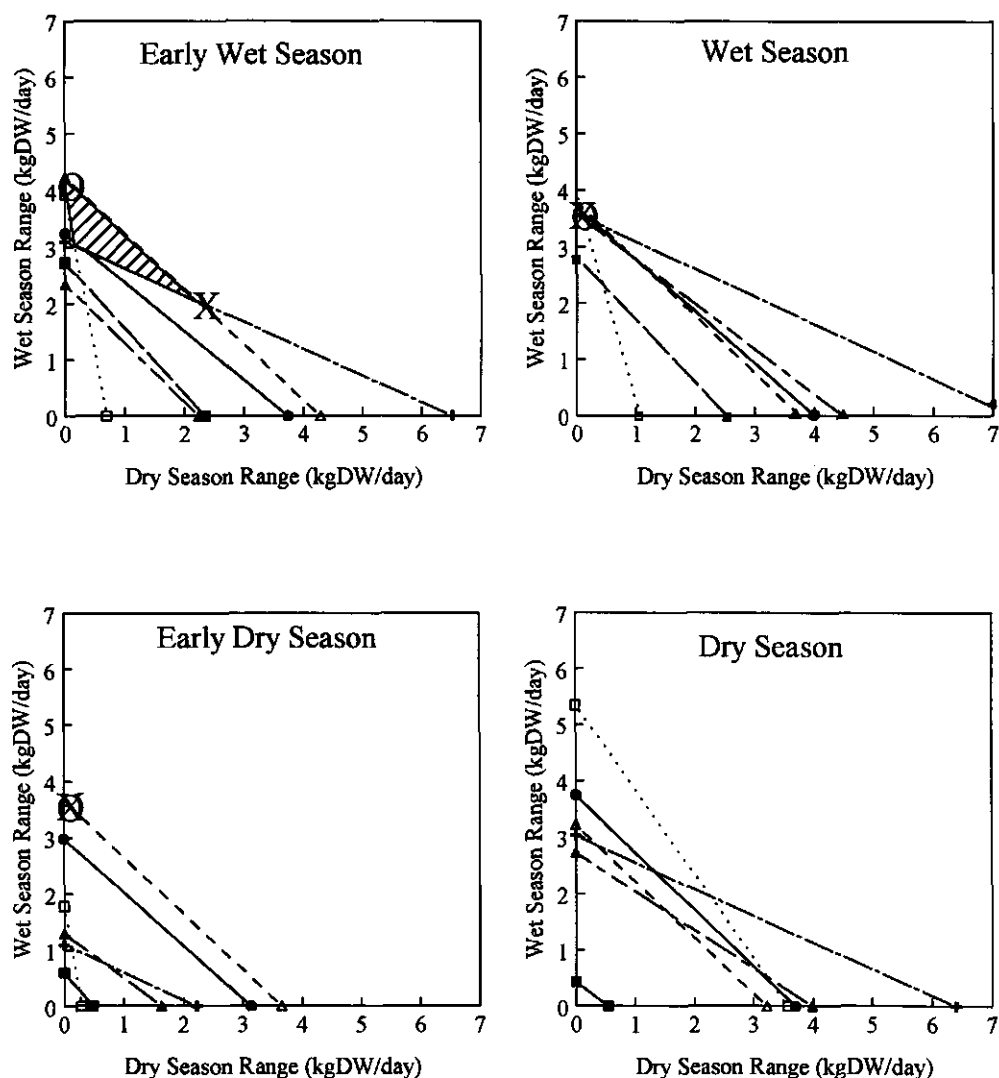


Figure 2. Outcome of the linear programming model, predicting in which area migratory wildebeest should forage during different seasons to simultaneously satisfy their nutritional requirements. To position the constraint lines during the early wet and wet season, the lactation requirements were used and during the early dry and dry season the maintenance requirements were used. X indicates the optimal diet if the animals would be maximizing protein intake and O indicates the optimal diet if the animals would be maximizing energy intake. The shaded area indicates the array of possible solutions. The model could not be solved for the dry season. Constant lines are marked with \blacktriangle for Protein, \triangle for Fibre, \square for Sodium, \bullet for Energy, \blacksquare for Calcium and $+$ for Phosphorus.

vegetation in the wet season range is slightly higher than that in the dry season range (Fig. 1) the metabolisable energy yield is higher in the wet season range. So, if the animals' goal is to maximize energy intake they should feed in the wet season range during the early dry season. The same reasoning applies to maximizing protein intake. Hence, the animals apparently leave the wet season range for other reasons.

The linear programming model could not be solved for the dry season (Fig. 2d), because in both the wet and dry season ranges the maximum fibre intake is reached before the other requirements are satisfied. So, in whichever area the animals would choose to forage, in both the wet season as well as the dry season range they would endure insufficient intake of energy and minerals, most notably sodium in the wet season range and phosphorus in the dry season range.

Discussion

We used linear programming to predict in which area migratory ungulates should forage to satisfy their nutritional requirements. The linear programming approach is conceptually useful to predict diet choice but the main difficulty is in positioning the constraint lines (see criticism by Hobbs 1990, Owen-Smith 1993, 1996). Much literature exists on nutrient and energy requirements of herbivores, which, however, mostly stems from agricultural use (see ARC/NRC). For this paper, these daily intake rates were adjusted for wildebeest or resulted from experimental work with wildebeest (Murray 1993), thereby assuring that we approximated the requirement levels as closely as possible based on the presently available information.

We solved the linear programming model for both maximization of energy intake and separately, for maximization of protein intake. We did not choose to set feeding time as a goal to minimize (Schoener 1971) since we do not consider wildebeest as being time limited when foraging (see also Beekman & Prins 1989, Prins & Iason 1989). Animals that forage constantly, except when avoiding predators, defending territories or engaging in reproductive activities, may be labelled energy maximizers (Hixon 1982). Large grazers, such as wildebeest, spend most of their time on foraging activities, their mating system is not very complex thus

8%; at this level digestion is severely limited (Van Soest 1994). Animals thus have to fall back on their reserves by catabolizing their muscle tissue. Indeed, during the dry season, most tropical herbivores lose physical condition (Chapter 6). For the migratory populations, it does not seem to be important in which area they are, regarding their nutritional requirements but is does for their access to drinking water. So, the dry season range is the only option during the dry season since Tarangire River maintains its flow. In addition, the herbivores will be able to supply their meagre diet with minerals from the river water. This seems especially important for sodium, because as can be seen from Fig.1, sodium concentrations in the vegetation are very low in the dry season. Sodium is not easily stored in body tissue and continuously excreted through urine so the animals need a constant intake of sodium. With a daily water intake of 1.78 litre, wildebeest would already cover their daily sodium requirements based on daily Na requirement of 1.07 gr. (Murray 1995) and an average Na concentration of 600 mg/l in the river water (M.M.Voeten, unpub.data). Phosphorus and calcium concentrations in the river water were too low for a substantial contribution to daily mineral requirements.

Since we used nutritional requirements during lactation to explain the migration to the wet season range, our results apply to females, who often during the wet season form separate herds from the males (Estes 1991). The question can than be posed why males migrate to the wet season range just like the females. Results of the linear programming model (not shown), using maintenance requirements of energy and nutrients during the early wet and wet season (which would be the requirements for males during that period), showed that the animals could satisfy all their requirements in the wet season range but also in the dry season range. The optimal diet though, for the maximization of energy or protein, could only be obtained in the wet season range. In addition, we consider mating success as an important factor in why the males migrate with the females. Mating takes place in the early dry season independent of where the animals are. To assure reproduction, males should stay close to the females because the females time of return to the dry season range is variable; when the rains have been abundant and pools do not dry up quickly, the wildebeest stay longer in their wet season range (M.M. Voeten, pers.obs.) and mating happens there.

We conclude that the causes of the seasonal migration are more complicated than just the drive to avoid mineral deficiencies, notably that of phosphorus (McNaughton 1990, Murray 1995). It is not likely that animals try to maximize the intake of a certain single mineral since

many nutritional constraints have to be overcome in order to satisfy all nutritional requirements simultaneously. By using a linear programming model we were able to correctly predict migratory movements of wildebeest in the Masai ecosystem in Tanzania. We showed that during the wet season the animals are able to satisfy simultaneously their energy, protein and mineral requirements only in the wet season range. And they do not migrate to the wet season range because of high concentrations of phosphorus in the vegetation there, but more so because the low concentration of phosphorus in the vegetation in the dry season range makes that range unsuitable for them in periods of high phosphorus requirements. The return to the dry season range is mainly related to water requirements.

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References

- AFRC (1991). AFRC Technical Committee on Responses to Nutrient, Report 6. A. Reappraisal of the calcium and Phosphorus Requirements of sheep and cattle Nutrition Abstracts and Reviews (Series B), Vol. 61, No. 9 September 1991.
- ARC (1980). Agricultural Research Council. The nutrient requirements of ruminant livestock. Commonwealth Agricultural bureaux, England.

- Beekman J.H. & Prins H.H.T. (1989). Feeding strategies of sedentary large herbivores in East Africa, with emphasis on the African buffalo, *Syncerus caffer* African Journal of Ecology 27: 129-147.
- Belovsky G.E. (1978). Diet optimization in a generalist herbivore: the moose. Theoretical population biology 14: 105-134.
- Chuwa S. (1996). Tarangire National Park, vegetation species composition mapping, General report. New York Zoological Society.
- Crampton E.W. & Harris L.E. (1969). Applied animal nutrition – the use of feedstuffs in the formulation of live stock rations (2nd ed.). Freeman, San Francisco.
- Delany M.J. & Happold D.C.P. (1979). Ecology of African mammals. Longman, London.
- Estes R.D. (1991). The behaviour guide to African mammals. The University of California Press, Berkeley.
- Forchhammer M.C. & Boomsma J.J.(1995). Foraging strategies and seasonal diet optimization of muskoxen in West Greenland. Oecologia 104: 169-180.
- Fryxell J.M. & Sinclair A.R.E. (1988). Seasonal migration by white-eared kob in relation to resources. African Journal of Ecology 26: 17-31.
- Fryxell J.M., Greever J. & Sinclair A.R.E. (1988). Why are migratory ungulates so abundant? American Naturalist 131: 781-798.
- Fryxell J.M. (1995). Aggregation and migration by grazing ungulates in relation to resources and predators. In : Sinclair A.R.E. & Arcese P. (eds.). Serengeti II: Dynamics, management and conservation of an ecosystem. The University of Chicago Press, Chicago, pp257-273.
- Goering H.K. & Van Soest P.J. (1970). Forage fiber analyses (apparatus, reagents, procedures and some applications). Agricultural handbook No.379, Agricultural Research Services, Washington.
- Hixon M.A. (1982). Energy maximizers and time minimizers: theory and reality. American Naturalist 119: 596-599.
- Hobbs N.T. (1990). Diet selection by generalist herbivores: a test of the linear programming model. In: Hughes R.N. (ed.), Behavioral mechanisms of food selection (NATO ASI series, vol. G20). Springer, Berlin Heidelberg New York, pp395-413.

- Hofer H. & East M. (1995). Population dynamics, population size, and the commuting system of Serengeti spotted hyena. In : Sinclair A.R.E. & Arcese P. (eds.). *Serengeti II: Dynamics, management and conservation of an ecosystem*. The University of Chicago Press, Chicago, pp332-363.
- Hunter L.T.B. & Skinner J.D. (1998). Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour* 135: 195-211.
- Kahurananga J. (1979). The vegetation of the Simanjiro plains, Northern Tanzania. *African Journal of Ecology* 17: 65-83.
- Kahurananga J. & Silkiluwasha F. (1997). The migration of zebra and wildebeest between Tarangire National Park and Simanjiro plains, Northern Tanzania, in 1972 and recent trends. *African Journal of Ecology* 35: 179-185.
- Kreulen D. (1975). Wildebeest habitat selection on the Serengeti plains, Tanzania, in relation to calcium and lactation: a preliminary report. *East African Wildlife Journal* 13: 297-304.
- Lamprey H.F. (1964). Estimation of the large mammal densities, biomass and energy exchange in the Tarangire Game Reserve and the Masai steppe in Tanganyika. *East African Wildlife journal* 2: 1-46.
- Maddock L. (1979). The "migration" and grazing succession. In: Sinclair A.R.E. & Norton-Griffiths M. (eds.). *Serengeti: Dynamics of an ecosystem*. The University of Chicago Press, Chicago, pp104-129.
- McNaughton S.J. (1990). Mineral nutrition and seasonal movements of African migratory ungulates. *Nature* 345: 613-615.
- Murray M.G. (1993). Comparative nutrition of wildebeest, hartebeest and topi in the Serengeti. *African Journal of Ecology* 31: 172-177.
- Murray M.G. (1995). Specific nutrient requirements and migration of wildebeest In : Sinclair A.R.E. & Arcese P. (eds.) *Serengeti II: Dynamics, management and conservation of an ecosystem*. The University of Chicago Press, Chicago, pp231-256.
- Nolet B.A., Van der Veer P.J., Evers E.G.J. & Ottenheim M.M. (1995). A linear programming model of diet choice of free-living beavers. *Netherlands journal of zoology* 45: 315-337.

- Novozamsky I., Houba V.J.G., Van Eck R. & Van Vark W. (1983). A novel digestion technique for multi-elemental plant analysis. *Communications in Soil Science and Plant Analyses* 14: 239-249.
- Owen-Smith N. (1993). Evaluating optimal diet models for an African browsing ruminant, the kudu: how constraining are the assumed constraints ? *Evolutionary Ecology* 7: 499-524.
- Owen-Smith N. (1996). Circularity in linear programming models of optimal diet. *Oecologia* 108: 259-261.
- Prins H.H.T. (1987). Nature Conservation as an Integral Part of Optimal land use in East Africa: The case of the Masai Ecosystem of Northern Tanzania. *Biological Conservation* 40: 141-161.
- Prins H.H.T. (1988). Plant phenology patterns in Lake Manyara National Park, Tanzania. *Journal of Biogeography* 15: 465-480.
- Prins H.H.T. & Iason G.R. (1989). Dangerous lions and nonchalant buffalo. *Behaviour* 108: 298-324.
- Reid R.L., Jung G.A. & Thayne W.V. (1988). Relationships between nutritive quality and fiber components of cool season and warm season forages: a retrospective study. *Journal of Animal Science* 66: 1275-1291.
- Schoener T.W. (1971). Theory of feeding strategies. *Annual review of ecology and systematics* 2: 369-343.
- Seagle S.W. & McNaughton S.J. (1992). Spatial variation in forage nutrient concentrations and the distribution of Serengeti grazing ungulates. *Landscape ecology* 7: 229-241.
- Taylor C.R. (1968). The minimum water requirements of some east African bovids. *Comparative nutrition of wild animals: Symposium Zoological Society of London*.
- Tilley J.M.A. & Terry R.A. (1963). A two-stage technique for the in vitro digestion of forage crops. *Journal of British Grassland Society* 18: 104-111.
- Van Soest P.J. (1994). *Nutritional ecology of the ruminant* (2nd ed.). Cornell University Press.
- Van Wijngaarden W. (1985). *Elephants-Trees-Grass-Grazers: relationships between climate, soils, vegetation and large herbivores in a semi-arid savanna ecosystem (Tsavo, Kenya)*. ITC Publication number 4, 159p.

- Watson R.M. (1967). The population ecology of the wildebeest (*Connochaetes taurinus albojubatus* Thomas) in the Serengeti. Ph.D. thesis, Cambridge University.
- Western D. (1975). Water availability and its influence on the structure and dynamics of a savannah large mammal community East African Wildlife Journal 13: 265-286.
- Westoby M. (1974). An analysis of diet selection by large generalist herbivores. American Naturalist 108: 290-304.
- Wilmshurst J. F. & Fryxell J.M. (1995). Patch selection by red deer in relation to energy and protein intake: A re-evaluation of Langvatn and Hanley's (1993) results. Oecologia 104: 297-300.

**EFFECTS OF GRAZING ON FORAGE QUALITY AND
FORAGE QUANTITY FOR MIGRATORY
UNGULATES IN THE MASAI ECOSYSTEM,
NORTHERN TANZANIA**

Margje M. Voeten, Claudius A.D.M. Van de Vijver and Han Olff

Abstract

Several observations in Africa indicate that restriction of seasonal movement of migratory ungulates can cause a significant decline in numbers of the populations involved. Causes for this decline have, however, hardly been addressed. We investigated if the dry season range of migratory wildebeest and zebra in the Masai Ecosystem, northern Tanzania, can sustain current populations when access to the wet season range would be restricted and migratory herds would reside in the dry season range year-round. Both forage quality and quantity were considered.

Grazing itself can affect herbivore forage quality and quantity. Presently, however, the dry season range is not grazed during the wet season by migratory ungulates. This will be the case when access to the wet season range is restricted. We therefore performed clipping experiments to investigate how grazing affects forage quality and quantity in the dry season range during the wet season.

Clipping had a positive effect on the quality of forage whereby the clipped vegetation had higher proportions of live and leaf material as compared to unclipped vegetation. Moreover, clipping increased the concentration of nutrients in leaf material, N and P in particular. However, the concentrations were not sufficient to meet herbivore nutrient requirements, especially P. Furthermore, the present study suggests that through grazing the annual production of forage in the dry season range would be reduced and that also forage quantity would be insufficient for the current herbivore numbers.

We therefore conclude that, if the animals were forced to stay year-round in their dry season range, current population numbers of migratory herds would decline. Consequently this study shows the necessity of protecting current wet season ranges from the expanding human activities to safeguard this migratory system.

Key words: *migratory system, savanna, East Africa, forage quantity and quality, simulated grazing, forage requirement.*

Introduction

East African savannas are (still) renown for the large-scale seasonal migration of large grazing ungulates (Lamprey 1964, Pennycuik 1975, Prins 1987, Fryxell & Sinclair 1988, Williamson et al. 1988). Generally, the annual cycle of migration involves a concentration in areas with permanent water availability during the dry season, followed by a movement and dispersion into surrounding grazing areas at the onset of the wet season. This movement into the wet season range has been explained by the higher nutritious quality of the grasslands in the wet season range as compared to the dry season range (Kreulen 1975, Bell 1982, McNaughton 1990, Murray 1995, Chapter 4). During the dry season, most grasses are in a senescent phase and forage quality and quantity are limited in both the wet season range and dry season range. The animals however concentrate in their dry season range probably because of its permanent supply of fresh water there, while most wet season ranges lack water in the dry season (Chapter 4). Table 1 shows the annual cycle of migratory herbivores in East Africa with the main factors involved: forage quantity, forage quality and drinking water.

Table 1. Migratory populations move between a wet season range in the wet season and a dry season range in the dry season. The suggested main factors involved are indicated. ++ = sufficient, -- = insufficient and ? = unknown when grazed.

		Area	
		Wet Season Range	Dry Season Range
Season	Wet	Forage quality : ++	Forage quality : ?
		Forage quantity : ++	Forage quantity : ?
		Water : ++	Water : ++
	Dry	Forage quality : --	Forage quality : --
		Forage quantity : --	Forage quantity : --
		Water : --	Water : ++

The once free roaming wildlife of East Africa has been greatly affected by increasing human populations and by expanding agricultural activities (Lamprey 1983, Prins 1992, Happold 1995, Newmark 1996). Nowadays most wildlife is confined to National Parks and the consequences of this confinement for migratory wildlife are becoming an important management issue. In some areas, like in the Serengeti-Mara migratory system in Tanzania and Kenya, large tracks of the wet season range lie within the protected area of the National Park.

In many other migratory systems, however, the wet season range is situated in unprotected areas and these areas are becoming less accessible for migratory ungulates.

A migratory system where this is occurring is the Masai Ecosystem, northern Tanzania (Prins 1987). Most migratory wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) in the Masai Ecosystem congregate in Tarangire National Park during the dry season. The Tarangire River, which runs through this park, is one of the few permanent dry season water sources in the 35,000 km² Masai Ecosystem. During the wet season most of the wildebeest and zebra move to the Simanjiro plains. Due to human settlement and agricultural activities the accessibility of these unprotected plains is increasingly becoming restricted (Borner 1985, TWCM 1995a). Consequently the question is if the dry season range, Tarangire National Park, would be able to sustain current migratory populations when the wet season range becomes inaccessible and migratory herds would be restricted to the dry season range year-round.

Research in the migratory systems of the Serengeti (McNaughton 1990, Murray 1995) and Masai Ecosystems (Chapter 4) shows that during the wet season, the forage quality in the wet season ranges meets herbivore nutritional requirements, while in the dry season range it does not during this period. However, most comparisons between forage quantity and quality in wet and dry season ranges were done during the wet season on grazed wet season range herbage and ungrazed dry season range herbage. Regarding this comparison, the absence of herbivory in the dry season range during the wet season can be of importance since vegetation production and mineral concentration in the vegetation in African savannas are not only determined by rainfall and soil nutrients (Bell 1982, Le Houerou et al. 1988) but also by herbivory itself. Indeed, much research has shown that grazing can keep the vegetation in an open, young, productive stage of growth and can improve plant available soil nutrients and water status, thus contributing to the maintenance of a high above ground production of good quality (McNaughton 1979, 1984, Hilbert et al. 1981, Coppock 1983, Georgiadis et al. 1989, Georgiadis & McNaughton 1990, Oesterheld & McNaughton 1991, Milchunas et al. 1995, Hobbs 1996, but see Belsky 1987, Verkaar 1988, Belsky et al. 1993). When the migratory herbivores would be forced to stay in the dry season range year-round, the animals will also graze there during the wet season which is the growing season. Therefore, this study investigated the effects of grazing on vegetation production and nutrient status during the wet season in the dry season range and if these effects would improve dry season range forage to

levels that meet herbivore requirements. This information subsequently was used to predict if current migratory populations could be sustained in the park when migratory routes were to be cut off and the animals would reside in the park year-round.

We investigated the effects of clipping on biomass production, composition of above ground standing crop and mineral concentrations. We simulated medium and heavy grazing pressure by frequently clipping the vegetation down to two different heights. The experiment was conducted on mixed grasslands on the three main soil types of the dry season range to incorporate possible differences between soil types in grass production, in mineral contents and in their response to clipping. Finally we placed the outcome of the clipping experiment in the context of forage requirements of the migratory herds and discussed if, through grazing, forage quantity and quality in the dry season range is sufficiently enhanced to sustain current migratory populations if their range would be restricted to Tarangire National Park.

Methods

Study area

Data were collected in Tarangire National Park (4° S, 36° E, and 1200 m above sea level), the dry season range of migratory herds of wildebeest and zebra. The Park is located in northern Tanzania on the eastern side of the Great Rift Valley and encompasses an area of approximately 2600 km². The Tarangire River runs through the Park and is the main permanent dry season water supply within the entire 35 000 km² Masai Ecosystem (Prins 1987) in which the Park lies. The vegetation mainly consists of grasslands and open savanna woodlands (Chuwa 1996). Dominant grass species of the grasslands and floodplains are *Bothriochloa insculpta*, *Brachiaria* spp., *Cenchrus ciliaris*, *Dactyloctenium aegypticum*, *Digitaria* spp., *Panicum* spp., *Pennisetum mezianum*, *Sporobolus* spp., and *Urochloa* spp. Dominant tree species of the woodlands in the riverine area are *Acacia tortilis*, *Balanites aegyptiaca*, *Adansonia digitata*, *Maerua triphylla* and *Grewia* spp. The woodlands on the ridges are dominated by *Combretum* spp. and *Commiphora* spp.. Soils are of lacustrine and alluvial origin underlain by pre-Cambrian gneiss rock.

Average annual rainfall is 620 mm with high temporal and spatial variability. Most rain falls between December and May. During the dry season (June-November) rainfall is very rare. Large migratory herds of wildebeest and plains zebra are present during the dry season but leave the Park at the onset of the wet season. Other abundant herbivores in Tarangire N.P. are African elephant (*Loxodonta africana*), African buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), Coke's hartebeest (*Alcelaphus buselaphus cokii*), giraffe (*Giraffa camelopardalis*), Grant's gazelle (*Gazella granti*), oryx (*Oryx gazella*) and eland antelope (*Tragelaphus oryx*). These species, although more sedentary also disperse over a larger area during the wet season and very few animals remain in the Park in this period.

Data collection

In Tarangire National Park we selected 3 study sites: one on the open plains, one on a ridge slope and one in the river valley area, close to Tarangire river. These sites were selected because the soil types on which these sites were located represent the main soil types on which the migratory ungulates congregate during the dry season (TWCM 1995a). The Plains site was situated on a brownish loam soil with medium fertility and medium drainage capacity. This site consisted of open grassland, dominated by *Chloris virgata*, *Dactyloctenium aegyptium*, *Urochloa mosambicensis* and *Sporobolus ioclados*. The Ridge site was located halfway up the ridge on red loamy sand soil with medium fertility and high drainage capacity in open woodland dominated the tree species *Combretum apiculatum*, *Balanites aegyptiaca*, *Adansonia digitata* and *Maerua triphylla*. The grass layer was dominated by *Dactyloctenium aegyptium*, *Urochloa mosambicensis*, *Cynodon nlemfuensis*, and *Cenchrus ciliaris*. The River site was located on a light clay soil with high fertility and low drainage capacity on a floodplain next to the Tarangire river, and the vegetation was dominated by the grasses *Pogonarthria squarrosa*, *Brachiaria decumbens* and *Urochloa mosambicensis*.

Clipping experiment

The experiment was started in January 1996 in the beginning of the wet season and lasted until September 1996, which is halfway the dry season. The 1995-1996 rainy season was wetter than average and annual rainfall was 943 mm. First rains came in the second half of December 1995 and last showers occurred at the end of May 1996. The Plains and Ridge sites were set up at the 15th of January and sampled 9 times. The River site was set up two weeks later and sampled 8 times. In each site, five chain-link fence exclosures of 2.4 m by 1.2 m were put up. Each exclosure was divided in three equal parts, each of them receiving a different clipping treatment: the heavy treatment was clipped to 3 cm, the medium treatment was clipped to 15 cm and the control treatment was left unclipped. The clipping height of the medium treatment was based on average grass height found in the Simanjiro plains, the area that the Tarangire ungulates use during the wet season (Voeten 1999).

The heavy and medium treatments were clipped every 3 to 4 weeks and the clipped biomass was collected. At each clipping date we also measured the above ground biomass of the control treatment. The control sample was harvested to ground level in a 0.5 m x 1.0 m frame in matched plots outside the experimental exclosures, because the exclosures were not big enough to harvest the control treatment inside the exclosure throughout the growing season. Since most large ungulates are outside the Park during most of the growing season, vegetation outside the exclosures could be considered as ungrazed. Only at the end of the growing season, when the animals had returned to the Park, the control was clipped inside the exclosures.

At the end of the experiment, when grasses had stopped growing, the medium treatment was also harvested to ground level to determine the above ground annual production. For the heavy treatment the biomass below 3 cm was negligible and not included in further analysis. All plant material was hand-sorted into green leaf, green stem and dead material, dried to a constant weight and weighed.

To describe the soil properties of the different sites, we collected soil samples from each site in May 1996. Samples were collected with a metal pipe ($\varnothing = 4.2$ cm) from 0-10 cm soil depth. All soil samples were taken in duplicate and mixed to account for spatial variability.

Bulked samples were sieved through a 2-mm mesh screen to remove small stones and root material. Samples were dried to a constant weight and stored for chemical analysis.

Chemical analysis

Prior to chemical analysis, plant material and soil samples were digested using a modified Kjeldahl procedure with Selenium as a catalyst (Novozamsky et al. 1983). Total nitrogen (N) and phosphorus (P) concentrations in plant and soil material were analysed colorimetrically using a continuous-flow analyser (Skalar SA-4000, The Netherlands). Total calcium (Ca) and sodium (Na) concentrations were analysed with an Atomic Absorption Spectrophotometer (Varian Spectra AA-600, The Netherlands). Soil organic matter content was determined via combustion of soil samples at 550 °C for 3 hours. Soil pH was determined in the extraction residue from soil, using a 0.01 M CaCl₂ solution (Houba et al. 1986).

Data analysis

Seasonal changes in total above ground biomass, proportion of leaves and proportion of live biomass were compared between clipping treatments and sites. The above-ground biomass of the medium clipping treatment was calculated as the regrowth from each period plus an estimated value of the biomass between ground level and 15 cm. The latter was calculated by interpolating the biomass harvested at the end of the experiment for the medium treatment to the biomass at the beginning of the experiment. The proportion of leaves was calculated as leaf biomass divided by the sum of the leaf and stem biomass. The proportion of live material was calculated as live biomass divided by the sum of live and dead biomass.

Annual above ground production was calculated for both total biomass and live biomass. For the control treatment, annual above ground production was calculated as the sum of the positive biomass increments between harvests (McNaughton 1979). For the heavy and medium clipping treatments, annual production was calculated as the sum of the removed regrowth plus, for the medium treatment, the biomass harvested at the end of the experiment. Differences in annual live and total production between treatments and sites were tested with a two-way analysis of variance followed by Tukey HSD contrasts.

Seasonal changes in the proportion of leaves, proportion of live biomass and nutrient concentrations (N, P, Ca and Na) in green leaf were analysed per site, using an analysis of covariance with clipping treatment as the independent factor and harvest time as a the co-variate. To analyse differences between treatments, we subsequently tested the treatments pair wise (medium-control, heavy-control and medium-heavy) per site, using an analysis of covariance with clipping treatment as the independent factor and harvest time as a co-variate.

Prior to statistical analysis, data were either log-transformed (biomass-data) or arcsine-transformed (proportions and mineral nutrient concentrations) to adjust for deviations of normality and to improve homogeneity of variance. All statistical calculations were performed with SPSS 7.0 for Windows.

Forage production and requirements

To calculate the total forage availability for herbivores, we first determined the total surface area of the soil types that we investigated in Tarangire NP (unpub. C.A.D.M. Van de Vijver). Other soil types were excluded since the vegetation in these areas, such as forest, dense woodlands and swamps, do not form important habitat types for the migratory herbivores (TWCM 1995a). Subsequently, we estimated the total annual production of the graminoid vegetation for the selected part of the Park by multiplying the measured annual production in each of the three study sites with the total area of the soil type of the study site and accordingly adding up the three figures. Total forage requirements of all large herbivore species were estimated by multiplying the individual intake requirements by the herbivore population numbers (TWCM 1995a,b). The intake requirements were estimated assuming an average daily intake of dry matter of 2.5 % of a herbivore's bodyweight (Van Wijngaarden 1985, p.102). Grass intake of the intermediate feeders (Hofmann 1989) such as elephant and Grant's gazelle were taken from Hofmann (1973), Drent & Prins (1987) and Estes (1991). Mineral requirements for P, Ca, and Na during lactation and pregnancy were taken from Murray (1995) who adjusted AFRC (1991) cattle requirements for wildebeest. The minimum nitrogen requirement for maintenance was set at 1.3 % (Van Soest 1994).

Results

Soils

The soil of the River site was more fertile than the Plains and Ridge sites with significantly higher concentrations of total nitrogen, phosphorus, calcium and sodium as well as a higher organic matter content (Table 2). Only total soil nitrogen and soil pH did not differ significantly between the River site and the Plains site.

Table 2. Mean values of total soil nutrients, soil organic matter and pH. Different letters denote significant differences (one-way ANOVA, $P < 0.001$ and Tukey-HSD contrasts).

Site	N (%)	P (%)	Ca (%)	Na (%)	Soil Organic Matter (%)	pH
Ridge	0.06 ^a	0.04 ^a	0.35 ^a	0.05 ^a	3.04 ^a	5.86 ^a
Plains	0.10 ^{ab}	0.02 ^a	0.35 ^a	0.03 ^b	4.96 ^b	6.24 ^b
River	0.16 ^b	0.11 ^b	0.63 ^b	0.10 ^c	10.61 ^c	6.16 ^b

Above ground biomass and production

In the beginning of the wet season, the vegetation recovered well from the clipping treatments (Fig. 1). This recovery especially occurred in the Ridge and River site (Fig 1b and 1c). At the end of the wet season however, the growth response of the clipped treatments in all sites declined. Compared to the results of the unclipped control, clipping resulted in a significantly lower annual production of live above ground biomass (Fig 2a) and total above ground biomass (Fig 2b) in all three sites. For both live and total biomass production, the response to clipping did however differ between sites (site x treatment interaction: $F_{4, 36} = 3.09$, $P < 0.05$; $F_{4, 36} = 3.45$, $P < 0.05$ respectively). In the River site, which had the highest annual production, the clipped treatments recovered relatively less, as compared to the control, than in the Plains and Ridge sites. This was especially so for the annual live production of the medium clipped treatment which produced only 36 % of the control treatment on the River site as compared to 64 % on the Plains site and 46 % on the Ridge site. The medium and heavy clipped plots did not show many significant differences. Only in the Plains and Ridge sites, the annual total production differed significantly between heavy and medium clipped plots.

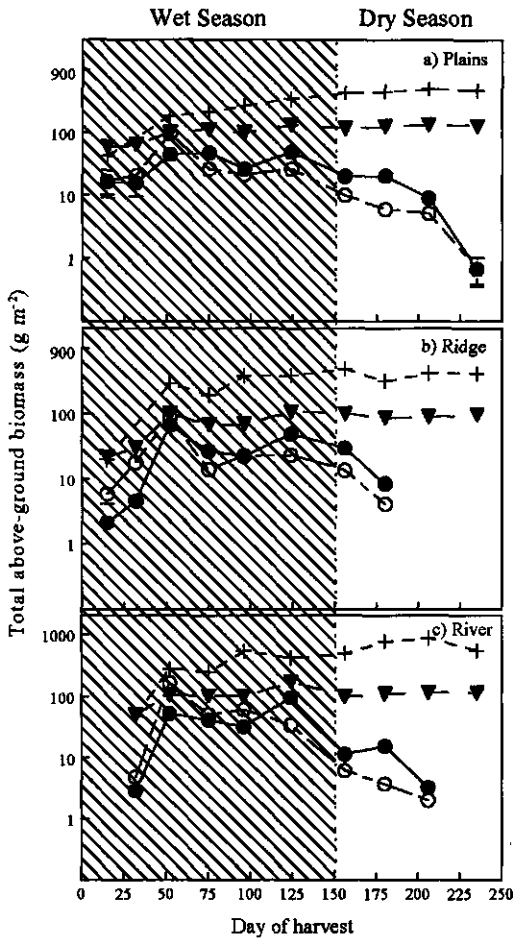


Figure 1. Average total above ground biomass (g m^{-2} , \pm SE) for the control, unclipped (+ — +) and medium clipped (\blacktriangledown — \blacktriangledown) treatment as well as regrowth of the medium clipped (\bullet — \bullet) and heavy clipped (O—O) treatments. Total above ground biomass for the medium clipped treatment is the sum of the regrowth plus the interpolated biomass under 15 cm. Day of harvest: day 0 = 1-01-1996 and day 235 = 22-08-1996.

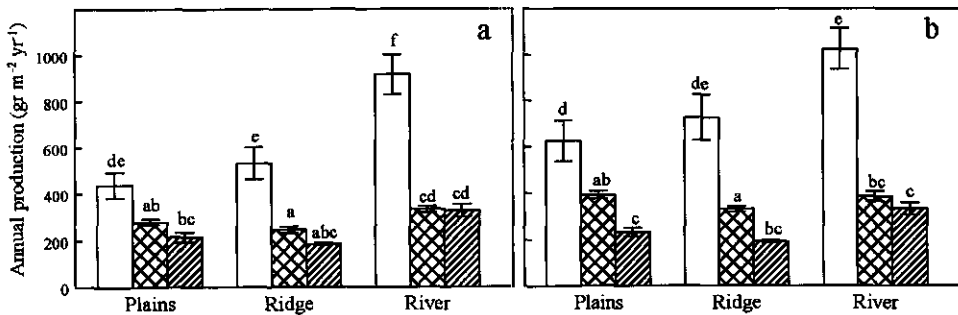


Figure 2. Mean annual live (a) and total (b) production ($\text{g m}^{-2} \text{ yr}^{-1}$, \pm SE) for the control unclipped, (= \square), medium (= \boxtimes) and heavy (= ▨) clipped in the Plains, Ridge and River site in Tarangire National Park. Different letters denote significant differences (Tukey HSD, $p < 0.05$). (see also data analysis in the material and methods section).

Composition of biomass

In general, clipping maintained the proportion of live material rather constant (Fig 3a,b,c). The proportion of live material was primarily affected by date of harvest, thus by the time in the growing season (Table 3). Pairwise comparisons between treatments per site showed that, in the course of the experiment, the unclipped plots decreased significantly more in the proportion of live material than both the clipped plots (date x treatment interaction for medium-control in the Plains site: $F_{1,76} = 94.76$, $P < 0.001$, in the Ridge site: $F_{1,59} = 61.80$, $P < 0.001$ and in the River site: $F_{1,58} = 16.97$, $P < 0.001$; date x treatment interaction for heavy-control in the Plains site: $F_{1,74} = 81.28$, $P < 0.001$ and in the Ridge site: $F_{1,61} = 93.56$, $P < 0.001$).

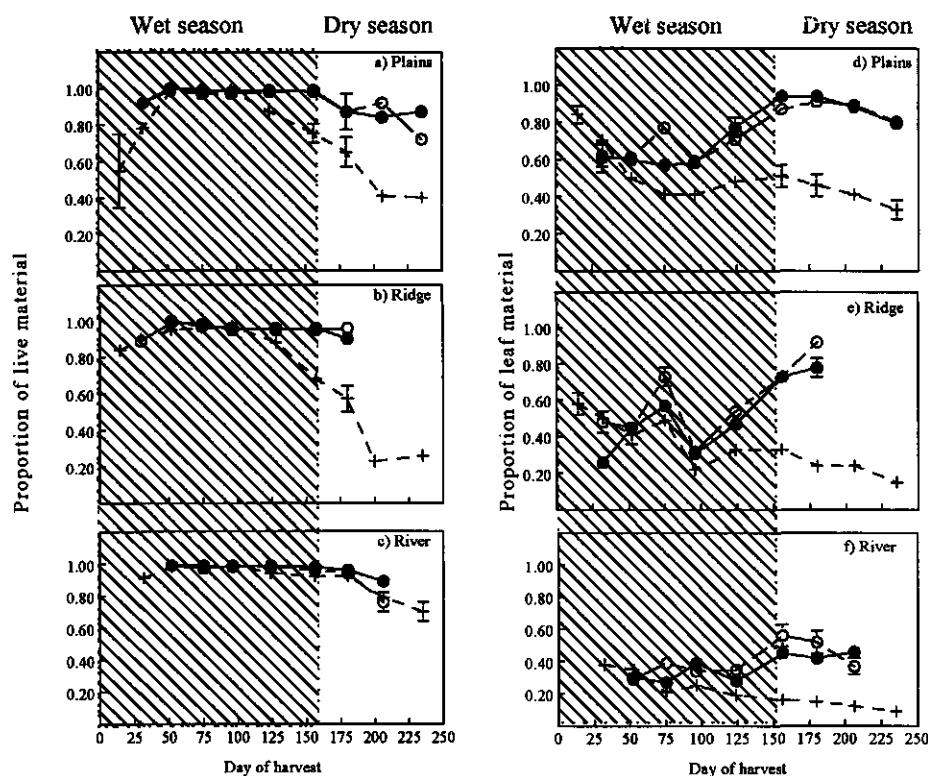


Figure 3. Mean proportions of live material (a,b and c) and leaves (d,e and f) for the control, unclipped (+ — +), medium clipped (●—●) and heavy clipped (O—O) treatments in the vegetation in the Plains, Ridge and River site respectively. The proportion live material was calculated as live biomass divided by live plus dead biomass. Medium and heavy proportions of live material refer to the regrowth. For the Ridge and River site, the proportion live in the clipped treatments at the end of the season could not be calculated because either no dead or live biomass was present. Day of harvest: as in Figure 1.

Only in the River site (Fig.3c), the decrease in proportion of live biomass for the heavy treatment and the control did not differ significantly. Also no significant differences were found between the medium and heavy clipping treatments. Clipping significantly increased the proportion of leaves (Fig.3a,b,c). For all three sites the proportion of leaves was primarily affected by the clipping treatments (Table 3) and less by date of harvest and date x treatment interaction. Pairwise comparisons between treatments showed that, in all the sites, the difference between clipped plots and unclipped plots significantly increased during the season, whereby the unclipped plots showed a decline in proportion of leaves while the clipped plots tended to show an increase in the proportion of leaves (date x treatment interaction for medium-control in the Plains site: $F_{1,74} = 30.95$, $P < 0.001$, in the Ridge site: $F_{1,66} = 87.85$, $P < 0.001$ and in the River site: $F_{1,66} = 100.38$, $P < 0.001$; date x treatment interaction for heavy-control in the Plains site: $F_{1,79} = 28.02$, $P < 0.001$, in the Ridge site: $F_{1,71} = 46.13$, $P < 0.001$ and in the River site: $F_{1,71} = 52.13$, $P < 0.001$). The proportion of leaves did not differ significantly between the heavy and medium clipped treatments in either of the sites.

Table 3. Results of analysis of co-variance in which the effect of clipping treatment (medium, heavy or unclipped) was tested on live/dead ratio, leaf/stem ratio and mineral concentrations (nitrogen (N), phosphorus (P), calcium (Ca) and sodium (Na)) in green leaves during the course of the season. Date of harvest was used as co-variable. Values indicate the percentage of variance explained per factor, summing up to the variance explained by the model (r^2). The explained variance per factor was calculated as the SS per factor divided by the SS of the corrected total. The significance levels refer to the F-test of the ANCOVA procedure. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

Site	Factor	df	Proportion		Grass leaf nutrient concentration			
			live	leaves	N	P	Ca	Na
Plains	Date (D)	1	0.35***	0.04***	0.32***	0.00 ^{ns}	0.37***	0.00 ^{ns}
	Treat (T)	2	0.19***	0.60***	0.29***	0.19***	0.00 ^{ns}	0.03 ^{ns}
	D x T	2	0.26***	0.10***	0.06***	0.02 ^{ns}	0.01 ^{ns}	0.06 ^{ns}
	r^2	5	0.79***	0.73***	0.67***	0.21***	0.39***	0.09 ^{ns}
Ridge	Date (D)	1	0.49***	0.00 ^{ns}	0.51***	0.06**	0.00 ^{ns}	0.00 ^{ns}
	Treat (T)	2	0.13***	0.38***	0.17***	0.30***	0.12**	0.07 ^{ns}
	D x T	2	0.25***	0.29***	0.01 ^{ns}	0.04*	0.02 ^{ns}	0.04 ^{ns}
	r^2	5	0.87***	0.67***	0.68***	0.40***	0.14**	0.11 ^{ns}
River	Date (D)	1	0.47***	0.02**	0.52***	0.15***	0.50***	0.31***
	Treat (T)	2	0.05**	0.51***	0.18***	0.06*	0.18***	0.12***
	D x T	2	0.06***	0.22***	0.04**	0.00 ^{ns}	0.10***	0.01 ^{ns}
	r^2	5	0.58***	0.74***	0.74***	0.21***	0.78***	0.44***

Plant mineral concentrations

Clipping resulted in higher nitrogen (N) concentrations in grass leaves (Fig 4a,b,c) but N concentrations were mainly affected by date of harvest (Table 3). In all three sites, plant N concentrations decreased in the course of the wet and dry season. Pairwise comparisons between most clipped and unclipped treatments showed that over time, the clipped plots decreased less in N concentration than the control treatment (date x treatment interaction for medium-control in the Plains site: $F_{1, 78} = 8.53$, $P < 0.01$ and in the River site: $F_{1, 71} = 8.23$, $P < 0.01$; date x treatment interaction for heavy-control in the Plains site: $F_{1, 79} = 20.45$, $P < 0.001$ and in the River site: $F_{1, 71} = 13.22$, $P < 0.01$). In other cases, only main treatment effects were significant (medium- control in the Ridge site: $F_{1, 68} = 20.68$, $P < 0.001$ and heavy-control in the Ridge site: $F_{1, 71} = 47.90$, $P < 0.001$). The differences between medium and heavy clipped plots were significant except in the River site (medium- heavy in the Plains site: $F_{1, 81} = 9.14$, $P < 0.01$ and in the Ridge site: $F_{1, 63} = 6.65$, $P < 0.05$).

Clipping also had a positive effect on grass leaf phosphorus (P) concentration (Fig.4d,e,f). The response however differed between sites and was not similarly affected by date of harvest or treatment (Table 3). In the Plains site grass leaf P concentration did not change significantly during the year while in the Ridge and River site they increased towards the dry season. Grass leaf P concentrations in the Plains site were considerably lower than in the Ridge and River site. Pairwise comparisons showed that in the Plains and River sites, plant P concentrations in clipped plots showed the same trend in time as the unclipped plots since only significant main effects were found (medium-control in the Plains site: $F_{1, 78} = 23.12$, $P < 0.001$ and in the River site: $F_{1, 71} = 4.97$, $P < 0.05$; heavy-control in the Plains site: $F_{1, 79} = 21.68$, $P < 0.001$ and in the River site: $F_{1, 71} = 6.78$, $P < 0.05$). Only in the Ridge site, P levels increased more in the clipped plots than in the unclipped plots (date x treatment interaction for medium- control in the Ridge site: $F_{1, 68} = 4.98$, $P < 0.05$ and for heavy-control in the Ridge site: $F_{1, 71} = 5.11$, $P < 0.05$). No significant differences between medium and heavy clipped plots in any of the sites were found.

Clipping negatively affected calcium (Ca) concentrations (Fig. 4g,h,i). Just as for P, the response differed between sites and concentrations were not similarly affected by date of harvest or treatment (Table 3). In the Plains site, Ca levels increased during the seasons but

clipping had no effect at all. In the River site, Ca levels also increased in the course of the season, but clipping resulted in a less steep increase (Table 3). In the Ridge site, Ca levels were lower as a result of clipping but stayed constant over the year. Pairwise comparisons between treatments showed that medium and heavy clipped plots on the River site increased less in Ca

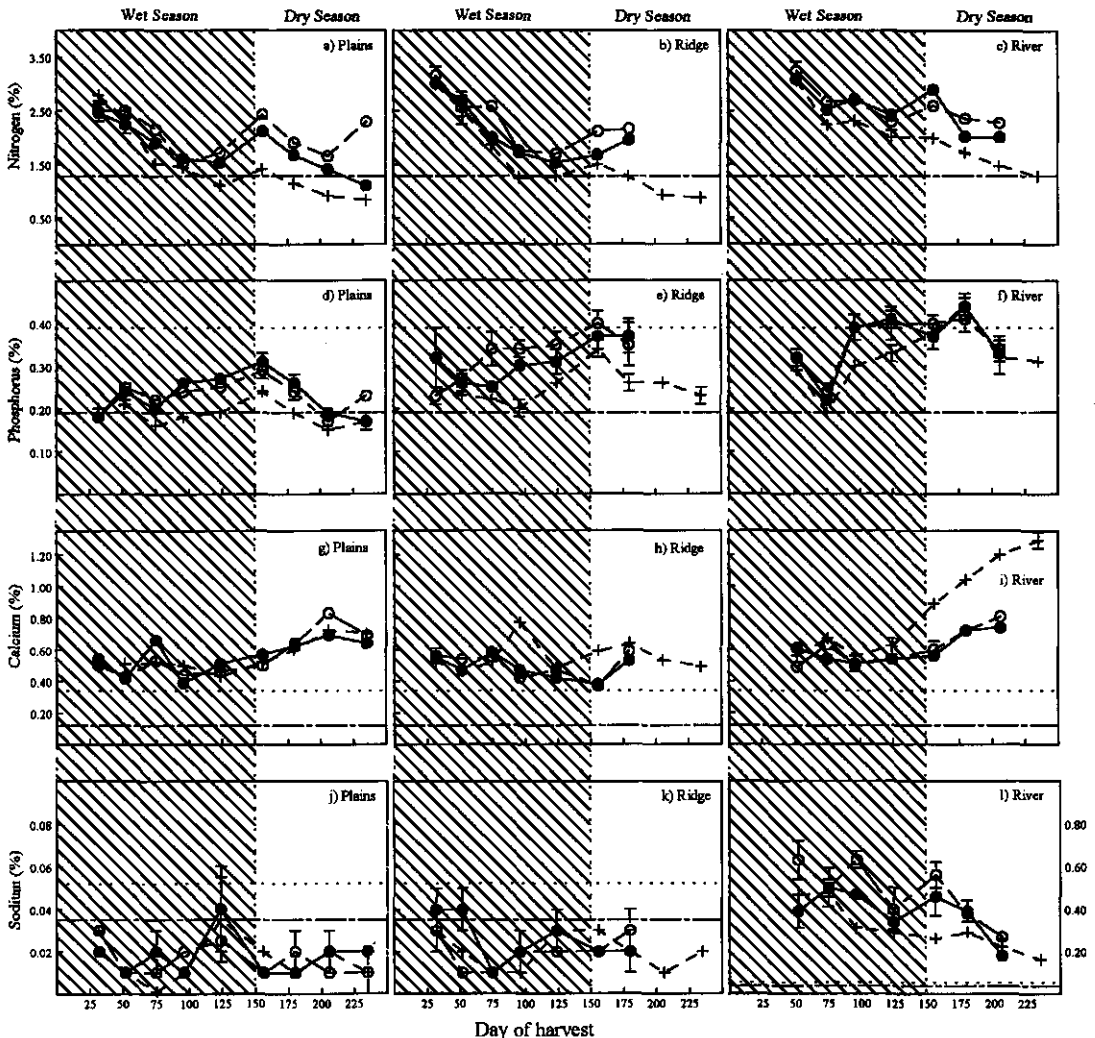


Figure 4. Concentration of Nitrogen (a,b,c), Phosphorus (d,e,f), Calcium (g,h,i) and Sodium (j,k,l) in green leaves in the Plains, Ridge and River site respectively for unclipped (+ — +), medium (●—●) and heavy clipped (O—O) treatments. Medium and heavy concentrations refer to the regrowth. No data are available for clipped treatments in the Ridge and River site at the end of the season due to lack of material. Minimum N requirement for maintenance (— — —) as well as minimum requirements of P, Ca and Na during pregnancy (— — —) and lactation (---) is indicated. Day of harvest as in Fig. 1.

levels than the unclipped plots (date x treatment interaction for medium-control in the River site: $F_{1, 71} = 23.26$, $P < 0.001$ and for heavy-control in the River site: $F_{1, 71} = 35.02$, $P < 0.001$). In the Ridge site, the heavy and medium clipped plots showed the same trends in time as the unclipped plots, since only the main effects of treatment were significant (for medium-control in the Ridge site: $F_{1, 68} = 7.42$, $P < 0.01$ and for heavy-control in the Ridge site $F_{1, 71} = 11.28$, $P < 0.01$). As with P, the medium and heavy clipped plots did not differ significantly in the concentration of Ca for all three sites investigated.

Clipping did not have a clear effect on the sodium (Na) concentrations in most sites and also no clear seasonal trends were found (Fig. 4j,k,l and Table 3). However, between sites large differences in grass leaf Na concentrations were observed. The River site had a ± 15 time's higher Na concentration as the Plains and Ridge site and also showed most differences between clipped and unclipped treatments. Pairwise comparisons showed that, only in the River site, clipped plots had higher Na concentrations and that Na concentrations decreased in the course of the season. This decrease was similar in all treatments since only the main effects were significant. (for heavy-control: $F_{1, 71} = 24.50$, $P < 0.001$, for medium-control $F_{1, 71} = 5.15$, $P < 0.05$ and for medium-heavy: $F_{1, 71} = 4.77$, $P < 0.05$). None of the other comparisons did differ significantly.

Consequences for herbivore forage availability and quality

Table 4 and Table 5 show that, when the animals do not graze in Tarangire National Park during the growing season (as is the present situation), they find upon their return to the park ample total standing biomass to satisfy their required consumption. However, under heavy grazing pressure during the growing season, as would be the case when the animals would stay year-round in Tarangire NP, and assuming that the herbivores only consume the green (live) biomass, the annual production of 211,000 ton/year is close to the total estimated consumption of 199,000 ton/yr.

The mineral requirements (see Fig. 4), show that the mineral concentrations in the plant material are not sufficient at all times to meet the animals' requirements (based on wildebeest requirements). In the wet season the females are lactating and have high mineral requirements,

Table 4. Estimates of the annual live and total above ground primary production on different soil types for Tarangire NP. Production was estimated for an ungrazed situation (based on the control plots) and for a medium and heavy grazed situation (based on the clipped plots, see also Fig. 2).

Soil description	Soil type area (km ²)	Ungrazed	Ungrazed	Medium grazed	Medium grazed	Heavy grazed	Heavy grazed
		Live prod. (ton/yr.)	Total prod. (ton/yr.)	Live prod. (ton/yr.)	Total prod. (ton/yr.)	Live prod. (ton/yr.)	Total prod. (ton/yr.)
Brownish loam soil (Plains)	632	277,000	396,000	176,000	248,000	136,000	146,000
Red loamy sand (Ridge-slope)	236	126,000	172,000	58,000	78,000	44,000	45,000
Light clay (Riverine)	96	88,000	98,000	32,000	37,000	31,000	32,000
Total	964	491,000	666,000	266,000	363,000	211,000	223,000

Table 5. Estimate of yearly dry matter intake by all large herbivores in Tarangire NP if they would be forced to stay in the Park. Population estimates for large herbivores were taken from aerial surveys of Tarangire NP (TWCM 1995ab). Body weight was taken for average adult animals from Estes (1991). % grass in diet of intermediate feeders was taken from Hofmann (1973), Drent & Prins (1987) and Estes (1991). Total dry matter intake per year was calculated as $(0.025 \text{ (in kg)} \times \text{body-weight} \times 365 \text{ (days)} \times \text{population} \times \text{proportion of grass in diet})/1000$.

species	Population numbers	Body weight (kg)	% of grass in diet	Total intake of grass for whole population (ton/yr.)
Grazers:				
Wildebeest	23,923	230	100	50,208
Zebra	29,835	240	100	65,339
Buffalo	5,321	630	100	30,589
Hartebeest	1,462	135	100	1,801
				sub total = 147,937
Intermediate feeders:				
Impala	2,973	55	95	1,417
Elephant	2,077	3,500	70	46,434
Grant's gazelle	1,311	40	40	191
Oryx	1,263	200	70	1,613
Eland antelope	438	475	65	1,234
				sub total = 50,890
				Total = 198,827

especially for phosphorus and calcium. The lactation period is approximately 3-6 months and in the beginning of the dry season the calves are weaned and mineral requirements drop to maintenance and pregnancy levels.

Clipping increased the nitrogen concentrations so that these were above maintenance levels for a longer period of time (Fig. 4a,b,c). Phosphorus levels were, however, continuously too low in the wet season when females are lactating (Fig. 4d,e,f). Calcium concentrations were well above or around lactation and pregnancy requirements throughout the wet and dry season (Fig. 4g,h,i). Sodium levels in the grasses in Plains and Ridge-slope soil types are too low for lactating and pregnant females but high enough in the Riverine soil types (Fig. 4j,k,l). For reasons of clarity, we did not include zebra requirements in Fig. 4. However, a zebra's nitrogen, phosphorus and sodium requirements are comparable to wildebeest's (Duncan 1990) while calcium requirements are slightly higher.

Discussion

East African savanna systems are well known for the large migratory herbivore populations. These populations, however, are increasingly being threatened by expansion of human activities in their migratory ranges, the wet season range in particular. Restricted access to the wet season range could have severe consequences for migratory population numbers since quality of ungrazed vegetation in the dry season range does not meet herbivore requirements (Chapter 4). However, it has long been recognized that through grazing herbivore forage quality and quantity can be enhanced (Vesey-FitzGerald 1960, McNaughton 1979, 1984, Georgiadis et al. 1989, Georgiadis & McNaughton 1990, Oesterheld & McNaughton 1991, Belsky 1987, Verkaar 1988, Belsky et al. 1993). Therefore, in this study, we questioned if grazing during the wet season in the dry season range of migratory herbivores in the Masai Ecosystem, Tarangire National Park, will improve herbage quality and quantity to levels that would be sustainable for current migratory herbivore numbers when migration routes to the wet season ranges were to be cut off.

Indeed, we found that grazing improved forage quality whereby the concentration of nitrogen and phosphorus in particular was enhanced. This positive effect of clipping on grass

leaf nitrogen and phosphorus concentrations can be partly explained by a reduced dilution, due to a lower biomass of standing plant material in the clipped treatments (Chapin & Van Cleve 1981, Wilson 1984, Rittenhouse & Roath 1987, Milchunas et al. 1995, Van de Vijver 1999). The younger age of leaves in the clipped treatments may also explain the higher tissue nutrient concentrations since nutrient concentrations decrease during ageing (McNaughton 1979, Georgiadis & McNaughton 1990, Van de Vijver 1999).

Nitrogen concentrations remained above maintenance requirements for a longer period of time through clipping but eventually also fell below the critical levels in the course of the dry season. In most semi-arid savanna systems, nitrogen concentration in the vegetation is well below maintenance levels during at least part of the dry season (Boutton et al. 1988, Prins 1996) and most animal species will use their reserves built up during the wet season (Chapter 6). So, the positive effect of grazing on nitrogen levels will delay the use of reserves and hence can be advantageous if the dry season is prolonged.

Although phosphorus concentrations were enhanced through clipping, they did not reach levels required by lactating females during the wet season. Short periods of limitation may be overcome by release of phosphorus that was previously stored in bones (Wallis de Vries 1996), but quantitative information on this is not yet available. Also Sodium concentrations, which were not consistently enhanced by clipping, remained below requirement levels, except for the River site where concentrations in all treatments were exceptionally high. Also for calcium concentrations no consistent clipping effects were found; here, however, concentrations were well above lactation requirements in all treatments and sites. Additional supplies of minerals by drinking (river)water (Chapter 4), soil consumption (Kreulen & Jager 1984) and licking on recently burned areas (Komarek 1969, Van de Vijver C.A.D.M. pers. obs.) may be important when nutrient concentrations in the vegetation are too low. Quantitative insight into the importance of these sources is however lacking. Since plant concentrations of phosphorus and sodium in Tarangire in the clipped treatments are, on average, still insufficient for lactating females, exclusive foraging on these grasses in the dry season range during the lactation period, the wet season, may result in repercussions for herbivore reproduction and survival of their young.

Quality parameters related to composition of vegetation material, such as the proportion of leaves and live material in the vegetation, were also higher in clipped treatments

as compared to the unclipped treatment (see also Coppock 1983, Hik & Jefferies 1990, Hamilton et al. 1998). This effect primarily was due to a larger build-up of stem and dead material in the unclipped treatment while regrowth after clipping primarily consisted of leaf material. Because of the increased proportion of leaves and live material, the most nutritious parts will be more readily available for herbivores. But, as discussed before, the mineral concentrations of leaf material, although higher than stem and dead material, were still not sufficient to meet the animals' requirements. Moreover, since our previous interpretation of forage quality was based on green leaf material and a herbivores diet also contains stem and dead material, the mineral intake will be even less and requirements will be even more difficult to meet than previously suggested.

Results of this study show that, for all three soil types investigated, clipping adversely affected forage quantity, with significantly lower annual production in both clipped treatments as compared to the unclipped control. Other studies have however shown that in semi-arid grazing systems grazed vegetation can compensate for the amount of material grazed and in some situations can even produce more than ungrazed vegetation (McNaughton 1979, Oosterheld & McNaughton 1991, Wegener & Odasz 1997). However, in this study no evidence of such (over)compensation was found.

Considering production of biomass in relation to herbivore consumption, Drent & Prins (1987) reported that 80 % of the above ground net primary production was being consumed by large herbivores in Manyara National Park in Tanzania. This figure seems exceptionally high (Prins 1989), and average consumption is more likely to be around 50 % (Lamprey 1983) or even lower (25 %), as was calculated for the Serengeti National Park (Prins 1989). Our own estimates show that, when the Park would not be grazed during the wet season, the estimated consumption by all large herbivores would be 20 % of the live annual production or 15 % of the total annual production (estimated consumption is hereby supposed to be half of that calculated in Table 5 since the animals would only graze for half of the year). Clearly, this is enough to satisfy the requirements as indeed the present-day situation shows. However, under a year-round medium grazing pressure, while consuming only the green biomass, the estimated consumption by large herbivores would already be 75 % of the estimated production. Moreover, since rainfall is a prime determinant of annual production and this research was performed in an exceptionally wet year (50 % above average), it may well be expected that the

annual production in a year of average rainfall will be lower and consequently herbivore forage availability will be even more limited.

This brings us to the central question posed in this study: can herbivore forage supply and quality in the dry season range of migratory herbivores be sufficiently enhanced through grazing to allow the current herbivore populations to reside year-round in the dry season range when access to the wet season range is cut off? Our data show that, although grazing in the dry season range during the wet season improved forage quality, both forage quantity and quality, phosphorus in particular, would not meet the herbivore's requirements. Here we should however consider the fact that no nutrient returns via dung or urine occurred in our experiment. This would be the case when the animals would graze year-round. Enhanced soil nutrient supply through dung and urine after grazing can contribute to increased nutrient concentrations and vegetation growth after grazing (McNaughton 1979, Georgiadis et al. 1989, Day & Detling 1990). It thus can be questioned if year-round nutrient input would have resulted in different conclusions regarding the effect of grazing on forage quality and quantity and the consequences for the migratory herbivores.

Since our experimental plots were situated on sites where large herds of ungulates congregate during the dry season, the deposition of nutrients through urine and accumulated faeces was high already. Moreover, Van de Vijver et al. (1999) found that in these relatively nutrient-rich savannas, where the majority of nutrients are below-ground, nutrient returns after biomass removal do not significantly contribute to enhanced nutrient status of regrowth. We therefore expect that additional nutrient returns via dung and urine will not lead to an additional increase in plant nutrient concentrations. If additional nutrient returns would have resulted in more regrowth after grazing can also be questioned, since we found that the most nutrient-rich site, the River site, showed least compensation after clipping as compared to the other sites investigated. We therefore postulate that increased input of nutrients through faeces and urine will not lead to higher vegetation production as compared to what we found in our experiment. Our production data are more likely to be higher than average due to the exceptionally wet year in which the experiment was performed, as was mentioned previously.

We conclude that if the current migratory populations of the Masai Ecosystem were to be confined to their dry season range year-round, their numbers would be negatively affected. Our conclusions are based on the short-term effects of simulated grazing on forage quantity

and quality and do not include the possible long-term changes, plant species composition amongst others. The latter deserves further attention. The present study does however clearly demonstrate that protection of migration routes and wet season grazing areas is essential to safeguard current migratory ungulate populations.

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References

- AFRC (1991). AFRC Technical Committee on Responses to Nutrient, Report 6. A. Reappraisal of the calcium and Phosphorus Requirements of sheep and cattle Nutrition Abstracts and Reviews (Series B), Vol. 61, No. 9 September 1991.
- Bell R.H.V. (1982). The effect of soil nutrient availability on community structure in African ecosystems. In: Huntley B.J. & Walker B.H. (eds.). Ecology of tropical savannas. Springer-Verlag, Berlin, pp193-216.
- Belsky A.J. (1987). The effects of grazing: confounding of ecosystem, community and organism scales. *American Naturalist* 129: 777-783.
- Belsky A.J., Carson W.P., Jensen C.L. and Fox G.A. (1993). Overcompensation by plants: herbivore optimisation or red herring? *Evolutionary Ecology* 7: 109-121.
- Borner M. (1985). The increasing isolation of Tarangire National Park. *Oryx* 19: 91-97.
- Boutton T.W., Tieszen L.L. and Imbamba S.K. (1988). Seasonal changes in the nutrient content of East African grassland vegetation. *African Journal of Ecology* 26: 103-115.

- Chapin F.S. and Van Cleve K. (1981). Plant nutrient absorption and retention under different fire regimes. In: Mooney H.A., Bonnicksen T.M., Christensen N.L., Lotan J.E. & Reiners W.A.(eds.). Proceedings of the conference: Fire regimes and ecosystem properties, December 11 – 15, 1978, Honolulu, Hawaii, pp301-326.
- Chuwa S. (1996). Tarangire National Park, vegetation species composition mapping, General report. New York Zoological Society.
- Coppock D.L., Detling J.K., J.E. Ellis & Dyer M.I. (1983). Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intra seasonal aboveground plant biomass and nutrient dynamics and plant species diversity. *Oecologia* 56: 1-9.
- Day T.A. & Detling J.K. (1990). Grasslands patch dynamics and herbivore grazing preference following urine deposition. *Ecology* 71: 180-188.
- Drent R.H. & Prins H.H.T. (1987). The herbivore as prisoner of its food supply. In: Van Andel J., Bakker J.P. & Snaydon R.W. (eds.). Disturbance in grasslands: species and population responses. Dr W Junk Publishers Co. Dordrecht, pp131-147.
- Duncan P. (1990). Horses and grasses; the nutritional ecology of equids and their impact on the Camargue, *Ecological studies* 87, Springer-Verlag, Berlin, 287p.
- Estes R.D. (1991). The behaviour guide to African mammals. The University of California Press, Berkeley, 611p.
- Fryxell J.M. & Sinclair A.R.E. (1988). Seasonal migration by white-eared kob in relation to resources. *African Journal of Ecology* 26: 17-31.
- Georgiadis N.J., Ruess R.W., McNaughton S.J. & Western D. (1989). Ecological conditions that determine when grazing stimulates grass production. *Oecologia* 81: 316-322.
- Georgiadis N.J. and McNaughton S.J. (1990). Elemental and fibre contents of savanna grasses: variation with grazing, soil type season and species. *Journal of Applied Ecology* 27: 623-634.
- Hamilton E.W., Giovannini M.S., Moses S.A., Coleman J.S. & McNaughton S.J. (1998). Biomass and mineral element responses of a Serengeti short-grass species to nitrogen supply and defoliation: compensation requires a critical [N]. *Oecologia* 116: 407-418.
- Happold D.C.D. (1995). The interactions between humans and mammals in Africa in relation to conservation: a review. *Biodiversity and Conservation*. 4: 395-414.

- Hilbert D.W., Swift D.M., Detling J.K. & Dyer M.I. (1981). Relative growth rates and the grazing optimisation hypotheses. *Oecologia* 51: 14-18.
- Hik D.S. and Jefferies R.L. (1990). Increases in the net above-ground primary production of a saltmarsh forage grass: a test of the predictions of the herbivore-optimisation model. *Journal of Ecology* 78:180-195.
- Hobbs N.T. (1996). Modification of ecosystems by ungulates *Journal of Wildlife Management* 60: 695-713.
- Hofmann R.R. (1973). The ruminant stomach vol. 2. East African Literature Bureau, Nairobi Kenya.
- Hofmann R.R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78: 443-457.
- Houba V.J.G., Novozamsky I., Huybregts A.W.M & Van der Lee J.J. (1986). Comparison of soil extracts by 0.01 M CaCl₂, by EUF and by some conventional extraction procedures. *Plant and Soil* 96: 433-437.
- Komarek E.V. (1969). Fire and animal behaviour. *Proceedings of the Tall Timbers and Fire Ecology Conference* 9: 161-207.
- Kreulen D.A. (1975). Wildebeest habitat selection on the Serengeti plains, Tanzania, in relation to calcium and lactation: a preliminary report. *East African Wildlife Journal* 13: 297-304.
- Kreulen D.A. and Jager T. (1985). The significance of soil ingestion in the utilization of arid rangelands by large herbivores. In: Gilchrist F.M.C. & Mackie R.I.(eds.). *Herbivore nutrition in the subtropics and tropics*. The Science Press, Johannesburg, pp204-221.
- Lamprey H.F. (1964). Estimation of the large mammal densities, biomass and energy exchange in the Tarangire Game Reserve and the Masai steppe in Tanganyika. *East African Wildlife Journal* 2: 1-46.
- Lamprey H.F. (1983). Pastoralism yesterday and today: the over-grazing problem. In Bourliere F. (ed.). *Tropical savannas*. Elsevier, Amsterdam, pp643-666.
- Le Houerou H.N., Bingham R.L. & Skerbek W. (1988). Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *Journal of Arid Environment* 15: 1-18.

- McNaughton S.J. (1979). Grazing as an optimisation process: grass-ungulate relationships in the Serengeti. *American Naturalist* 113: 691-703.
- McNaughton S.J. (1984). Grazing lawns: animals in herds, plant form and co-evolution. *American Naturalist* 124: 863-886.
- McNaughton S.J. (1990). Mineral nutrition and seasonal movements of African migratory ungulates. *Nature* 345: 613-615.
- Milchunas D.G., Varnamkhasti A.S., Lauenroth W.K. & Goetz H. (1995). Forage quality in relation to long-term grazing history, current-year defoliation and water resource. *Oecologia* 101: 366-374.
- Murray M.G. (1995). Specific nutrient requirements and migration of wildebeest In: Sinclair A.R.E. & Arcese P. (eds.). *Serengeti II: Dynamics, management and conservation of an ecosystem*. The University of Chicago Press, Chicago, pp231-256.
- Newmark W.D. (1996). Insularization of Tanzanian parks and the local extinction of large mammals. *Conservation Biology* 10: 1549-1556.
- Novozamsky I., Houba V.J.G., Van Eck R. & Van Vark W. (1983). A novel digestion technique for multi-elemental plant analysis. *Communications in Soil Science and Plant Analyses* 14: 239-249.
- Oosterheld M. and McNaughton S.J. (1991). Effect of stress and time for recovery on the amount of compensatory growth after grazing. *Oecologia* 85: 305-313.
- Pennycuik L. (1975). Movements of the migrating wildebeest population in the Serengeti area between 1960 and 1973. *East African Wildlife Journal* 13: 65-87.
- Prins H.H.T. (1987). Nature Conservation as an Integral Part of Optimal land use in East Africa: The case of the Masai Ecosystem of northern Tanzania. *Biological Conservation* 40: 141-161.
- Prins H.H.T. (1989). East African grazing lands: overgrazed or stably degraded? In: Verwey W.D. (ed.). *Nature Management and sustainable development, Proceedings of the international congress, IOS, Amsterdam, The Netherlands*, pp281-307.
- Prins H.H.T. (1992). The pastoral road to extinction: competition between wildlife and traditional pastoralism in East Africa. *Environmental Conservation* 19: 117-123.
- Prins H.H.T. (1996). *Ecology and behaviour of the African buffalo: social inequality and decision making*. Chapman and Hall, London, 293p.

- Rittenhouse L.R. and Roath L.R. (1987). Forage quality: primary chemistry of grasses. In: Capinera J.L. (ed.). Integrated pest management on rangeland -a shortgrass prairie perspective. West-view, Boulder, pp25-37.
- TWCM (1995a). Tanzania Wildlife Conservation Monitoring: Aerial Wildlife Census of Tarangire National Park, Wet and Dry Season 1994. Frankfurt Zoological Society, P.O. Box 3134, Arusha, Tanzania.
- TWCM (1995b). Tanzania Wildlife Conservation Monitoring and Tarangire Conservation project: Total count of buffalo and elephant in the Tarangire Ecosystem, September 1995. FZC/EC Report. TWCM/FZC, P.O. Box 3134, Arusha, Tanzania.
- Van Soest P.J. (1994). Nutritional ecology of the ruminant, second edition. Cornell University Press, Ithaca, New York, 476p.
- Van de Vijver C.A.D.M. (1999). Fire and life in Tarangire: the effects of burning and herbivory on an East African savanna system. PhD Thesis, Wageningen Agricultural University, The Netherlands.
- Van de Vijver C.A.D.M., Poot P. & Prins H.H.T. (1999). Causes of increased nutrient concentrations in post-fire regrowth in an East African savanna. Plant and Soil, in press.
- Van Wijngaarden W. (1985). Elephants-Trees-Grass-Grazers: relationships between climate, soils, vegetation and large herbivores in a semi-arid savanna ecosystem (Tsavo, Kenya). ITC Publication number 4, 159p.
- Verkaar H.J. (1988). Are defoliators beneficial for their host plants in terrestrial ecosystems ? - a review. Acta Botanica Neerlandica 37: 137-152.
- Vesey-FitzGerald D.F. (1973). Browse production and utilisation in Tarangire National Park. East African Wildlife Journal 11: 291-305.
- Wallis de Vries M.F. (1996). Nutritional limitations of free-ranging cattle: the importance of habitat quality. Journal of Applied Ecology 33: 688-702.
- Wegener C. & Odasz A.M. (1997). Effects of laboratory simulated grazing on biomass of the perennial Arctic grass *Dupontia fisheri* from Svalbard: evidence of overcompensation. Oikos 79: 496-502.
- Williamson D., Williamson J. & Ngwamotsoko K.T. (1988). Wildebeest migration in the Kalahari. African Journal of Ecology 26: 269-280.

Wilson J.R. (1984). Environmental and nutritional factors affecting herbage quality. In: Hacker J.B. (ed.) Nutritional limits to animal production from pastures. Commonwealth Agricultural Bureaux , Slough, pp111-131.

**THE POTENTIAL FOR COMPETITION BETWEEN
WILD HERBIVORES AND LIVESTOCK IN THE
MASAI ECOSYSTEM**

Margje M. Voeten

Abstract

This paper presents a case study on the potential of competition between wildlife (wildebeest and zebra) and livestock (Zebu-cattle) in the Masai Ecosystem in Northern Tanzania. Overlap both in habitat and in diet between wildlife and livestock was studied in combination with food availability and food requirements. In addition, body condition of a wildebeest population co-occurring with livestock and one isolated from livestock was compared. We found a large overlap in diet and habitat during the wet season and we found that resources are limited. Hence, a large potential for competition between wildebeest, zebra and cattle is inferred. Zebra and cattle showed most overlap and wildebeest and zebra least. Although the necessary conditions for competition to occur are met, it is concluded that, in this special case wildlife is able to avoid competition during the dry season because they move then to areas where cattle do not have access. They do not move, however, because of competition but because of differences in resource availability between areas.

Key words: *habitat and dietary overlap; faecal analysis; body condition; food requirements; ungulates*

Introduction

Many of the savanna systems in East Africa are dominated by pastoral economies, which share the same resources with abundant and diverse wildlife populations. Many authors have stated that pastoralists have been able to live in a harmonious relationship with their environment for centuries without severely affecting vegetation and wildlife (Osemeobo 1988, ole Parkipuny 1989, Homewood & Rodgers 1991). In the last decades however, it has become recognised that livestock populations are an important factor in the ecological degradation prevailing in many of the arid and semi-arid grazing lands of the world (UNEP 1977, Lamprey 1983, Prins 1989). This will clearly not only affect human subsistence, but also the survival of wildlife in unprotected areas, where wildlife still coexists with livestock. Already, it has been observed that in areas with increased livestock numbers, wild herbivore populations are decreasing (Ecosystems LTD 1980, Prins 1992, Happold 1995). Research on the effects of increased pastoralism has mainly been focused on the influence exerted by livestock on vegetation and the consequences for habitat (Werger 1977, leHouérou 1989, de Bie 1991). Loss of habitat and deterioration of habitat conditions may eventually lead to a decrease in wildlife numbers (and livestock). However, little is known about the role of competition for resources between wildlife and livestock and how this affects the coexistence of wildlife and livestock. The introduction of an exotic species in a native faunal assemblage may cause strong competitive interactions and since livestock did not evolve in Africa south of the Sahara, livestock can be viewed as such an exotic species and hence there is reason for concern about competition between wildlife and livestock (Voeten & Prins 1999).

For the occurrence of interspecific competition the following conditions must be met: the species must show an overlap in habitat and in diet and resources must be limited (Wiens 1989). In addition, as a consequence either of exploitation of a shared resource or of interference related to that resource, competition has a negative effect on fitness related characteristics of at least one species. Very few studies have actually measured overlap in habitat and diet between wildlife and livestock in East-Africa. These studies concentrated on dietary overlap (Casebeer & Koss 1970, Hoppe et al. 1977) or on overlap in habitat (Fritz et al. 1996, Machange 1997), but not in combination with availability of resources and requirements of the species involved. This study, however, considered overlap, both in habitat and in diet between wildlife and livestock and resource availability and presents a case study

on competition between wildlife and livestock in the Masai Ecosystem, located in Northern Tanzania. Here, large herds of wildebeest (*Connochaetes taurinus*) and plains zebra (*Equus burchelli*), coexist with livestock, especially cattle (*Bos indicus*). Overlap in habitat and diet between these species was determined. We also studied diet quality and estimated forage production and food requirements for a wildlife population within a National Park isolated from livestock, and for wildlife populations co-occurring with livestock. Finally, we studied possible consequences of this overlap and resource availability by comparing the body condition of two populations of wildebeest: inside and outside a National Park.

Study area

Data were collected in the Mto-wa-Mbu Game Controlled Area (GCA) and Lake Manyara National Park (NP), both located in Northern Tanzania within the eastern part of the Great Rift Valley. The Mto-wa-Mbu GCA (lat. 3°35' S, long. 35°55' E, 1000 m above sea level) is an area of about 720 km² and used by traditional Masai and Warusha pastoralists for livestock grazing, small scale agricultural activities and firewood collection. The area is also used as a wet season range by wildebeest and plains zebra from the nearby Tarangire NP and Lake Manyara NP (Chapter 2). Resident game, such as giraffe (*Giraffa camelopardalis*), Grant's gazelle (*Gazella granti*) and Thomson's gazelle (*Gazella thomsonii*) are the next most abundant species (Chapter 2). African elephant (*Loxodonta africana*) and African buffalo (*Syncerus caffer*), still occurred in considerable numbers before the nineties (H.H.T. Prins, pers.com), but are very rare nowadays. Most large herbivores are found on the extensive grasslands and flood plains, which are dominated by grass species such as *Brachiaria xantholeuca*, *Cenchrus ciliaris*, *Chloris* spp., *Dactyloctenium aegypticum*, *Odysea jaegeri*, *Panicum* spp., *Pennisetum mezianum* and *Sporobolus* spp. (M.M. Voeten, unpub. data).

Lake Manyara NP (lat. 3°30' S, long. 35°45' E, 1000 m a.s.l.) consists of a narrow strip of land (100 km²) situated between Lake Manyara and the steeply rising escarpment of the Rift Valley. Most abundant large herbivores include wildebeest, zebra, elephant, buffalo and impala (*Aepyceros melampus*), while Grant's and Thomson's gazelle do not occur in this Park. Livestock do not have access to the Park. The wildebeest and zebra populations here are partly sedentary and partly migratory. The park is characterised by open grasslands along the lake dominated by

Sporobolus spicatus and *Cynodon dactylon* and woodlands further away from the lake (Loth & Prins 1987).

The average yearly rainfall for both areas is 650 mm (Prins & Loth 1988) and two seasons can be distinguished. During the wet season (November to May) rainfall is highly variable and erratic. During the dry season (June to October) rainfall is very rare.

Methods

Habitat preference and overlap in habitat

Animal road counts (Prins et al. 1994) were conducted from November 1994 until September 1995 in both the Mto-wa-Mbu GCA and Lake Manyara NP, using the road's network of these areas. Each road was driven two to three times per month and all animal groups that were spotted were recorded. Records were made of species, number of animals in the group, habitat type (see below), distance to the road, road name, date and time. In Lake Manyara NP 1561 km was driven and 1868 observations were made. In the Mto-wa-Mbu GCA only the Northern part was sampled, an area of 440 km². Here a total of 2521 km was driven and 1278 observations were made. Observations were made on all wild herbivores heavier than about 20 kg, including Thomson's gazelle but excluding hippopotamus (*Hippopotamus amphibius*). In the Mto-wa-Mbu GCA also groups of cattle, sheep and goats were observed. The latter two species often occur in mixed herds and are difficult to distinguish at a distance: therefore, data on sheep and goats were collected indifferently of the herd composition and are referred to as shoats.

Habitat types were defined on basis of vegetation types (grassland, wooded grassland, wooded bush, forest, etc.) and delineations based on percentage cover by woody species, according to Loth & Prins (1987). Habitat preference was calculated for cattle, wildebeest and zebra by means of Ivlev's electivity index (Ivlev 1961):

$$E_i = \frac{r_i - n_i}{r_i + n_i}$$

where E_i = Ivlev's electivity measure for species i , r_i = percentage of habitat type i selected and n_i = percentage of habitat type i of the total surface area. Values of electivity between 0 and +1

indicate preference and values between 0 and -1 indicate avoidance. The advantage of Ivlev's measure is that several habitat types can be included. The surface areas of the different habitat types for Lake Manyara NP were taken from Prins & Iason (1989) and for the Mto-wa-Mbu GCA from TWCM (1995a). Preference was calculated per month and for the whole year. Since the preference indexes did not change during the different months, only the preference over the whole year will be presented in this paper.

Overlap in habitat was calculated with Pianka's (1973) formula:

$$O_{jk} = \frac{\sum (P_{ij} * P_{ik})}{\sqrt{[\sum (P_{ij}^2) * \sum (P_{ik}^2)]}}$$

Where O_{jk} = Pianka's measure of niche overlap between species j and k , p_{ij} = proportion resource i of the total resources used by species j , p_{ik} = proportion resource i of the total resources used by species k and n = total numbers of resource states. This measure of overlap ranges from 0 (no resources used in common) to 1 (complete overlap). Overlap in habitat between animal species was determined for the beginning of the wet season (January), the middle of the wet season (April) and the beginning of the dry season (July).

Overlap in diet and diet quality

Data on diet composition were obtained by identifying plant epidermis fragments in the faeces and data on diet quality by determining the faecal protein. Wildebeest, zebra and cattle faeces were collected in both areas from November 1994 until September 1995. We collected 10-15 samples per area, per month, per species. Each sample was made up by grab samples from 3-4 fresh dung piles. Faeces were air-dried, grounded through a 2-mm mesh mill and stored until further analysis. For identifying the epidermis fragments, methods by Stewart (1967) and by de Jong et al. (1995) were used. Of each faecal sample, a 1.5 gram sub-sample was taken, boiled for one hour and washed for one minute in a Waring blender to separate epidermis/cuticle fragments from underlying parenchym tissue. The washed sample was then poured over a 0.01 mm sieve and stored in 60%-70% ethanol. Each sample was mounted on a microscopic slide and 100 plant fragments per sample were examined, identified and measured under 100-400 X magnification. 100 identified fragments per sample should suffice

to find plant species, which account for more than 5 % of the diet (Stewart 1967). Identification of the plant species was facilitated by making a reference collection of the most abundant grass species from both areas (i.e., the stem, adaxial and abaxial sides of leaf and leaf sheath and the inflorescence). Dietary overlap between animal species was determined for the beginning of the wet season (January), the middle of the wet season (April) and the beginning of the dry season (July) by also using Pianka's measure of niche overlap.

Faecal nitrogen was determined after a modified Kjeldahl analysis (Novozamsky et al. 1983) and N concentrations were measured colorimetrically using a continuous-flow analyser (Skalar SA-4000). Faecal crude protein (%FCP) was calculated as $6.25 \times \%N$ in faeces and dietary crude protein (%DCP) was derived with the following formulas:

For wildebeest: $\%DCP = 2.61 \times \%FCP - 11.90$ (Sinclair 1977, p234)

For zebra: $\%DCP = 1.09 \times \%FCP - 0.32$ (Duncan 1992, p242).

Dietary crude protein was calculated per month and seasonal changes were analysed per animal species using a covariance analysis with area (Mto-wa-Mbu GCA or Lake Manyara NP) as the independent factor and month as the co-variate. Since, we were mainly interested in differences in the course of the season, data were analysed from January onwards (i.e., November and December were not included)

Population size estimates

Population sizes of the different species were estimated by means of the stratified random sampling method (Norton-Griffiths 1978, Prins & Weyerhaeuser 1987) from the data on animal numbers collected during the road counts. Roads were considered as transects with a fixed width, depending on the visibility in the different vegetation types along the roads. Visibility per vegetation type was based on Prins & van der Jeugd (1993) who worked in the same area. Per stratum (i.e. vegetation type) and animal species the density per km² was calculated as the sum of observed animals divided by the sampled area (km driven x transect width). Total population size was estimated by multiplying the density with the total surface area of the vegetation type and by summing these up for the different vegetation types. It is acknowledged that road counts are not the ideal way of counting animals with a clumped distribution (Norton-Griffiths 1978). Therefore, for elephant and buffalo we used data on total counts (TWCM 1995b) and we conducted total counts for wildebeest along the lakeshore by

car. Population estimates were calculated for April and for November which are representative of respectively the wet and dry season.

Annual grass production, grass quality and forage requirements

Annual grass production was estimated by using peak-standing crop measurements (McNaughton et al.1996). In Lake Manyara NP and the Mto-wa-Mbu GCA, vegetation was sampled in June 1995 at the end of the growing season. In each area, 3 sites were sampled per vegetation type and at each site five 1 m x 1 m frames were harvested. It was assumed that peak-standing crop is 70% of the annual production (Ketner 1972). Total annual production was then calculated by multiplying the standing crop per vegetation type and the surface area of the vegetation types, and by summing these up for the different vegetation types. It is realised that this is an approximate way of estimating the annual production. However, when comparing these production data to Prins (1996) and Chapter 5, which refer to measurements of annual production in the same area, it was found that results were very similar.

The vegetation was hand-sorted into green leaf, green stem and dead material, air-dried and weighed. Total nitrogen and phosphorus concentration in leaves was determined after a modified Kjeldahl analysis (Novozamsky et al. 1983). Nitrogen and phosphorus concentrations were measured colorimetrically, using a continuous-flow analyser (Skalar SA-4000). Neutral detergent fibre (NDF) was determined according to Goering and Van Soest (1970). Grass quality was only analysed for the grasslands, which was the habitat type most used by the animals. Differences in grass quality between areas were tested with a one-way analysis of variance after arcsine-transformation.

Total food intake requirements of all large herbivore species were estimated by multiplying the individual intake requirements by the herbivore population numbers. The intake requirements were estimated, assuming an average daily intake of dry matter of 2.5 % of a herbivore's bodyweight (van Wijngaarden 1985, p102). Grass intake of the intermediate feeders (Hofmann 1989), such as elephant and Grant's gazelle, were taken from Hofmann (1973), Drent & Prins (1987) and Estes (1991).

Body condition

Video recordings were made of both the wildebeest population in the Mto-wa-Mbu GCA and in Lake Manyara NP in July and November 1995. July can be considered as the end of the wet season (or beginning of the dry season), when most of the animals are in prime condition. November is the end of the dry season and the animals have been using their body reserves during the dry season, since during this period forage availability is limited. The video-recordings were viewed on a regular television screen and each adult animal, which was clearly visible, was appointed a condition score. Five classes of body condition were distinguished, based on Prins (1988) and adapted for wildebeest by the author and H.H.T. Prins:

- 1.0 very poor : haunch muscle and abdominal cavity concave, spinal ridge and ribs visible
- 2.0 poor : haunch muscle concave, abdominal cavity less concave as 1, ribs just visible
- 3.0 moderate : haunch muscle straight, abdominal cavity not concave, ribs not visible
- 4.0 good : body contours convex, haunch muscle convex
- 5.0 very good : body contours and haunch muscle more convex than 4, rump muscle convex

In the analysis of the body condition, the index values (1,2,3 etc.) of the condition scores were used. These index values were treated as ordinary numerical values since there is a linear relationship between body condition scores and percentage fat in Bovini (Herd & Sprott 1986, Prins 1988). The index values were log-transformed to adjust for deviations of normality and to improve homogeneity of variance. Differences in body condition between areas and seasons were tested with a two-way analysis of variance followed by Tukey's HSD contrasts.

Results

Cattle, wildebeest and zebra all preferred the open grasslands (Table 1) of the Mto-wa-Mbu GCA. Wildebeest avoided habitat types with a higher cover by shrubs while cattle and zebra only avoided wooded bush grassland and wooded bush and not so much the bushed grasslands. Similar habitat preferences were also illustrated by the large amount of habitat overlap (Table 2). Cattle-zebra showed a consistent high overlap in habitat in all three seasons. Cattle-wildebeest and zebra-wildebeest showed less overlap, which in addition decreased as the season progressed.

Overlap in diet was based on 16 grass species of which the epidermis could be determined in the faeces. *Sporobolus spp.* and *Chloris spp.* were the two most common genera found in the faeces, respectively 33% and 22% of the identifiable fragments and dicots made up less than 3%. Most overlap in diet was found for cattle-zebra (Table 2) and least for cattle-wildebeest and zebra-wildebeest. Seasonal differences were not apparent for cattle-zebra while overlap for cattle-wildebeest and zebra-wildebeest tended to increase as the season progressed.

Table 1. Habitat preference of wildebeest, zebra and cattle in the Mto-wa-Mbu Game Controlled Area, indicated by means of Ivlev's electivity index E_i . Habitat types are classified based on % cover by shrubs. E_i with values between 0 and +1 indicate preference and values between 0 and -1 indicate avoidance.

Habitat type	Cover by shrubs	E_i Wildebeest	E_i Zebra	E_i Cattle
Grassland	2 %	0.59	0.30	0.33
Wooded bush grassland	8 %	-0.28	-0.36	-0.26
Bushed grassland	10 %	-0.76	0.02	-0.06
Wooded bush	18 %	-0.91	-0.72	-0.47

Table 2. Seasonal overlap in habitat and diet of wildebeest, zebra and cattle in the Mto-wa-Mbu Game Controlled Area by means of Pianka's measure of overlap. Values range from 0 (no overlap) to 1 (complete overlap). Habitat types are classified based on % cover by shrubs. Overlap in diet was based on 16 grass species, of which epidermis fragments could be identified in faeces.

Season	Cattle- Wildebeest		Cattle-Zebra		Wildebeest-Zebra	
	Habitat	Diet	Habitat	Diet	Habitat	Diet
Early wet	0.83	0.83	0.88	0.98	0.82	0.76
Wet	0.65	0.91	0.96	0.96	0.71	0.99
Early dry	0.68	0.97	0.91	0.98	0.40	0.98

When comparing the diet quality of wildebeest and zebra in the Mto-wa-Mbu GCA and in Lake Manyara NP (Fig1) on the basis of the faecal protein, it was found that the decrease in dietary crude protein from January onwards was slightly stronger in the Mto-wa-Mbu GCA than in Lake Manyara NP (area x month interaction for wildebeest: $F_{1, 318} = 4.46$, $P < 0.05$ and for zebra: $F_{1, 287} = 7.44$, $P < 0.05$) but main significant differences between areas were not found. Dietary crude protein was around requirement levels for both wildebeest and zebra in the driest months (July-October) in both areas. However, the percentage nitrogen in the green leaves of the vegetation, the leaf-stem ratio and the live-dead ratio, were significantly lower in the Mto-wa-Mbu GCA at the beginning of the dry season (Table 3), while no significant differences were found between percentages phosphorus and fibre.

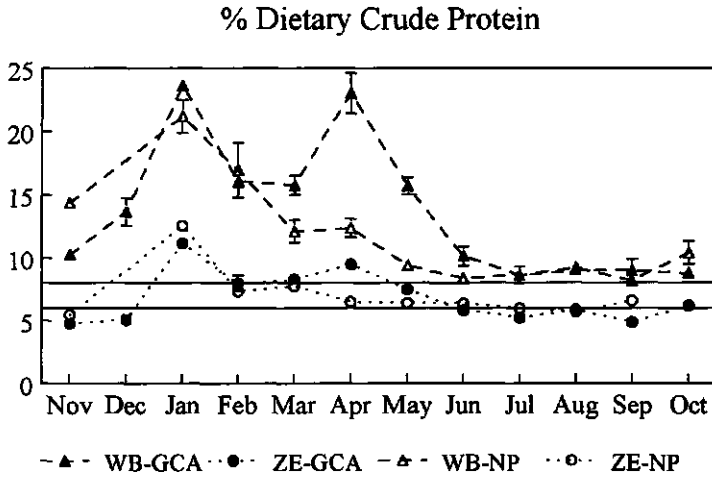


Figure 1. Mean dietary crude protein \pm 95 % confidence levels of wildebeest (WB) and zebra (ZE) in the Mto-wa-Mbu Game Controlled Area (GCA) and Lake Manyara National Park (NP). Horizontal lines indicate maintenance levels of crude protein for wildebeest (8 %) and for zebra (6 %).

Table 3. Forage quality parameters for the Mto-wa-Mbu Game Controlled Area (GCA) and Lake Manyara National Park (NP) at the beginning of the dry season (June). Values are means \pm 95 % confidence limits. Different letters denote significant differences, $P < 0.01$.

Forage quality parameters	Game Controlled Area	Manyara National Park
% Nitrogen	1.35 ^a \pm 0.14	2.00 ^b \pm 0.22
% Phosphorus	0.33 ^a \pm 0.04	0.25 ^a \pm 0.03
% Fibre	76.50 ^a \pm 1.08	77.49 ^a \pm 1.03
Leaf-stem ratio	0.51 ^a \pm 0.05	0.63 ^b \pm 0.06
Live-dead ratio	2.05 ^a \pm 0.12	3.03 ^b \pm 0.16

Table 4. Estimated populations size of all large herbivores from the Mto-wa-Mbu Game Controlled Area. Body weight (BW) was taken for average adult animals from Estes (1991). % grass in diet as indicated in brackets behind species name, was taken from Drent & Prins (1987), Estes (1991) and Hofmann (1973). Food requirements per season were calculated as $(0.025 \text{ (in kg)} \times \text{body-weight} \times 183 \text{ (days)} \times \text{population} \# \times \text{proportion of grass in diet})/1000$. Herbivore biomass density was calculated as $(\text{population} \# \times \text{BW})/440 \text{ km}^2$. For estimation of annual production see methods.

Season	Population size		BW (kg)	Requirements (ton/yr)		Herbivore biomass (kg/km ²)	
	Wet	Dry		Wet	Dry	Wet	Dry
Cattle (90%)	6,049	10,213	225	5,589	9,436	3,093	5,223
Shoats (40%)	2,967	6,952	20	108	254	135	316
Impala (95%)	177	157	55	42	37	22	20
Wildebeest (100%)	3,379	280	230	3,546	294	1,766	146
Zebra (100%)	2,026	526	240	2,219	576	1,105	287
Thomson's Gazelle (90%)	541	1,094	20	44	90	25	50
Grants gazelle (40%)	226	90	40	17	7	21	8
Sum :				11,564	10,693	6,167	6,049
Total requirements per year ton/yr:				22,258			
Estimated production (ton/yr):				201,115			

Table 5. Estimated populations size of all large herbivores from Lake Manyara National Park. Body weight (BW) was taken for average adult animals from Estes (1991). % grass in diet as indicated in brackets behind species name, was taken from Drent & Prins (1987), Estes (1991) and Hofmann (1973). Food requirements per season were calculated as $(0.025 \text{ (in kg)} \times \text{body-weight} \times 183 \text{ (days)} \times \text{population} \# \times \text{proportion of grass in diet})/1000$. Herbivore biomass density was calculated as $(\text{population} \# \times \text{BW})/100 \text{ km}^2$. For estimation of annual production see methods.

Season	Population size		BW (kg)	Requirements (ton/yr)		Herbivore biomass (kg/km ²)	
	Wet	Dry		Wet	Dry	Wet	Dry
Impala (95%)	435	435	55	104	104	239	239
Wildebeest (100%)	179	3,307	230	188	3,470	412	7,606
Zebra (100%)	229	440	240	251	482	550	1,056
Buffalo (100%)	1,010	1,010	630	2,903	2,903	6,363	6,363
Elephant (70%)	261	261	3,500	2,918	2,918	9,135	9,135
Warthog (90%)	75	75	75	23	23	56	56
Sum :				6,386	9,900	16,755	24,456
Total requirements per year (ton/yr) :				16,286			
Estimated production (ton/yr) :				25,706			

The seasonal movements of wildebeest, zebra but also cattle and shoats are clearly reflected in the population sizes for the Mto-wa-Mbu GCA and Lake Manyara NP. Wildebeest and zebra numbers are highest in the Mto-wa-Mbu GCA during the wet season (Table 4); their numbers are much smaller during the dry season, while a larger number of especially wildebeest is observed in Lake Manyara NP during the dry season (Table 5). This corresponds with the observation that in the beginning of the wet season (January) large herds of wildebeest and zebra first appear in the Mto-wa-Mbu GCA, while their numbers there decrease again at the beginning of the dry season (June/July), at the same time an influx of wildebeest is observed in Lake Manyara NP. Cattle and shoats disperse over a larger area during the wet season and concentrate again in the Mto-wa-Mbu GCA during the dry season (Table 4). Although large differences between seasons in numbers of wildebeest, zebra, cattle and shoats were found, the combined forage requirements of all species are similar during the wet and dry season in the Mto-wa-Mbu GCA (Table 4) while in Lake Manyara NP forage requirements during the dry season increase (Table 5). The total forage requirements of all large herbivores in the Mto-wa-Mbu GCA are only 12 % of the estimated annual production. In Lake Manyara NP, the total forage requirements of all large herbivores are 73 % of the estimated annual production. This much higher consumption in Lake Manyara NP is also illustrated by calculating the herbivore biomass per km², which is 2.5 as high in Lake Manyara NP as in the Mto-wa-Mbu GCA during the wet season and 4 times as high during the dry season.

At the beginning of the dry season, wildebeest in both the Mto-wa-Mbu GCA and Lake Manyara NP had the same body condition, which was classified as good (Fig 2). Body condition decreased during the dry season but more so in the Mto-wa-Mbu GCA than in Lake Manyara NP (area x season interaction: $F_{1, 19} = 11.46$, $P < 0.01$). At the end of the dry season body condition was classified as between moderate and good.

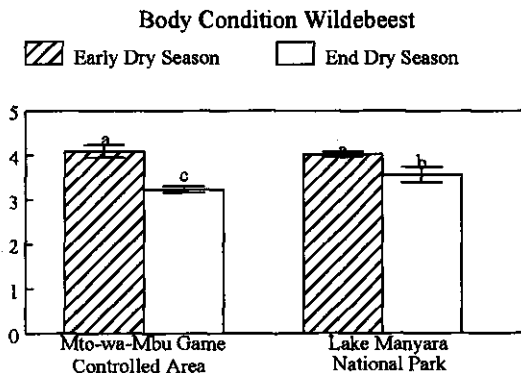


Figure 2. Mean body-condition \pm 95 % confidence levels of wildebeest in the Mto-wa-Mbu Game Controlled Area (GCA) where they co-occur with cattle and in Lake Manyara National Park (NP) where they are isolated from cattle. Different letters denote significant differences $P < 0.05$.

Discussion

The aim of this study was to explore the potential of competition between wildlife and livestock by determining overlap in habitat and diet and studying resource availability and forage requirements. Furthermore we looked for evidence of competition by comparing body condition of wildlife (in this case wildebeest) co-occurring with livestock and isolated from livestock. We found large overlap between cattle, wildebeest and zebra in diet as well as in habitat. Forage availability seemed to be larger than the demands (but see further discussion) and data on dietary crude protein showed that throughout the year levels are above or around maintenance requirements. However, differences in body condition between wildebeest co-occurring with cattle and isolated from cattle, in combination with distribution patterns, implies that competitive relationships may exist.

Prins (1999), in an extensive review on competition between wildlife and livestock in Africa, concluded that, although information on competition is scarce, wildlife numbers are negatively affected by livestock numbers due to human activities and to denial of access to resources. Voeten & Prins (1999, Chapter 3) by studying the overlap in resource use by comparing the feeding sites of wildebeest, zebra and Zebu-cattle co-occurring in the same area, also concluded that there was a strong potential for competition.

When co-occurring species are similar in feeding habits, like the species studied, a large overlap in habitat and diet can be expected. Interestingly, cattle and zebra showed consistently most overlap in habitat and diet and wildebeest and zebra least, resulting in less potential for competition between the native species (see also Voeten & Prins 1999, Chapter 3). However, when resources became scarcer, overlap in habitat decreased between wildebeest-zebra and cattle-wildebeest but overlap in diet increased, implying that the species still select similar diets but avoid each other by foraging in different habitats.

The potential for competition however, further depends on, resources being limited or not. Our estimates of forage production and requirements in the Mto-wa-Mbu Game Controlled Area show that production is ample as compared to requirements. However, the production of the Mto-wa-Mbu GCA is so much larger than what is actually consumed by the animals that at the end of the growing season most of the standing biomass turns into dead standing crop (pers.obs). Hence, although forage quantity may satisfy the requirements, forage quality may not. This is substantiated by the finding that nitrogen levels in the

vegetation at the end of the growing season are just above maintenance levels and that also dietary crude protein is just above maintenance requirements during the dry season. We conclude that resources are limited at the beginning of the dry season or become so during the dry season in the Mto-wa-Mbu GCA. Thus, all conditions for competition to occur between wildlife and livestock are met. It is questionable however, if this also actually leads to competitive interactions.

In Lake Manyara National Park, due to a high grazing pressure (see also Drent & Prins 1987) the vegetation is maintained at a young productive growth stage and can be considered a grazing lawn (McNaughton 1984). The high grazing pressure in Lake Manyara NP during the wet season results in higher leaf/stem ratio's, live/dead ratio's and higher nitrogen levels as compared to ungrazed (Chapter 5) or, in this case, undergrazed vegetation as in the Mto-wa-Mbu GCA. In addition, upwelling groundwater in Lake Manyara NP results in vegetation of higher forage quality (Prins 1996). These differences in forage quality become most apparent at the beginning of the dry season and are likely to consolidate during the rest of the dry season. At this time of the year, wildebeest and zebra start to leave the Mto-wa-Mbu GCA and move to Lake Manyara NP. Assuming that the animals distribute themselves in an ideal free manner (Fretwell & Lucas 1970, Parker 1970), the highest animal densities are expected in Lake Manyara NP because of the higher forage quality: and this is indeed what we found. We postulate that wildebeest and zebra, by moving to Lake Manyara NP, are able to avoid competition. Finally, Lake Manyara NP will reach its limits so that a further increase of immigrants will not result in benefits for the newcomers anymore. The wildlife which then remains in the Mto-wa-Mbu GCA is confronted with the presence of cattle, limited resources and very probably competition. This might explain why we found a difference in body-condition between wildebeest of the Mto-wa-Mbu GCA and Lake Manyara NP at the end of the dry season.

We conclude that there is a large potential for competition between wildebeest, zebra and cattle but that wildlife is able to avoid competition during the dry season when moving to other areas, not because of competition but because of a difference in forage availability. Understanding competitive relationships between wildlife and livestock requires that large-scale movements be taken into account. In the Masai-Ecosystem, such movements of wild herbivores occur between protected areas such as Lake Manyara National Park, Tarangire National Park and surrounding areas which are dominated by livestock. One could argue that

since the National Parks are not accessible for livestock, livestock in fact is negatively affected by wildlife or more precisely, by conservation laws. However, the exclusive use of the National Parks by wildlife is necessary to survive the dry season. We think that if livestock would be allowed to graze in such protected areas this would result in competition between wildlife and livestock.

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References

- Casebeer R.L. & Koss G.G. (1970). Food habits of wildebeest, zebra, hartebeest and cattle in Kenya Masailand. *East African Wildlife Journal* 8: 25-36.
- Ecosystems Ltd (1980). Livestock, wildlife and landuse, survey in the Arusha region Tanzania. Final report (3 volumes). Ecosystems Ltd, Nairobi.
- De Bie S. (1991). Wildlife resources of the West African Savanna. PhD-thesis, Agricultural University of Wageningen, the Netherlands.
- De Jong C.B., Gill R.M.A., Van Wieren S.E. & Burlton F.W.E. (1995). Diet selection by roe deer (*Capreolus capreolus* L.) in Kielder forest in relation to plant cover. *Forrest Ecology and Management* 79: 91-97.
- Drent R.H. & Prins H.H.T. (1987). The herbivore as prisoner of its food supply. In: Van Andel J., Bakker J.P. & Snaydon R.W. (eds.). *Disturbance in grasslands: species and population responses* Dr W Junk Publishers Co. Dordrecht, pp131-147.

- Duncan P. (1992). Horses and grasses; the nutritional ecology of equids and their impact on the Camargue, Ecological studies 87, Springer-Verlag.
- Estes R.D. (1991). The behaviour guide to African mammals. The University of California Press, Berkeley.
- Fretwell S.D. & Lucas H.L. (1970). On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheorica* 19:16-36.
- Fritz H., De Garine-Wichatitsky M. & Letessier G. (1996). Habitat use by sympatric wild and domestic herbivores in an African savanna woodland: the influence of cattle spatial behaviour. *Journal of Applied Ecology* 33: 589-598.
- Goering H.K. & Van Soest P.J. (1970). Forage fiber analyses (apparatus, reagents, procedures and some applications). Agric. Handb. No.379, Agric.Res.Serv. Washington.
- Happold D.C.D. (1995). The interactions between humans and mammals in Africa in relation to conservation: a review. *Biodiversity and Conservation* 4: 395-414.
- Herd D.B. & L.R. Sprott (1986). Body condition, nutrition and reproduction of beef cows. Texas agricultural extension service, B-1526. Texas A&M University System, College Station (Texas).
- Hofmann R.R. (1973). The ruminant stomach vol. 2. East African Literature Bureau, Nairobi Kenya, 354p.
- Hofmann R.R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78:443-457.
- Homewood K.M. & Rodgers W.A. (1991). Maasailand ecology: pastoral development and wildlife conservation in Ngorongoro, Tanzania. Cambridge University Press, Cambridge, 298p.
- Hoppe P.P., Qvortrup S.A. & Woodford M.H. (1977). Rumen fermentation and food selection in East African Zebu cattle, wildebeest, Coke's hartebeest and topi. *Journal of Zoology* 181: 1-9.
- Ivlev V.S. (1961). Experimental ecology of the feeding of fishes. Yale University Press, New Have, Conn.
- Ketner P. (1972). Primary production of Salt-Marsh Communities on the Island of Terschelling in the Netherlands. Research Institute for Nature Management. Verhandeligen Nummer 5.

- Lamprey H.F. (1983). Pastoralism yesterday and today: the overgrazing problem. In: Bourliere F. (ed.). Ecosystems of the world 13, Tropical savannas, Elsevier scientific publishing company, Amsterdam, pp643-666.
- leHou  rou H.N. (1989). The grazing land ecosystems of the African Sahel (ecological studies 75). Springer-Verlag.
- Loth P.E. & Prins H.H.T. (1986). Spatial patterns of the landscape and vegetation of Lake Manyara National Park. ITC Journal 1986: 115-130.
- Machange J. (1997). Livestock and wildlife interactions. In: Thompson D.M. (ed.). Multiple landuse, the experience of the Ngorongoro Conservation Area Tanzania,. IUCN, Gland Switzerland and Cambridge, pp127-141.
- McNaughton S.J. (1984). Grazing lawns: animals in herds, plant form and co-evolution. American Naturalist 124: 863-886.
- McNaughton S.J., Milchunas D.G. & Frank D.A. (1996). How can net primary productivity be measured in grazing ecosystem ?. Ecology 77: 974-977.
- Norton-Griffiths M. (1978). Counting animals, 2nd ed. African Wildlife Leadership Foundation, Nairobi, 110p.
- Novozamsky I., Houba V.J.G., Van Eck R. & Van Vark W. (1983). A novel digestion technique for multi-elemental plant analysis. Communications in Soil Science and Plant Analyses 14: 239-249.
- OleParkipuny M.S. (1989). So that the Serengeti shall never die ? In: Verwey W.D. (ed.). Nature Management and sustainable development, Proceedings of the international congress, IOS, Amsterdam, The Netherlands, pp256-264.
- Osemeobo G.J. (1988). Animal wildlife conservation under multiple land-use systems in Nigeria. Environmental Conservation 15: 239-249.
- Parker G.A. (1970). The reproductive behaviour and the nature of sexual selection in *Scatophaga stercoraria* L. (Diptera: Scatophagidae) II. The fertilization rate and the spatial and temporal relationships of each sex around the site of mating and oviposition. Journal of Animal Ecology 39: 205-228.
- Pianka E.R. (1974). The structure of lizard communities. Annual Review of Ecology and Systematics 4: 53-74.

- Prins H.H.T. & Weyerhaeuser F.J. (1987). Epidemics in populations of wild ruminants: anthrax and impalas, rinderpest and buffalo in Lake Manyara National Park, Tanzania. *Oikos* 49: 28-38.
- Prins H.H.T. & Loth P.E. (1988). Rainfall patterns as background to plant phenology in northern Tanzania. *Journal of Biogeography* 15: 451-463.
- Prins H.H.T. (1988). Condition changes and choice of social environment in African buffalo bulls. *Behaviour* 108: 297-324.
- Prins H.H.T. (1989). East African grazing lands: overgrazed or stable degraded ? In: Verwey W.D. (ed.). *Nature Management and sustainable development, Proceedings of the international congress, IOS, Amsterdam, The Netherlands*, pp281-307.
- Prins H.H.T. & Iason G.R. (1989). Dangerous lions and nonchalant buffalo. *Behaviour* 108: 262-296.
- Prins H.H.T. (1992). The pastoral road to extinction: competition between wildlife and traditional pastoralism in East Africa. *Environmental Conservation* 19: 117-123.
- Prins H.H.T. & Van der Jeugd H.P. (1993). Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology* 81: 305 - 314.
- Prins H.H.T., Van der Jeugd H.P. & Beekman J.H. (1994). Elephant decline in Lake Manyara National Park, Tanzania. *African Journal of Ecology* 32: 185-191.
- Prins H.H.T. (1996). Ecology and behaviour of the African buffalo: social inequality and decision making. Chapman Hall, London UK. 293p.
- Prins H.H.T. (1999). Competition between wildlife and livestock in Africa. In: Prins H.H.T., Grootenhuis J.G. & Dolan T. (eds.). *Conservation of wildlife by sustainable use*, Kluwer Academics, Boston, in press.
- Sinclair A.R.E. (1977). *The African buffalo: a study in resource limitations of populations*. Chicago University Press, Chicago.
- Stewart D.R.M. (1967). Analysis of plant epidermis in faeces: a technique for studying the food preference of grazing herbivores. *Journal of Applied Ecology* 4: 83-111.
- TWCM (1995a). *Tanzania Wildlife Conservation Monitoring: Aerial Wildlife Census of Tarangire National Park, Wet and Dry Season 1994*. Frankfurt Zoological Society, P.O. Box 3134, Arusha, Tanzania.

- TWCM (1995b). Tanzania Wildlife Conservation Monitoring and Tarangire Conservation project: Total count of buffalo & elephant in the Tarangire ecosystem, September 1995. FZC/EC Report. TWCM/FZC, P.O. Box 3134, Arusha, Tanzania.
- UNEP (1977). Ecological change and desertification. UN Conference on Desertification. Background document, Nairobi, 124p.
- Van Wijngaarden W. (1985). Elephants-Trees-Grass-Grazers: relationships between climate, soils, vegetation and large herbivores in a semi-arid savanna ecosystem (Tsavo, Kenya). ITC Publication number 4. 159p.
- Voeten M.M. & Prins H.H.T. (1999). Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia* 120: 287-294.
- Werger, M.J.A. (1977). Effects of game and domestic livestock on vegetation in East and Southern Africa. In: Krause W. (ed.). Application of vegetation science to grassland husbandry, Handbook of vegetation science, part XIII, Junk (Den Haag).
- Wiens J.A. (1989). The ecology of bird communities, vol. 2 processes and variations. Cambridge studies in ecology. Cambridge University Press.

SYNTHESIS:
LIVING WITH WILDLIFE

In East Africa large tracks of land are still populated by diverse and abundant wildlife and by pastoralists with their livestock. Although we lack actual data on how harmonious or stable this situation has been in the past, it is clear that presently conflicts do arise. Grazing land is becoming relatively scarce for both wildlife and pastoralists due to the large increase in human population, livestock numbers and large-scale agricultural activities. A number of people have given recommendations about how to solve the two apparently contrasting problems of a continued existence of wildlife outside the protected area system and the legitimate wish of the indigenous people to continue a pastoral mode of production even in the face of environmental and economic stress. The areas outside the protected area system are in East Africa crucial for the preservation of wildlife in the National Parks because they form part of the migratory ranges of these wild animals. So people and wildlife need the same space. Before recommendations can be given on how to solve conflicts between wildlife and livestock it is of major importance first to answer the question of how compatible wildlife and livestock(keeping) are.

Major conclusions

A fundamental question raised in the Introduction of this thesis is how well non-indigenous species such as livestock fit into a natural assemblage of wild species. The native herbivore assemblage shows a large variety in group size, body mass, feeding style and habitat choice. Body mass, through its effect on food requirements and on how animals experience the distribution of food, can explain most variation in group size (Chapter 2). Differential use of (food)resources may also explain how species coexist despite extensive overlap in ecological requirements. It has been shown (Chapter 3 and Chapter 6) that wildebeest, zebra and cattle show substantial overlap in resource use by selecting similar feeding sites, foraging on the same grass species and preferring the same habitat types. More overlap was found between cattle and either wildebeest or zebra than between wildebeest and zebra. This overlap, in combination with limited resources, implicates a strong potential for competition between cattle and the native species. However, ecological theory predicts that overlap in resource use under food limited conditions should not be expected between native species and indeed this

was not found (Chapter 3). This was substantiated by the finding that, when resources became scarcer, the overlap decreased stronger between native species than between cattle and the native species (Chapter 6). It is concluded that the niche that cattle occupy within the natural system gives potentially rise to more competitive interactions between cattle, wildebeest and zebra than between wildebeest and zebra.

In the Masai Ecosystem, where this study was performed, wildlife is able to avoid competition with livestock by moving during the dry season to areas where cattle do not have access to (Chapter 6). During the dry season, resources are very scarce and competition is expected to be strongest. This seasonal movement, however, is not because of competition, but is a result of differences in resource availability between areas. The migratory wildebeest select a foraging area where they can satisfy their nutritional requirements simultaneously (Chapter 4). During the wet season, the animals move to their wet season range because only there they can satisfy all their nutritional needs, which are high at this time of the year since the females are lactating. The return to the dry season range in the dry season is related to the year-round availability of drinking water in these areas. Most of the zebra population of the Masai Ecosystem shows the same seasonal migration pattern as wildebeest. Zebra nutritional requirements are similar to those of wildebeest (Duncan 1992) and I therefore propose that also the migration of zebra can be explained in the same way.

In the Masai Ecosystem the seasonal migration of wildebeest and zebra results in a movement from National Parks in the dry season (which are not accessible for livestock) to unprotected areas during the wet season. It is during this period and in these areas that the wild herbivores frequently interact with livestock. That these wet season ranges are necessary for the survival of the migratory wild herbivore herds is substantiated by the finding that if the animals were forced to stay year-round in their dry season range, forage quality as well as forage quantity would not be sufficient to satisfy their nutritional requirements (Chapter 5).

Summarizing, I conclude that there is a large potential for competition between cattle, wildebeest and zebra and that specific areas in the Masai Ecosystem, where these species frequently interact, are of major importance for the survival of the wild herbivores.

Consequences

If the present situation of increasing human populations, 53% between 1978 and 1988 (Mwalyosi 1991), and encroachment of settlements and agricultural activities in the rural areas in the Masai Ecosystem continues, without doubt major consequences for the existing wildlife populations can be expected. More and more land will be occupied by humans or human activities and less and less land will be available for wildlife. The foreseen and actual decline in wildlife populations is not simply proportional to the amount of habitat lost over time since certain areas, such as the migratory grounds, are of much more importance than other areas. Observations in other parts of Africa indicate that loss of part of the range of migratory ungulates can have severe repercussions for the populations involved. In Kruger NP in South Africa, the migratory wildebeest population declined with more than 80% between 1965 and 1979, after fences erected in 1961 and 1966, closed off the wet season grazing areas. Although other factors, such as a drought during the seventies, may have contributed to this decline, the population never recovered to former numbers (Whyte & Joubert 1988). Fences erected in the Kalahari in Botswana during the fifties restricted the access to the dry season range of the migratory wildebeest and population numbers severely declined (Williamson et al. 1988). In the Masai Ecosystem not only wet season ranges are becoming less accessible to wildlife (Borner 1985) but also the dry season ranges, which are so important because of their perennial rivers, are under threat. Due to agricultural activities in areas surrounding Tarangire National Park and Lake Manyara National Park the water flow of the main rivers has decreased (Loth 1999, pers.com. J.Simonson).

As mentioned above, strongest competition is expected when resources are most scarce, that is, during the dry season. Currently, most wildlife is then spatially separated from livestock so that competition cannot take place. However, evidence has been found that resources might not only be limited in the dry season but also in the beginning of the wet season (food quantity) and the beginning of the dry season (food quality), (Chapter 3). During both these seasons, wildlife and livestock occupy the same areas. Since loss of habitat in general will lead to higher local densities of wildlife and livestock and since competition is a density-dependent process, the potential for competition between wildlife and livestock in other seasons than the dry season will increase. Furthermore, I suggest that if competition would take place, cattle are very likely to be the stronger competitor; not because of intrinsic

competitive characteristics of cattle but because cattle are rather independent of natural regulation mechanisms and also because of the presence of herdsman who can protect livestock from predators, can dig waterwells, can search for good pastures or just because of their mere presence frightening wildlife (pers. obs.).

Returning to the main issue of this thesis, it is concluded that cattle do not fit into the natural assemblage of native wild herbivores without negatively affecting them: compatibility between wildlife and livestock per se can therefore be seriously questioned but is dependent on densities.

Multiple land-use

What options and tools do we have to prevent the eventual decline in wildlife, which is bound to happen if no measures are taken? From the wildlife point of view it is obvious that expansion of protected areas would be the best solution. This will involve rather large areas especially when migratory ungulate populations are concerned and moreover, areas which are inhabited already by people. Prohibition of human habitation is increasingly being called into question. For example Mustafa (1997) describing the eviction of pastoralists from the Mkomazi Game Reserve in Tanzania and Neumann (1992) describing community resentment at the creation of Arusha National Park in Tanzania. These conflicts between protected areas authorities and local communities have prompted growing calls for protected areas and for the government to play a greater role in the development of adjacent local communities (IUCN 1994, Thompson 1997). Two examples will illustrate this approach.

The Ngorongoro Conservation Area (NCA) in northern Tanzania is considered a pilot model for multiple land-use management, being established already in 1958 to promote the conservation of natural resources as well as the development of its Masai pastoralist inhabitants. Prior to 1974, human habitation was combined with natural resource conservation throughout the NCA. Since 1974, however, permanent habitation and livestock grazing was prohibited in the Ngorongoro Crater itself, although Masai were permitted to continue to bring livestock into the Crater to access salt licks. From 1975 onwards cultivation was completely banned from the whole NCA. In 1992 this ban was temporarily lifted to improve the food security situation and has not been reinstalled yet. There has been a considerable

change in numbers of certain herbivore species since the 1960s (Perkin 1995, Runyoro et al. 1995, Moehlman et al. 1997). From the seventies onwards, wildebeest numbers, elephant and black rhinoceros numbers have decreased while buffalo numbers have increased. The number of most other species has remained more or less the same. Populations of elephant and rhino were certainly affected by poaching and probably nowadays also the buffalo and wildebeest population (Campbell & Hofer 1995). The main changes in buffalo and wildebeest numbers in the 1970s however, coincided with the eviction of cattle and settlements from the Crater floor. On the other hand, the total amount of wild herbivore biomass (in kg body mass) remained rather constant (see also Prins 1990), suggesting a total fixed carrying capacity (in the broad sense) of the combined herbivore assemblage. The number of livestock has increased resulting primarily from an increase in small stock numbers while cattle numbers did not change much until recently their numbers started to increase again (Prins 1992, Kijazi 1997b). The number of people has been almost five-folded since the early sixties. The general conclusion is that under the multiple land-use strategy of the NCA the natural resources, and in particular, wildlife have been maintained rather well (Perkin & Thompson 1997). The negative effect of poaching on wildlife is not a problem specifically related to the NCA management strategy, but happens in all areas where large populations of wildlife still occur. On the other hand, human development objectives have been lagging behind and problems exist with livestock diseases, food security and social services (Kijazi 1997a). It must be mentioned though that the overall economic status of the NCA Masai appears to be little different from that of pastoral groups elsewhere in eastern Africa (Thompson 1997a), so that the NCA strategy at least did not impair their situation but apparently, also did not improve it. Within the NCA, management activities have been oriented primarily towards conservation and not so much to human development. It is important to realise that the reverse could have occurred: from 1968 until 1969, the NCA fell under the Ministry of Agriculture and was nearly dissolved and large sections of the area were converted to intensive cultivation and livestock ranching (Arhem 1985 cited in Perkin 1995).

In Kenya, land-use issues in the arid and semi-arid rangelands were differently approached. Besides setting apart Game Reserves, the colonial government adopted policies aimed at sedentarising the semi-nomadic pastoralists and increasing the productivity and national participation of their livestock economy in the areas surrounding the protected areas (Lindsay 1987). In the early 1970s the government introduced a new land tenure system to

commercialise livestock production and group ranches were created in order to assign the rights and responsibilities of land ownership to the specified pastoral communities. Ottichilo et al. (1999) in a nation-wide assessment of animal numbers in the rangelands over the period 1970-1990 showed that wildlife numbers had decreased by over 30 % and that livestock numbers had remained rather constant. De Leeuw et al. (1998) confirmed these trends. Ottichilo concluded that the main factors contributing to the decline were poaching (especially elephant and rhino) and land-use changes. The impact of the creation of group ranches and individual landholders was that overall wildlife was systematically excluded from properties in order to minimise livestock/wildlife competition and because wildlife was not directly benefiting the private landowners in terms of economic returns. Heath (1999) reported on ranching enterprises on the Laikipia Plateau in central Kenya. He concluded that most ranches perform within very narrow margins and that in the case of the smaller ranches (6,000 to 8,000 ha) the occurrence of wildlife makes the difference between a marginal and profitable enterprise and that the owners of these ranches have mostly cleared their land of wildlife. To address the issue of landowners, who do not want wildlife on their land due to lack of financial benefits from wildlife, the Kenyan wildlife Service now has adopted a strategy that encourages integration of wildlife management objectives with those of the land owners. Partly due to political changes in Kenya, the results of these programmes are not unequivocal (pers.com. H.H.T. Prins).

Final conclusions

Linking conservation of wildlife to the process of rural development has become an important issue world-wide since it has been recognised that not only wildlife but also the traditional pastoral societies experience pressures due to high population growth and grazing land becoming scarce or less accessible. Community-based wildlife management, that is, consultation and direct participation of local communities in decision-making and sharing resources and revenues, is becoming generally accepted as an essential component of sustainable wildlife management, and in particular maybe the only option for managing livestock-wildlife interactions. As is clear from the described examples in the Ngorongoro Conservation Area and the Kenyan rangelands, there is still much to learn and to do. A

contribution to the future success of this approach could be a better understanding of the differences between sharing resources and sharing revenues.

Sharing the resources refers to sharing the rangelands and the forage these rangelands produce for wild herbivores and livestock. This thesis has shown, however, that there is a large potential for competition for food between wildlife and livestock. Competition is a density-dependent process and I argued that if livestock numbers keep increasing, as they have done in most areas during the last decades, then this would inevitably lead to competition whereby eventually livestock will replace the wild herbivores. In addition, loss of habitat due to settlements and agriculture accelerates this process. Only sharing the natural resources that govern animal production will lead to pure livestock enterprises where tangible human benefits come mainly from meat, hides and milk. The left site of figure 1 depicts this situation. However, the number of animals that can be kept in a certain area is limited because food (i.e. plant production) and space are limited. In addition, no extra tangible benefits can be generated through livestock keeping. Ultimately it can be questioned how sustainable pure livestock enterprises will be if livestock numbers can not be strictly controlled and activities which threaten the livestock economies, such as large scale agriculture, can not be stopped.

If wildlife populations could be maintained however, then revenues generated by wildlife could be shared. Sharing revenues refers to the equitable distribution of the benefits from wildlife to the people inhabiting the areas where wildlife occurs and is to be protected. These benefits could be generated through meat selling, safari hunting or wildlife viewing (see right site of fig.1). For a wildlife enterprise the tangible benefits resulting from meat, skins and curios are similar to livestock enterprises. However, the extra benefits through safari hunting, wildlife viewing and general services related to tourism, add substantially to the total amount of benefits. Moreover, in the long run this will be more sustainable: although the number of animals is still limited by food, water and space, revenues related to wildlife can be generated and extended in many different ways and are therefore much less limited. A mixed enterprise with wildlife and livestock would be in the middle of figure 1 and would also generate extra benefits. Again since food and space are limited resources over which wildlife and domestic herbivores will compete to the detriment of wildlife, these mixed enterprises can only be maintained by strict control of livestock numbers and people, so that the demand for and availability of resources by both wildlife and livestock could be balanced.

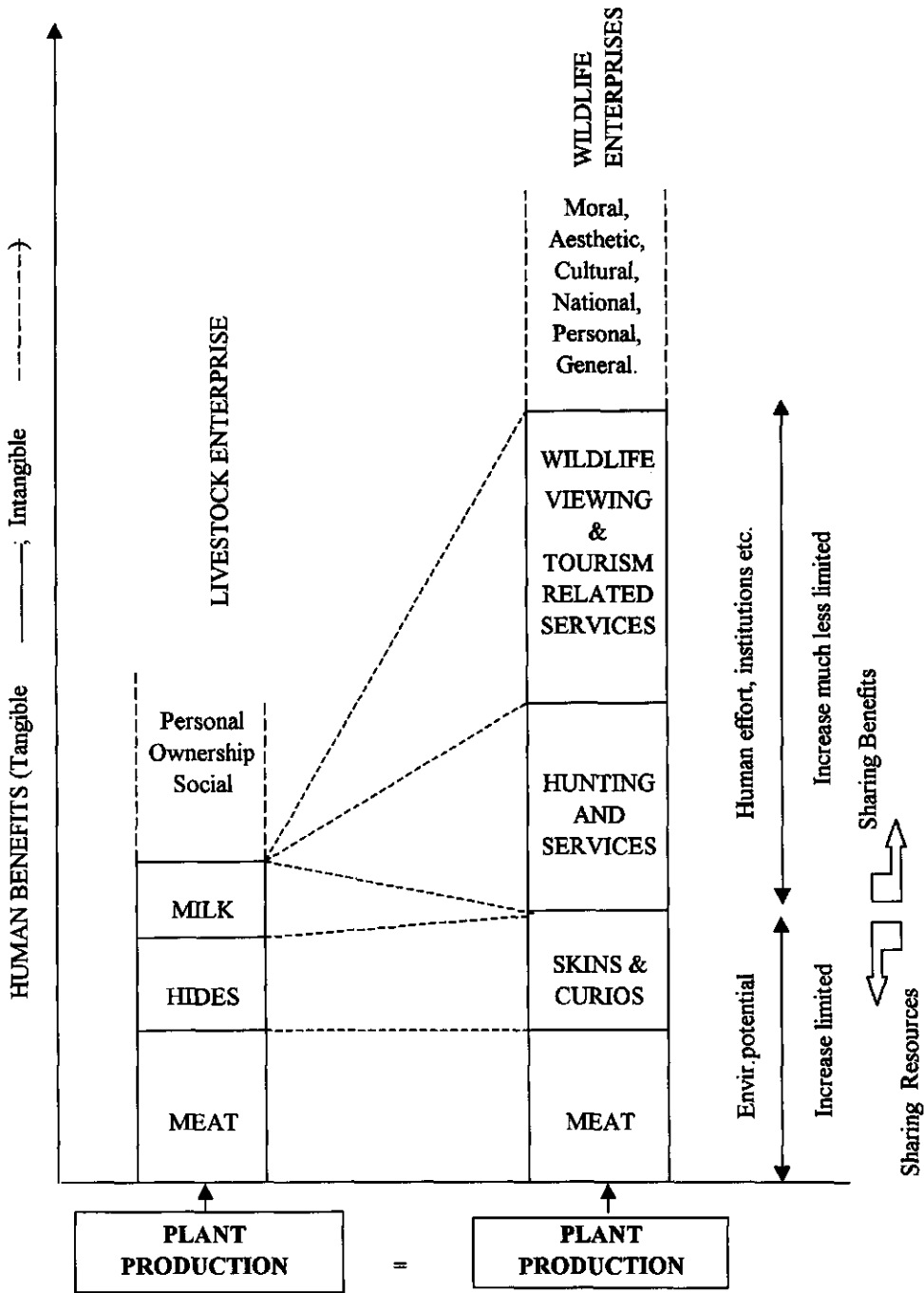


Figure 1. After Child (1999).

So far, the emphasis of management strategies where sharing revenues generated by wildlife is a principal element, has been on distributing economic benefits from protected areas to local communities as a means to compensate local inhabitants for restricted use of the protected areas. Transferring financial or infrastructure benefits in the form of waterholes, dispensaries and schools has provided economic benefits. Some small-scale projects of this sort have succeeded in the sense that certain facilities have been provided. At the same time this has induced some settlements, bordering protected areas, of having become attractive centres for immigrants; this only aggravates the problem of increasing human populations. Part of the benefits related to wildlife will also eventually return through the national government as public facilities, such as roads and electricity supplies. However, the benefits are generally not felt directly at the local level, but are rather enjoyed in the capitals and regional centres of the countries involved (Thompson 1997), which has led to resentment within the local communities.

Maybe in sharing the benefits of wildlife one should go one step further. The emphasis should not be on compensation, but rather, the local communities of rangelands surrounding protected areas, should become the custodian of wildlife in these rangelands; the ones who will own the benefits by setting up their own enterprises to exploit the natural resources. Although this will involve many practical and political issues and might be particularly a social problem, I think that the conflicts resulting from the incompatibility of wildlife and livestock could be settled in this manner so that "living with wildlife" becomes a way of life.

References

- Borner M. (1985). The increasing isolation of Tarangire National Park. *Oryx* 19: 91-97.
- Campbell K. & Hofer H. (1995). People and wildlife: spatial dynamics and zones of interaction. In: Sinclair A.R.E. & Arcese P. (eds.). *Serengeti II: Dynamics, management and conservation of an ecosystem*. The University of Chicago Press, Chicago, pp534-570.
- De Leeuw J., Prins H.H.T., Njuguna E.C., Said M.Y. & De By R.A. (1998). Interpretation of DRSRS animal counts (1977-1997) in the rangeland districts of Kenya. International Institute for Aerospace Survey and Earth Science (ITC), Enschede, The Netherlands. Department of Resource Surveys and Remote Sensing (DRSRS), Nairobi, Kenya, p187.
- Duncan P. (1992). Horses and grasses; the nutritional ecology of equids and their impact on the Camargue, *Ecological studies* 87, Springer-Verlag.
- Child G. (1999). "Ownership" of wildlife. In: Prins H.H.T., Grootenhuis J.G. & Dolan T. (eds.). *Conservation of wildlife by sustainable use*, Kluwer Academics, Boston, in press.
- Heath B. (1999). Livestock ranching: an economic and ecological yardstick. In: Prins H.H.T., Grootenhuis J.G. & Dolan T. (eds.). *Conservation of wildlife by sustainable use*, Kluwer Academics, Boston, in press.
- IUCN (1994). Parks for live. In : proceedings of the IV world parks congress, Caracas, Venezuela. International Union for Conservation of Nature, Gland, Switzerland and Cambridge, UK.
- Kijazi A.(1997a). Principal management issues in the Ngorongoro conservation area. In: Thompson D.M. (ed.). *Multiple landuse, the experience of the Ngorongoro Conservation Area Tanzania*, IUCN, Gland, Switzerland and Cambridge, UK, pp33-44.
- Kijazi A., Mkumbo S. & Thompson D.M. (1997b). Human and livestock trends. In: Thompson D.M. (ed.). *Multiple landuse, the experience of the Ngorongoro Conservation Area Tanzania*, IUCN, Gland, Switzerland and Cambridge, UK, pp169-180.

- Loth P.E. (1999). The vegetation of Manyara: scale-dependent states and transitions in the African Rift Valley. PhD thesis, Agricultural University of Wageningen, The Netherlands.
- Lindsay W.K. (1987). Integrating parks and pastoralists. In: Anderson D. & Grove R. (eds.). *Conservation in Africa: people, policies and practice*. Cambridge University Press, Cambridge, UK, pp149-167.
- Machange J. (1997). Livestock and wildlife interactions. In: Thompson D.M. (ed.). *Multiple landuse, the experience of the Ngorongoro Conservation Area Tanzania*, IUCN, Gland, Switzerland and Cambridge, UK, p127-141.
- Moehlman P.D., Runyoro V.A. & Hofer H. (1997). Wildlife population trends in the Ngorongoro Crater. In: Thompson D.M. (ed.). *Multiple landuse, the experience of the Ngorongoro Conservation Area Tanzania*, IUCN, Gland, Switzerland and Cambridge, UK, pp59-69.
- Mwalyosi R.B.B. (1991). Population growth, Carrying capacity and sustainable development in South-West Masailand. *Journal of Environmental management* 33: 175-187.
- Mustafa K. (1997). Eviction of pastoralist from the Mkomazi Game Reserve in Tanzania: A historical review. Pastoral land tenure series No. 8. International Institute for environment and development, drylands programme. London, UK.
- Neumann R.P. (1992). Political ecology of wildlife conservation in the Mt. Meru area of northeast Tanzania. *Land degradation and rehabilitation* 3: 85-98.
- Ottichilo W.K., Grunblatt J., Said M.Y. & Wargute P.W. (1999). Population trends and distributions of large mammals on the Kenya rangelands. In: Prins H.H.T., Grootenhuis J.G. & Dolan T. (eds.). *Conservation of wildlife by sustainable use*, Kluwer Academics, Boston, in press.
- Perkin S.L. & Thompson D.M. (1997). Summary of the Ngorongoro Conservation Area's Multiple Land-Use Experience. In: Thompson D.M. (ed.). *Multiple landuse, the experience of the Ngorongoro Conservation Area Tanzania*. IUCN, Gland, Switzerland and Cambridge, UK, pp455-467.
- Perkin S. (1995). Multiple land use in the Serengeti region. In: Sinclair A.R.E. & Arcese P. (eds.). *Serengeti II: Dynamics, management and conservation of an ecosystem*. The University of Chicago Press, Chicago, pp571-587.

- Prins H.H.T. (1992). The pastoral road to extinction: competition between wildlife and traditional pastoralism in East Africa. *Environmental Conservation* 19: 117-123 .
- Prins H.H.T. & Douglas-Hamilton I. (1990). Stability in a multi-species assemblage of large herbivores in East Africa. *Oecologia* 83: 392-400.
- Runyoro V.A., Hofer H., Chausi E.B. & Moehlman P.D. (1995). Long-term trends in the herbivore populations of the Ngorongoro crater, Tanzania. In: Sinclair A.R.E. & Arcese P. (eds.). *Serengeti II: Dynamics, management and conservation of an ecosystem*. The University of Chicago Press, Chicago, pp146-168.
- Thompson D.M. (1997b). Integrating conservation and development. In: Thompson D.M. (ed.). *Multiple landuse, the experience of the Ngorongoro Conservation Area Tanzania*. IUCN, Gland, Switzerland and Cambridge, UK, pp7-18.
- Whyte I.J. & Joubert S.C.J. (1988). Blue wildebeest trends in the Kruger National Park and the effects of fencing. *South African Wildlife Research* 18 :78-87.
- Williamson D., Williamson J. & Ngwamotsoko K.T. (1988). Wildebeest migration in the Kalahari. *African Journal of Ecology* 26: 269-280.

SUMMARY

In the savannas of East Africa, diverse and abundant wildlife populations share their grazing land with pastoralists and their livestock. Although we lack actual data on how harmonious or stable this situation has been in the past, it has become clear that since the last decades conflicts do arise. The protected areas are often too small to sustain current wild herbivore populations and they need the surrounding rangelands for their survival, while also the local communities need these rangelands for their sustenance. Grazing land is becoming relatively scarce for both wildlife and pastoralists due to the large increase in human population, livestock numbers and large-scale agricultural activities. Linking conservation of wildlife and the natural habitats where they live into the process of rural development has become an important issue in the areas where wildlife and livestock frequently interact. If one wants to integrate wildlife conservation with development of rural areas dominated by pastoral economies, it is of major importance to first answer the question of how compatible wildlife and livestock(keeping) are. I investigated this issue in the Masai-ecosystem in northern Tanzania.

Livestock and African wild herbivores have not shared a long common evolutionary history. The wild herbivore species presently found in East-Africa have evolved together since the Pliocene approximately 5 million years ago while domestication of wild ungulates is estimated to have begun in the Middle-East about 10,000 years ago. Furthermore, the earliest evidence of pastoralism in East-Africa dates from 3000-2500 BP. Hence it can be questioned how well non-indigenous species, such as livestock, fit into a native assemblage of wild herbivore species. Among long-term coexisting native herbivores, complete overlap in resource use is not expected when resources are limited and hence, no competition can occur. In a native assemblage to which an exotic species has been introduced however, overlap in resource use can occur under food-limited conditions between exotic and native species and consequently implies competition.

The native herbivore assemblage shows a large variety in group size, body mass, feeding style, habitat choice and density. I investigated the relationship between these factors by analysing all these factors simultaneously. Body mass, or rather metabolic mass, explained most variation in group size. This relationship was found to be similar for grazers and intermediate feeders although group size of grazers increased more with an increase in metabolic mass than was the case for intermediate feeders. That metabolic mass is an important determinant of group sizes can be explained through the relation of metabolic mass with food

requirements and how different-sized animals experience the distribution of food.

Differential use of (food)resources, i.e. resource partitioning, may explain how species coexist despite extensive overlap in ecological requirements. The effect of the introduction of an exotic species (cattle) into a native African herbivore assemblage was investigated by studying resource partitioning between Zebu-cattle, wildebeest and zebra. This was investigated by analysing grass sward characteristics (such as sward height, digestibility and percentage nitrogen in leaves) of feeding sites selected by the different herbivore species. Linear discriminant analysis was used to determine whether a distinction could be made between feeding sites selected by the different animal species or whether the animal species showed overlap in resource use by selecting similar feeding sites. Wildebeest and zebra did not show overlap in resource use except in the wet season when resources were ample. Cattle showed overlap in resource use with zebra in the early wet season and with wildebeest in the early dry season, seasons when food limitation is likely.

In addition, overlap both in habitat and in diet between wildlife and livestock were studied in combination with resource availability and food requirements. Also, body condition of a wildebeest population co-occurring with livestock and isolated from livestock was compared. I found a large overlap in diet and habitat during the wet season and that resources are limited. Hence, a large potential for competition between wildebeest, zebra and cattle is inferred. Zebra and cattle showed most overlap and wildebeest and zebra least. Although the conditions for competition to occur are met, it is concluded that, in the Masai Ecosystem where this study was performed, wildlife is able to avoid competition during the dry season because they move then to areas where cattle do not have access. They do not move because of competition but because of differences in resource availability between areas.

A linear programming model was used to study these differences in resource availability between areas, in relation to the seasonal migration of wildebeest and zebra. The model was used to predict in which area, the wet season range or the dry season range, migratory wildebeest should forage to satisfy all their nutritional requirements while at the same time maximizing their energy or protein intake. The model correctly predicted the seasonal movements to the wet season range. In this period of the year phosphorus and fibre intake constraints determine the possible outcomes of the model. High phosphorus requirements of lactating females prevent the animals to satisfy their requirements in the dry season range. In the early dry season, the animals can satisfy their requirements in the wet as

well as in the dry season range. I showed that the movement back to the dry season range is related to water requirements. In the dry season, fibre content of the vegetation severely restricts intake and the animals are not able to fulfil their nutritional requirements in any of the ranges.

Since especially these wet season ranges are threatened by expanding human activities, I investigated if the dry season range of migratory wildebeest and zebra could sustain current populations when access to the wet season range would be restricted and migratory herds would reside in the dry season range year-round. Grazing itself can affect herbivore forage quality and quantity. Presently, however, the dry season range is not grazed during the wet season by migratory ungulates. This would be the case when access to the wet season range would be restricted. I therefore performed clipping experiments to investigate how grazing affects forage quality and quantity in the dry season range during the wet season. Clipping had a positive effect on the quality of forage whereby the clipped vegetation had higher proportions of live and leaf material and higher concentrations of nutrients in leaf material, nitrogen and phosphorus in particular, as compared to unclipped vegetation. However, the concentrations were not sufficient to meet herbivore nutrient requirements, especially phosphorus. Furthermore, clipping reduced the annual production of forage in the dry season range so that also forage quantity would be insufficient. I therefore concluded that, if the animals were forced to stay year-round in their dry season range, both forage quality and quantity would not be sufficient and current population numbers of migratory herds would decline.

In summary, I conclude in this thesis that the niche that cattle occupy within the natural system gives potentially rise to more competitive interactions between cattle, wildebeest and zebra than between wildebeest and zebra and that the areas in the Masai Ecosystem where these species frequently interact, are of major importance for the survival of the wild herbivores. Therefore, major impact is to be expected from the loss of habitat due to increasing human populations and human activities. The important migratory grounds will become less accessible and locally densities of livestock and wild herbivores will increase. Particularly the latter will add to the potential of competition between wildlife and livestock, since competition is a density dependent process. Furthermore, livestock is likely to be the stronger competitor, not because of intrinsic competitive characteristics but because of the presence of herdsmen.

As a means of managing conflicting livestock-wildlife interactions, several projects in East Africa have tried to involve local pastoral communities in wildlife conservation by consultation and direct participation of the communities in decision-making and sharing resources and revenues of protected areas and the surroundings. I suggests that sharing the benefits of wildlife should go one step further. The emphasis should not be on distributing economic benefits from protected areas to local communities as a means of compensating local inhabitants for restricted use of the protected areas or for any other confining regulations. Rather, the local communities of rangelands surrounding protected areas, should become the ones who will own the benefits of these rangelands by setting up their own enterprises to exploit the natural resources.

SAMENVATTING

Op de savannes van Oost Afrika delen grote kuddes van diverse wilde grote grazers de graslanden met het vee van de nomadische herdersvolken. Hoewel er weinig bekend is over de mate van harmonie en stabiliteit welke deze situatie in het verleden zou hebben gehad, is het wel duidelijk geworden dat gedurende de laatste decennia conflicten zijn ontstaan over het landgebruik. De Nationale Parken zijn dikwijls te klein om levensvatbare populaties van wilde dieren in stand te houden en voor hun overleving zijn de gebieden rondom de Parken onmisbaar. Maar ook de lokale herdersgemeenschappen zijn van deze gebieden afhankelijk voor hun levensonderhoud. Door de grote toename van de bevolking, van de aantallen vee en door grootschalige landbouwactiviteiten wordt de ruimte beschikbaar om te grazen zowel voor de wilde dieren als voor het vee steeds kleiner. In die gebieden waar wild en vee veelvuldig samen voorkomen wordt er steeds meer naar gestreefd om natuurbeheer te koppelen aan het proces van ontwikkeling van de lokale herdersgemeenschappen. Als men natuurbeheer wil integreren met de ontwikkeling van deze pastorale gebieden moet men echter eerst de kapitale vraag beantwoorden in hoeverre deze twee manieren van landgebruik verenigbaar zijn. Dit vraagstuk werd door mij onderzocht in het Masai ecosysteem in Noord Tanzania.

Op de evolutionaire tijdschaal gezien, is de gemeenschappelijke geschiedenis van vee en Afrikaanse wilde grazers, of herbivoren, nog kort. De wilde herbivoren die tegenwoordig voorkomen in Oost-Afrika zijn zo'n vijf miljoen jaar geleden tijdens het Pliocen ontstaan en zijn sindsdien samen verder geëvolueerd. De domesticatie van wilde herbivoren tot het huidige rundvee is echter pas zo'n 10.000 jaar geleden begonnen in het Midden Oosten en de allereerste bewijzen van de aanwezigheid van herdersvolken in Oost-Afrika dateren pas van 3000-2500 jaar geleden. Men kan zich dus afvragen hoe goed niet-endemische soorten, zoals vee beschouwd moet worden, passen in de oorspronkelijke assemblage van Afrikaanse wilde herbivoren.

De oorspronkelijke assemblage van wilde herbivoren vertoont per diersoort een grote variatie in groepsgrootte en ook in foerageerstrategie, habitatkeuze, lichaamsgewicht en aantallen. De relatie tussen deze factoren heb ik onderzocht door al deze factoren tegelijkertijd te analyseren. Het blijkt dat het lichaamsgewicht, of eigenlijk het metabolisch gewicht, de belangrijkste verklarende factor voor groepsgrootte is: hoe groter het dier hoe groter de groepen zijn waarin het dier leeft. De gevonden relatie tussen groepsgrootte en gewicht is van gelijke aard voor de pure grazers en voor de dieren die zowel gras als kruiden

en struiken eten ("intermediate feeders"), alhoewel de groepsgrootte in vergelijking met de gewichtstoename bij grazers sterker toeneemt dan bij de "intermediate feeders". Dat de gemiddelde groepsgrootte van een diersoort voorspeld kan worden op grond van het gewicht kan men verklaren door de relatie tussen het metabolisch gewicht en de voedselbehoefte van een dier en ook door de wijze waarop diersoorten van verschillende grootte de ruimtelijke verspreiding van hun voedsel ervaren.

"Resource partitioning" is het verschillend gebruik van, in dit geval, voedselbronnen, bijvoorbeeld door het eten van verschillend voedsel of door een andere manier van voedselvertering en zou kunnen verklaren hoe dieren die een grote overeenkomst in ecologische behoeften vertonen toch kunnen coëxisteren. Door de "resource partitioning" tussen Zebu-koeien, gnoes en zebra's te onderzoeken kan het uiteindelijke effect van de introductie van een niet-endemische soort (Zebu) in een assemblage van endemische Afrikaanse herbivoren bestudeerd worden. Met dit doel voor ogen werd de vegetatie op de plekken waar de verschillende diersoorten grazen nauwkeurig beschreven aan de hand van parameters zoals bijvoorbeeld grashoogte, stikstofgehalte en verteerbaarheid. Een statistische techniek, lineaire discriminanten analyse genaamd, werd daarna gebruikt om vast te stellen of de graasplekken van de verschillende diersoorten op grond van de gemeten graskarakteristieken konden worden onderscheiden of dat de verschillende diersoorten overeenkomst vertoonden in het gebruik van hun voedselbronnen door selectie van dezelfde typen graasplekken. Het bleek dat gnoes en zebra's verschillende typen graasplekken selecteerden behalve in het regenseizoen, wanneer het voedselaanbod ruim voldoende is. Zebu's selecteerden in het begin van het regenseizoen dezelfde typen graasplekken als zebra's en in het begin van het droge seizoen dezelfde typen graasplekken als gnoes, dus in seizoenen waarin het voedselaanbod waarschijnlijk beperkt is. Tussen diersoorten die al heel lang samen voorkomen zoals gnoes en zebra's wordt niet verwacht dat ze precies dezelfde voedselbronnen gebruiken indien het voedselaanbod beperkt is, en concurrentie kan dan dus ook niet optreden. Tussen niet-endemische soorten en endemische soorten daarentegen kan overeenkomst in het gebruik van voedselbronnen wel voorkomen als het voedselaanbod beperkt is; dit kan dus leiden tot concurrentie tussen koeien enerzijds en gnoes en zebra's anderzijds.

Ook de overeenkomsten in leefgebied (habitat) en dieet zijn bestudeerd voor Zebu-koeien, gnoes en zebra's in samenhang met het voedselaanbod en de voedselbehoeften.

Daarnaast heb ik de lichaamsconditie van gnoes die samen met koeien voorkomen en gnoes die niet samen met koeien voorkomen vergeleken. Alle drie de soorten vertoonden veel overeenkomst in habitat en dieetkeuze gedurende het regenseizoen: zebra's en koeien de meeste en gnoes en zebra's de minste. Tevens toonden berekeningen aan dat er niet voldoende voedsel beschikbaar is om het gehele jaar door in de behoeften te voorzien. Aan het begin van het droge seizoen zijn derhalve alle voorwaarden voor het ontstaan van concurrentie aanwezig en misschien vindt er ook al concurrentie plaats. Voor het Masai ecosysteem waar dit onderzoek werd uitgevoerd, kom ik echter tot de conclusie dat juist in de periode dat de sterkste concurrentie verwacht zou worden, namelijk in het midden of einde van het droge seizoen, het wild in staat is concurrentie te vermijden. Het wild trekt dan namelijk naar andere (beschermde) gebieden waar koeien geen toegang hebben; niet wegens voedselconcurrentie maar omdat de gebieden waar het wild naar toe trekt in voedselaanbod verschillen van de gebieden waar ze vandaan komen.

Een lineair programmeermodel werd gebruikt om dergelijke verschillen in voedselaanbod tussen gebieden te bestuderen in relatie tot de jaarlijkse migratie van gnoes en zebra's in het Masai ecosysteem. Het model werd met name gebruikt om te voorspellen in welk gebied, het verspreidingsgebied tijdens het regenseizoen of het verspreidingsgebied tijdens het droge seizoen, de populatie van deze migrerende gnoes zou moeten foerageren om in al hun voedselbehoeften te voorzien en tegelijkertijd zoveel mogelijk energie of eiwit op te nemen. De jaarlijkse migratie naar het verspreidingsgebied tijdens het regenseizoen werd correct voorspeld door het model. Gedurende de regentijd worden de mogelijke uitkomsten van het model bepaald door de beperkende voorwaarden die in het model zijn ingevoerd ten aanzien van de opname van fosfor en ruwe vezel. De hoge fosfor behoeften van lacterende vrouwtjes tijdens het regenseizoen hebben tot gevolg dat de dieren in het droge seizoens-verspreidingsgebied niet in hun behoeften kunnen voorzien en dus naar het regenseizoens-verspreidingsgebied moeten trekken. Aan het begin van de droge tijd kunnen de dieren in beide verspreidingsgebieden in al hun voedselbehoeften voorzien. Er is verder aangetoond dat de migratie terug naar het droge seizoens-verspreidingsgebied dan ook niet met voedsel verband houdt maar met waterbehoeften. Gedurende het droge seizoen beperkt het hoge ruwe-vezelgehalte van de vegetatie de voedselopname en de dieren zijn dan noch in het regenseizoens-verspreidingsgebied, noch in het droge seizoens-verspreidingsgebied in staat om aan hun voedselbehoeften te voldoen.

Het zijn op dit moment vooral de regenseizoens-verspreidingsgebieden van de migrerende gnoes en zebra's die bedreigd worden door steeds toenemende menselijke activiteiten. Tijdens dit onderzoek is dan ook nagegaan of de huidige migrerende kuddes het gehele jaar rond zouden kunnen overleven in het droge seizoens-verspreidingsgebied indien in de toekomst de regenseizoens-verspreidingsgebieden niet meer toegankelijk zouden zijn. Al grazende beïnvloeden de herbivoren zelf de hoeveelheid en de kwaliteit van het beschikbare voedsel. Op dit moment echter wordt er tijdens het regenseizoen niet gegraasd in het droge seizoens-verspreidingsgebied omdat de dieren zijn weggetrokken. Om toch het effect van begrazing op voedselbeschikbaarheid en -kwaliteit in het droge seizoens-verspreidingsgebied tijdens het regenseizoen te bestuderen heb ik knipexperimenten uitgevoerd. Aangetoond werd dat knippen, met de bedoeling om begrazing te simuleren, de kwaliteit van het gras verhoogde, hetgeen bleek uit een verhoogde verhouding van blad/stengel, van levend/dood plantenmateriaal en van bladstikstof- en bladfosforgehalte, vergeleken met het ongeknipte (onbegraasde) gras. Maar ondanks de verbeterde kwaliteit was met name het fosfor gehalte niet voldoende om aan de behoeften van de dieren te voldoen. Verder bleek dat knippen de jaarlijkse biomassaproductie van het gras in het droge seizoens-verspreidingsgebied dusdanig verlaagde dat ook de totale voedselbeschikbaarheid onvoldoende zou zijn. Mijn conclusie is dan ook dat, als de dieren gedwongen zouden worden om het gehele jaar door in het droge seizoens-verspreidingsgebied te grazen, zowel de kwaliteit als de kwantiteit van het gras niet voldoende zouden zijn om de huidige aantallen gnoes en zebra's in stand te houden.

Samengevat concludeer ik in dit proefschrift dat de niche die koeien innemen binnen het natuurlijke systeem meer aanleiding geeft tot concurrentie tussen koeien, gnoes en zebra's dan tussen de wilde soorten onderling. Daarnaast concludeer ik dat de gebieden in het Masai ecosysteem waar deze drie soorten een frequente wisselwerking op elkaar uitoefenen, voor het voortbestaan van de wilde herbivoren onmisbaar zijn. De toename van de menselijke bevolking en de daarmee gepaard gaande activiteiten zullen dus belangrijke consequenties hebben voor het wild door verlies van levensruimte. De belangrijke voor migratie benodigde graasgronden zullen kleiner en minder toegankelijk worden en de dichtheden van vee zowel als wild zullen lokaal sterk toenemen. Aangezien concurrentie een dichtheidsafhankelijk proces is, zal vooral door dit laatste de concurrentiedruk tussen wild en vee toenemen. Vee zal daarbij de sterkste concurrent zijn, niet door intrinsieke competitieve eigenschappen, maar alleen al door de aanwezigheid van veehouders.

Met verschillende projecten in Oost-Afrika is geprobeerd om de conflicten tussen veehouderij en natuurbeheer op te lossen door de lokale herdersgemeenschappen te betrekken bij het natuurbeheer. Dit is gedaan door de gemeenschappen te raadplegen bij en te laten participeren in de besluitvorming en door het samen delen van de hulpbronnen en opbrengsten van beschermde gebieden zoals de Nationale Parken. Ik denk echter dat men nog een stap verder zou moeten gaan. De nadruk zou niet moeten komen te liggen op het delen van opbrengsten van Nationale Parken met de lokale bevolking als een compensatie voor het feit dat de lokale bevolking geen gebruik kan maken van deze beschermde gebieden, maar de nadruk zou moeten liggen op de graasgebieden die de Nationale Parken omgeven omdat juist deze gebieden zowel voor het wild als voor de lokale bevolking van levensbelang zijn. In deze gebieden zou de lokale bevolking zelf de uitbater moeten worden van het wild bijvoorbeeld, door toeristische activiteiten te ontwikkelen en te beheren waarvan de inkomsten direct bij hunzelf terechtkomen.

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Curriculum Vitae

Margje Voeten was born on the 27th of August 1965 in Boxtel, the Netherlands. She finished her high school studies at the Jacob Roelands Lyceum in 1983 and thereafter started to study Biology at the University of Utrecht. During her graduate studies she was involved in three research projects. The first project concerned an educational programme about chemical waste for technical colleges. The second was a study on the dominance relationships within a captive group of Java-monkeys within the Department of Ethology and Social Ecology under supervision of Drs. W. Netto. The third project brought her to the Department of Wildlife and Range Sciences of the University of Florida in Gainesville, USA. There, she studied the feeding ecology of the Florida Woodrat under supervision of Professor J. Eisenberg. After her graduation in 1990 she was involved in various educational projects in Zoo's and environmental organizations and she worked as a research assistant in the Department of Ecophysiology of the University of Utrecht. In 1993 her PhD-research proposal was granted by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO) and the University of Wageningen. She conducted three years fieldwork in Tanzania under supervision of Professor H.H.T. Prins of the Department of Tropical Nature Conservation and Vertebrate Ecology, which resulted in this thesis. Currently she is working as the PR and Communications officer for the Space Research Organization of the Netherlands (SRON) and she is a member of the Utrecht District Committee of the Dutch Nature Conservation Society (Natuur Monumenten).

Epwo m-baa pokin in-gitin'got
Everything has an end
(Masai saying)
