COMPRESSED NATURE
Co-existing grazers in a small reserve in Kenya

Shem Mwawaka Mwasi

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Promotor:	Prof. Dr. H.H.T.Prins Hoogleraar in het Natuurbeheer in de Tropen en Ecologie van Vertebraten
Co-promotor:	Dr. Ir. I.M.A Heitkönig Universitair docent, Leerstoelgroep Natuurbeheer in de Tropen en Ecologie van Vertebraten

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Centrum voor Milieukunde, Leiden

Dr. G. W. T. A. Groot-Bruinderink
Alterra, Wageningen Universiteit

NN08201,3223

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Proefschrift

ter verkrijging van de graad van doctor
op gezag van de rector magnificus
van Wageningen Universiteit,
prof. dr. ir. L. Speelman,
in het openbaar te verdedigen
op dinsdag 25 Juni 2002
des voormiddags te 13:30 uur in de Aula.

Mwasi, S. M.
Compressed nature: co-existing grazers in a small reserve in Kenya
Wageningen University, The Netherlands.
Doctoral Thesis (2002); ISBN 90-5808-669-0

To my wife Catherine, children Beryl and Ronald by S. M. Mwasi, 2002

“Compressed nature: co-existing grazers in a small reserve in Kenya”

Pg. 80 alinea 3, the first sentence should read:

Chances of potential competitive interactions in Lake Nakuru NP among the grazers are high considering their high biomass densities in a fixed-**size area where emigration or immigration is impossible.**

Abstract

Mwasi, S. M. 2002. Compressed nature: co-existing grazers in a small reserve in Kenya. Doctoral Thesis, Wageningen University, The Netherlands. ISBN 90-5808-669-0

Wildlife habitats in Kenya are getting more fragmented and isolated due to increasing human activities within them. This has resulted in the establishment of several small nature reserves where wildlife is protected from human interference. Grazers contribute a large proportion of total herbivore biomass in these reserves, and their populations are likely to increase due to stoppage of migration and reduction in their home range sizes (for large home range holders) caused by fencing, human settlements or cultivation on the periphery of the reserves. This might lead to changes in dynamics of grass-grazer or grazer-grazer interactions, which are useful to understand for successful management of these populations to take place. It was in view of this, that I conducted a study with the following hypotheses: that a decline in a grazer species biomass in an isolated small reserve is due to an increase in biomass of other co-existing grazers, and that there is a high resource overlap among co-existing grazers in an isolated small reserve. I considered an isolated grazer assemblage comprising of ten co-existing grazers: defassa waterbuck (*Kobus defassa*), African buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), Grant's gazelle (*Gazella granti*), Thomson's gazelle (*Gazella thomsoni*), warthog (*Phacocoerus aethiopicus*), Burchell's zebra (*Equus burchelli*), eland (*Taurotragus oryx*), Chanler's reedbuck (*Redunca fulvorufula chanleri*), and Bohor reedbuck (*Redunca redunca*) in Lake Nakuru National Park. An analysis of the development of the assemblage over a 24-year period (1976-1999) showed that by 1999, its total biomass had reached 134 kg ha^{-1} and that it was dominated by species above 300 kg (buffalo and eland). Population growth rate of waterbuck and warthog has declined, and Bohor reedbuck appears to have now disappeared from the system. The study shows that larger grazer species did not facilitate smaller ones despite having high habitat overlaps with them during the wet season when grass regrowth after cropping is possible. There were also no indications of habitat segregation among grazers, but competition was apparent through directional habitat use overlap indices. Large similarities in diet composition were found between grazers across all seasons. Niche breadth for diet was smallest during the dry season, and combined (diet + habitat use) overlap was high between all pairs of grazers during all seasons indicating that there is a high possibility of competitive interactions among grazers in Nakuru. However, despite utilising similar feeding sites, competitive interactions between impala and zebra might have been reduced by their foraging strategy where they feed at different plant structure (leaf/stem/flowering stalk) levels. In conclusion, it appears that the structuring of this assemblage is most likely due to competitive interactions among the grazers, which might increase in intensity during years of average or below average rainfall.

Acknowledgements

As this PhD project comes to an end, I feel obliged to express my gratitude to various individuals as well as institutions without whose support I would probably have been unable to complete it successfully considering the fact that these 5½ years have been anything but gruelling to say the least. First and foremost, I feel indebted to Prof. Herbert Prins who not only accepted me as his student in the Tropical Nature Conservation and Vertebrate Ecology Group, Department of Environmental Sciences of Wageningen University (The Netherlands) way back in June 1996, but also for agreeing to be my PhD project supervisor. Indeed, I feel honoured to have worked under him as well as with other members of his group 'The toppers'. Secondly, I cannot forget Prof. Shyam Manohar of the Biological Sciences Division, School of Environmental Studies of Moi University (Kenya) for encouraging me to undertake this PhD study as well as for his unwavering support.

There were times when things did not go as 'smooth' as I would have wanted them to, but save for one person, Dr. Ignas Heitkönig who really encouraged me and ensured that I never gave up. He guided me whenever I encountered difficulties in the field and during the write-up by giving useful advice following recommendations from Prof. Prins. For this, I will always consider him an invaluable academic friend whom I will never forget. Thanks for that Ignas and God bless you!

In the field, I found myself criss-crossing between Lake Nakuru National Park, the Kenya Wildlife Service Training Institute and Hell's Gate National Park all managed by Kenya Wildlife Service. I am therefore, grateful to Kenya Wildlife Service and the management of these nature reserves for allowing me to conduct my research freely and for their support without which my fieldwork might have been rather difficult. My gratitude also go to Mr. Daniel Kilonzo, former Warden of Lake Nakuru National Park and his management team, rangers and auxiliary staff.

My work at the Kenya Wildlife Service Training Institute was made particularly easy by the co-operative staff initially under Dr. Bob Wishitemi, the then principal in 1997/1998. I will forever be grateful for his kind gesture in early 1998 when he agreed to allow me to use the e-mail facility at the institute, upon the request of my supervisors in the Netherlands. By then, access to e-mail facilities in Kenya was very limited. His gesture thus saved the day and solved the communication problems I earlier had with my supervisors! The principal's secretaries (Jane Mwangi, Margaret Eliud and Margaret Obura) made my use of the e-mail facility even easier; thanks ladies. Miss Anne Kahihia, the then Warden of Hell's Gate National Park and her entire staff helped me a lot while I conducted research in the Park, for which I am grateful. I am also grateful to all those who assisted in the actual field data collection. They ensured that I was able to collect high quality ecological data. These include Job Mwakio, Herbert Mwawana and many others whom I cannot mention by name.

The laboratory work proved to be tedious, however, Andrew Kulecho of the Nakuru Water and Sewerage Laboratory persevered and analysed hundreds of samples within the required time frame. Micha Linssen did the microhistological analyses of faeces at Moi University and Tjakkie Laan-Hazelhoff in the Netherlands performed other chemical analyses. To the three of you, I say thanks.

I did the data analyses and write-up of this PhD thesis in the Netherlands, specifically in the famous 'barak' of the Terrestrial Ecology and Nature Conservation (TON) building in Wageningen. Here life could be very stressful at times but I learnt to 'share' some of this stress through jokes and laughter with my fellow PhD colleagues: Theodore Mayaka, Irma Wynhoff, Charudutt Mishra, Euridice Leyequien, Juul Limpens, Fulco Ludwig, Liesbeth Bakker, Karin Kurk, Michael Drescher, and Barend van Gemerden. It was a pleasure studying with you guys in the 'barak'. Other people I sought assistance in the 'barak' quite frequently and were willing to help include Pieter Ketner, Frank van Langevelde, Max Rietkerk, André Schaffers and Christien de Jong.

Dr. Sip van Wieren played an instrumental role in ensuring that my speed for manuscript writing improved. Sip, I owe you a debt of gratitude for that. Dr. Arend Brunsting provided useful insights on various aspects of my work whenever I called on him. Administrative matters can at times become unnecessarily complicated, but two people among the 'troppers': Willemien Schouten and Gerda Martin, dealt with the administrative matters related to my stay in Wageningen University diligently. Willemien also designed the cover of my PhD thesis and assisted in its publication for which I am grateful. I think it would have been very rough for me with computers hadn't Herman van Oeveren, been very helpful to me. He was always willing to assist whenever I had a computer-related problem since 1996 to date. Aldo Bergsma drew all the maps for this thesis for which I am grateful.

I will now turn to the institutions, which in the first place made it, possible for me to pursue this PhD. The Netherlands Organisation for International Co-operation in Higher Education (NUFFIC) fully sponsored me financially through the Moi University (School of Environmental Studies)-University of Amsterdam (Faculty of Environmental Sciences) project which was co-ordinated by Annemieke van Haastrecht. She organised for the visas to the Netherlands, field research money, air tickets among other things and for that I am personally grateful to her, and to Moi University for giving me a 5-year study leave and the 'Suzuki' to enable me complete the PhD project. Thank you NUFFIC and Moi University.

Studying in a foreign country can be very lonely and one often misses home and the traditions that go with it. However, in Wageningen I was lucky to have the company of a few Kenyans who made some of the weekends real 'Kenyan' with *nyama choma* and *ugali*! Thank you all for being such good friends! I also cannot forget the company of fellow colleagues from Tanzania, Uganda and Zimbabwe.

Finally, this project will never have been completed without the full support of my wife Catherine. She has stood by me ever since it started and even when things got very rough. She and my children: Beryl and Ronald persevered throughout my long absence from home when I was in the field or in the Netherlands. They constantly urged me to 'push' on even during times when I was almost breaking down! For that matter, this piece of work is dedicated to them. My parents, my brothers and sisters have supported me in various ways throughout, and I am grateful to them. Lastly, thank you Isaac Kosgey for proof reading the last draft version of this thesis, and to Daniel Njaga and Jim Kairu for taking interest in my PhD work since it started.

S. M. Mwasi
April 2002
Nakuru, Kenya.

Chapter 1

General introduction

Shem M. Mwasi

Introduction

Wildlife reserves in Kenya are becoming increasingly isolated by activities associated with the expansion of human population in their neighbourhood. Infrastructure development, livestock rearing, cash and subsistence crop farming, poaching and fencing can exert varied pressure on wildlife and its habitat. This pressure may in turn cause fragmentation of wildlife ranges, closure of wildlife migratory routes (Bell 1971; Borner 1985) and excessive harvesting of wildlife leading to extinction of some animal varieties, such as the Nakuru hartebeest (*Alcelaphus buselaphus nakurae*)(Gosling 1969; Kutilek 1974). These activities, if allowed to continue unabated, will pose a serious threat to the survival of wildlife and ecological integrity of their habitats. This potential threat has made the government of Kenya realise the urgent need to conserve the remaining wildlife populations, even in areas already encroached by human activities. Since late 1960s the government has embarked on an ambitious programme to set aside some of these areas as wildlife reserves that are protected by law. Some of these reserves have either partially or completely been fenced.

Fencing of reserves often leads to their complete isolation and in most cases, wildlife habitats getting compressed (the reduction in wildlife home range size). Compression might lead to an increase in wildlife biomass densities, although the ecological mechanisms behind this expected increase are not clearly understood. It is worth noting that some of the recently isolated reserves have now become important as focal points of wildlife conservation in Kenya because of their localised high wildlife diversity and close proximity to urban centres. In most cases, co-existing grazers contribute the highest proportion of the herbivore biomass in these reserves and thus are expected to play a crucial role in the functioning of the plant-herbivore subsystems found here.

Co-existence

It is intriguing to observe how different grazer species whose needs are closely related utilise similar resources (forage and habitat) 'harmoniously' in the African savanna. There is evidence that apart from sharing habitats, grazers in the savanna also share the same food resources (Gwynne and Bell 1968; Bell 1970; Hansen et al. 1985) Mechanisms of co-existence (the condition of 'living together' at the same time) as suggested by (Harden 1960; Lamprey 1963; Bell 1971; Dunbar 1978; Leuthold 1978; Jarman and Sinclair 1979; Schoener 1982; French 1985; Jenkins and Wright 1988; Putman 1996; Prins and Olff 1998; Ritchie and Olff 1999) involve two basic principles which ensure that herbivore species do not compete for similar resources. Firstly, the species may utilise different parts of the same resource and secondly, for similar sized species with similar metabolic needs, their diets are expected to differ from one another (Schwartz and Ellis 1981) especially during periods when the amount of forage is limited. In other words as Putman (1996) puts it, if species are to co-exist then there should be no potential for competitive interaction. For co-existing herbivores to have maximal niche differentiation, several species-specific adaptations have been suggested to play a role.

Feeding styles among different herbivores, for example, can be used to explain niche differentiation. Hoffman (1973) proposed three different feeding styles based on various anatomical differences in ruminants. These are concentrate selectors, intermediate mixed feeders, and grass and roughage feeders. Most co-existing grazers in East Africa belong to the intermediate mixed feeder and the grass and roughage feeder type of Hoffman's feeding styles. They have adaptive features (e.g., a large stomach capacity and a long gut retention time) that enable them digest slow fermenting grass cell walls. It is worth noting that despite these co-existing grazers being 'lumped' together into broad similar feeding styles, species-specific differences in their digestive physiology within each class allow further niche differentiation among them so that they are able to utilise distinct parts of the same food resource in the same habitat. Differences in digestive strategies, i.e., browser-ruminants, grazer-ruminants, mixed grazer-ruminants and non-ruminants hind-gut fermenters among co-existing grazers make them utilise only a particular range of food items (Hoffman 1973; Van Soest 1982; Van Wieren 1996; Iason and Van Wieren 1999). On the other hand, interspecific differences in incisor arcade width, bite depth, bite volume and bite area are important morphological characteristics that cause differences in feeding strategies among co-existing grazers (Illius and Gordon 1987; Gordon and Illius 1988; Schuette et al. 1998).

Prins and Olff (1998) used weight ratio (mean body weight ratio between successive grazing species) from lightest to heaviest to explain species richness of grazer assemblages in Africa. A low weight ratio is correlated with high species packing and consequently a high number of co-existing species in the grazer assemblage. They predicted that there is an optimum weight ratio between two species by which niche differentiation is maximal. At this point, interspecific competition is expected to be minimal.

Food facilitation by co-existing species might also reduce the potential for competitive interaction. During facilitation, for example, as suggested by (Gywnne and Bell 1968; Bell 1970; McNaughton 1976; Maddock 1979; Sinclair and Norton-Griffiths 1982) for co-existing grazers in Serengeti NP (National Park), four species of ungulates feed on the same grass patch without showing signs of competition. These species utilise the patch in an almost sequential manner. Burchell's zebra (*Equus burchelli*) is always the first to utilise the patch by foraging mostly on upper parts of grass which comprise mainly of stems, inflorescence, and mature leaves which are low in quality (crude protein concentration). Burchell's zebra is able to tolerate a poorer quality diet because of its digestive system's ability to digest fibrous forage. The next grazer to utilise the patch is topi (*Damaliscus korrigum*) which feeds on the lower parts of grass which are better in quality than the upper parts which zebra utilised as forage earlier. The third to follow in this sequence is the wildebeest (*Connochaetus taurinus*) which feeds on the leaves, and lastly the patch is occupied by Thomson's gazelle which feeds on the highly nutritious new shoots which sprout a day or two after the grass is cropped by the other species. However, a grazing succession of this nature is difficult to prove since data are generally lacking and for the little that are available, they do not clearly show facilitation. De Boer and Prins (1990) did not observe facilitation by zebra in Lake Manyara NP, probably due to grass always being kept short by the heavy grazing pressure, and rarely do stem and flower parts that are expected to be eaten by coarse grass feeders such as zebra during a typical grazing succession observed (Drent and Prins 1987; Prins and Beekman 1989).

Jarman (1974) proposed that the nature of dispersion of forage resources is partly responsible for allowing co-existence. Jarman had in mind the fact that small-bodied herbivores would have an advantage over large-bodied ones while selecting forage resources that are more discretely dispersed and therefore, too scarce for large-bodied animals to rely on. High quality forage is usually more discretely distributed than low to medium quality forage that large-bodied herbivores rely on. Small-bodied herbivores need higher quality forage to satisfy their relatively high metabolic requirements. Therefore, they have to search more for discrete forage resources and in doing so separate themselves from the large-bodied herbivores that utilise patches with contiguously dispersed resources. Jarman's proposition is plausible in explaining co-existence of herbivores which feed on resources that are multi dimensional (different in size), e.g., fruits or seeds. However, it falls short in explaining co-existence of herbivores that feed on grass which is considered a single dimensional (same sized) resource.

Gordon and Illius (1989) demonstrated the need for the availability of an alternative forage resource which can be utilised by a subordinate (a herbivore species which is excluded from a mutually preferred resource) if co-existence was to occur at least partly during the year. The alternative resource should be able to meet the metabolic requirements of the excluded species after it has been forced out from the mutually preferred resource at a time when there is no co-existence. In this case, the excluded species is the bigger bodied herbivore. According to Gordon and Illius, if the dominant species is capable of effectively utilising both resources (the mutually preferred and the alternative), then there would be no co-existence at all between these two herbivore species, because the dominant one would force the subordinate to extinction. Gordon and Illius went further to demonstrate that red deer (*Cervus elaphus*) was the dominant herbivore, which excluded cattle from the mutually preferred species-rich *Agrostis-Festuca* grassland to the alternative species poor *Agrostis-Festuca* grassland during winter. However, in summer when mutually preferred resource is abundant, both herbivores heavily grazed on it and therefore co-existed. Gordon and Illius (1989) concluded that cattle would not be able to fulfil their metabolic requirements if they foraged on the species rich grassland during winter because of its reduced sward surface height. The species poor *Agrostis-Festuca* grassland where they move to during winter could instead meet their maintenance requirements, because it was taller and hence had a higher biomass per unit area despite being of poorer quality.

Co-existence among grazers has been shown in some cases to enhance chances of detection of predators and self defence. De Boer and Prins (1990) suggested that the association between herds of different species of grazers while feeding on certain food patches might increase their ability to detect predators. They even went further to show that zebra, wildebeest and African buffalo (*Synceros caffer*) associated positively on *Cynodon datylon* patches, where there was a lower chance of predation by lion (*Panthera leo*) on buffalo compared to *Sporobolus spicatus* patches where there was no positive association between these grazers. Sinclair (1985) suggested that zebra associated with wildebeest in the Serengeti-Mara ecosystem in order to gain protection from predators. Therefore, predation to some extent can be presumed to play a role in enhancing co-existence of large grazers in the savanna of East Africa.

Problem statement

Since most wildlife reserves where co-existing grazers inhabit are getting closed up and isolated with time under the prevailing socio-economic conditions in Kenya, it is imperative for conservation biologists to try and understand the dynamics of plant-herbivore interaction after isolation so that appropriate strategies for future management of these grazers can be formulated. Under circumstances where fewer habitats are available, one would expect shared resources to dwindle, especially when herbivore populations increase considerably without the option of emigration. Prins and Olff (1998) predicted that species packing of an ecosystem that gets smaller due to increased pressure from human activities (e.g., cultivation) would decrease because of an increase in weight ratios of local assemblages in it. Increase in weight ratio is indicative of species loss probably through resource competition. So far, there is little evidence to suggest that resource competition has led to species loss in any of these recently isolated small reserves, may be because species have not yet reached equilibrium (Western 1979). Despite this, I expect that with increased fragmentation and reduction of wildlife habitats, and the subsequent reduction in spatial heterogeneity, competitive interactions among co-existing species in local grazer assemblages within isolated reserves become more pronounced. With this in mind, and the fact that there is lack of information about how grazer species interact with one another and with their habitats when they get compressed, and on their comparative population structures and dynamics after habitat compression, I formulated a study with the following hypotheses to try and gain insights into how apparently closely related grazers continue to co-exist in isolated small reserves:

(i) *that a decline in a grazer species biomass in an isolated small reserve is due to an increase in biomass of other co-existing grazers*
(ii) *that there is a high resource overlap among co-existing grazers in an isolated small reserve.*

In order to test these hypotheses, I selected two isolated small reserves located on the floor of the Rift Valley in Kenya as study areas. They were Lake Nakuru NP and Kenya Wildlife Service TI (Training Institute) (Fig. 1.1). I selected the latter specifically for a foraging behaviour study since this could not be done in Lake Nakuru NP due to unavailability of a suitable study site. I then considered a grazer assemblage comprising ten co-existing grazers: defassa waterbuck (*Kobus defassa*), African buffalo, impala (*Aepyceros melampus*), warthog (*Phacocoerus aethiopicus*), Grant's gazelle (*Gazella granti*), Thomson's gazelle (*Gazella thomsoni*), Burchell's zebra, eland (*Taurotragus oryx*), Chanler's reedbuck (*Redunca fulvorufula chanleri*) and Bohor reedbuck (*Redunca redunca*).

Ecological history of study areas

Lake Nakuru National Park

The Nakuru wildlife area (the area occupied by the Park and the surrounding areas) used to be a haven for wildlife in the early 1900s according to the limited documentary evidence provided by early European explorers. The area was a habitat for a diversity of large wild ungulate species including defassa waterbuck, impala, Bohor reedbuck, Chanler's reedbuck, hippopotamus (*Hippopotamus amphibius*), Thomson's gazelle, Grant's gazelle, Burchell's zebra, Coke's hartebeest (*Alcelaphus buselaphus cokii*), Nakuru hartebeest, Jackson's hartebeest (*A.b. jacksoni*) which were abundant while Masai giraffe (*Giraffa camelopardalis tippelskirchi*), African buffalo and black rhino (*Diceros bicornis*) were uncommon. However, Coke's hartebeest and Jackson's

hartebeest which Chapman (1908); Meinertzhagen (1957) observed in early 1900s in the area which is now Lake Nakuru NP have since gone locally extinct. The Nakuru hartebeest is no longer found anywhere else in Kenya and is considered extinct.
Percival (1924) also reported that elephant (*Loxodanta africana*) used to make frequent visits to Nakuru area from the Laikipia plains. It no longer makes such visits.

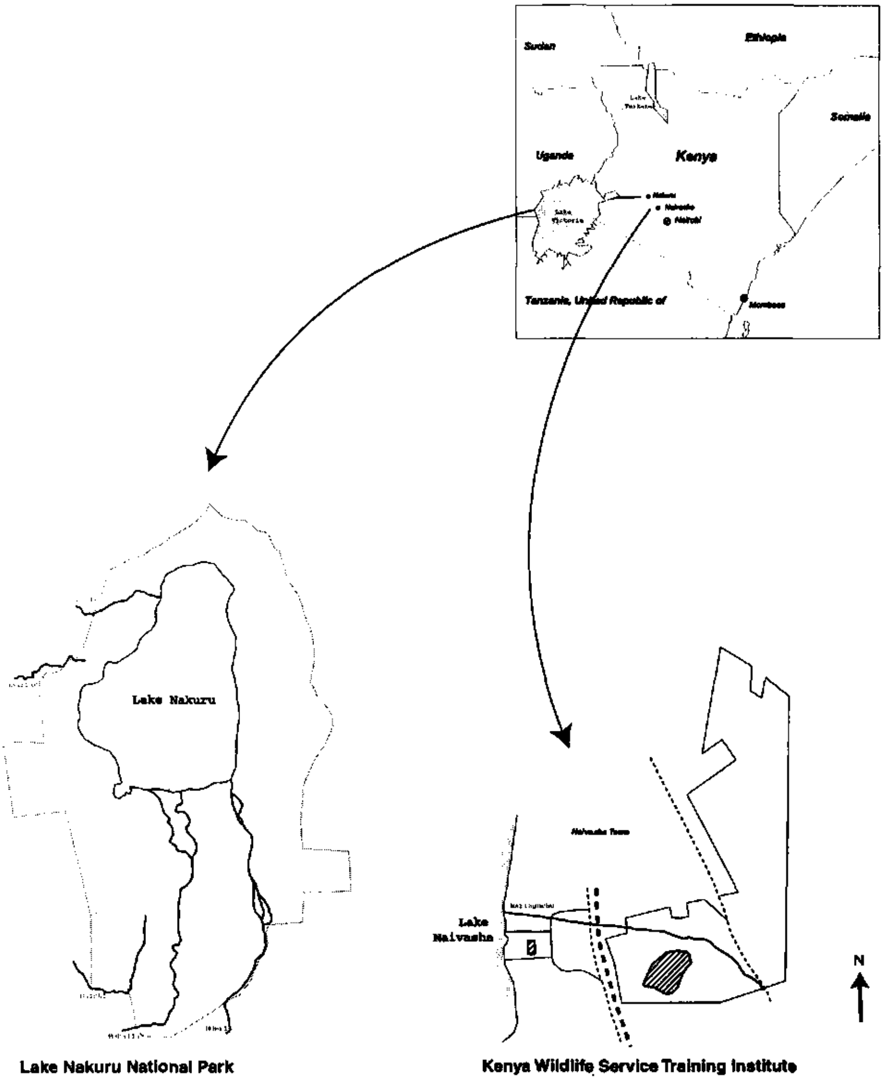

Fig. 1.1 Location of Lake Nakuru National Park and Kenya Wildlife Service Training Institute. Both wildlife reserves are found on the floor of the East African rift valley in close proximity to large urban and farming areas where human settlements are ever increasing

The Masai giraffe, which William (1970) observed in Nakuru, disappeared from this area probably towards the end of 1960s. Park census records from 1970 onwards do not indicate the presence of Masai giraffe. However, its place might have since been taken over by the Rothschild's giraffe (*G.c. rothschildi*) that was introduced into the Park in 1977.

According to Percival (1928), Burchell's zebra and Thomson's gazelle from the area where Lake Nakuru NP is located, used to undertake extensive seasonal migration to Lake Baringo (*ca.* 100 km to the north) and Lake Elementeita (*ca.* 30 km to the south). The east-west movements of large herbivores from this area are not documented anywhere and chances are that they did not move much in this particular direction probably because the steep escarpments found on both sides acted as formidable barriers. However, the north-south movements alone give an indication of how expansive the old Nakuru wildlife area might have been before increased human activities led to its fragmentation and subsequent closure of the migratory routes.

Ecosystem processes operating in this reserve have become a subject of intense biological interest during the past one decade or so. Most of this interest has been ignited by this Park's ability to host a high biomass density of large grazers in a fixed sized habitat where emigration is no longer possible. The biomass density of species which constitute the grazer assemblage in this study have been observed to fluctuate from 1974 when the Park was extended to its present size to the time this study was conducted. Buffalo has shown a sustained rise in its biomass density over the years since 1974 with no apparent sign of reaching its peak. The situation, however, has been different for waterbuck, which showed an 'exponential' increase in biomass density between 1974 to 1990, followed by a decline since then. Biomass densities of the other co-existing grazers in the assemblage have exhibited fewer fluctuations.

Kenya Wildlife Service Training Institute

Kenya Wildlife Service TI is a small isolated reserve established in 1985. It comprises three portions of land adjacent to one another, separated by the old and new Nairobi-Nakuru roads and the Nairobi-Nakuru railway (Fig. 1.2). The reserve is located about 70 km south of Lake Nakuru NP. The three blocks of land are Main campus, Annex and Game farm. Main campus (2.2 km^2) is centrally located and completely fenced except for five wildlife passages which allow Burchell's zebra, impala and eland to move in and out. Adjacent to it to the east and north east is the Game farm. It is the largest of the three blocks, consisting of a land area of 4.1 km^2. To the west of Main campus separated by the old Nairobi-Nakuru road and its adjoining old Nairobi-Nakuru railway and a small undeveloped parcel of land belonging to Kenya Agricultural Research Institute, lies the Annex (Fig. 1.2). It is the smallest block measuring 0.2 km^2 in size.

Large grazers observed in this area in the past (Williams 1970), but not anymore, include Coke's hartebeest, steinbok (*Raphicerus campestris*), Bohor reedbuck and Chanler's reedbuck. Bushbuck (*Tragelaphus scriptus*), which is now rare, is only found at the Annex. Wildebeest, which Meinertzhagen (1957) observed in the area in 1902, has since gone locally extinct. Other herbivores that have recently gone locally extinct include baboon (*Papio* spp.) and monkey (*Cercopithecus* spp.) (Abiya, pers. com.). The fact that Naivasha area was mainly used as a hunting ground by European settlers in the early 1900s (Meinertzhagen 1957) suggests that it might have had a high diversity and density of large herbivores.

In the Kenya Wildlife Service TI, large herbivores can move from one block to another but the high vehicular traffic and human disturbance associated with the old and new Nairobi-Nakuru roads might make it dangerous for them to attempt crossing. However, eland, Burchell's zebra and impala regularly cross between the three blocks (pers. obs.). There is a possibility that Coke's hartebeest, African buffalo, Masai giraffe and defassa waterbuck used to have larger home ranges than they presently do.

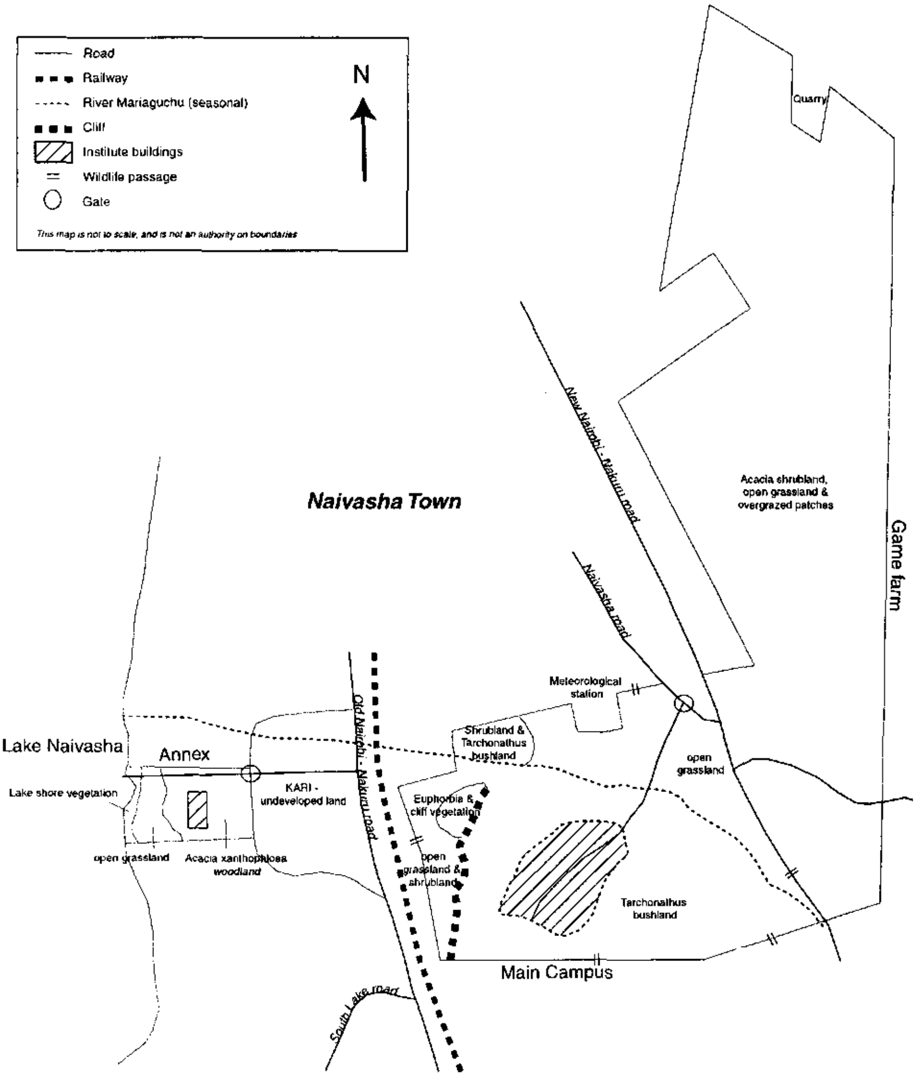

Fig. 1. 2 Map of Kenya Wildlife Service Training Institute, Naivasha

I observed these species in Main campus in 1999 but only once, an area about 1 km east of the Annex where buffalo, giraffe and waterbuck permanently inhabit. Coke's hartebeest does not usually occur in Kenya Wildlife Service TI but is instead found in the Delamare estates to the north and Kedong ranch further south west. How it managed to get to Main campus remains a mystery because of the many barriers it had to pass before reaching there.

In the past, there might have been relatively free movement of large wild herbivores from the area where Kenya Wildlife Service TI is located, to those further away from its immediate surroundings, e.g., Kedong ranch and the Delamere estates (These extend all the way from Naivasha to the neighbourhood of Lake Nakuru NP). This is because of the similar composition of large herbivore species and the almost similar vegetation types, which these areas have. This movement might have been unhindered until recently (1980s and 1990s) when human settlements, cultivation and fencing within the larger Naivasha wildlife area intensified.

Thesis outline

Grass-grazer and grazer-grazer interactions in isolated small reserves, being the main object of this study were investigated in a variety of ways and the results are presented and discussed in this thesis. **Chapter 2** explains the development of the grazer assemblage in Lake Nakuru NP from the time the Park became completely isolated to the present. The process of structuring of the different co-existing grazer populations and how ecological interactions between the grazers in the assemblage influence their respective populations and biomass densities are examined. **Chapter 3** examines seasonal habitat utilisation by the co-existing grazers in Lake Nakuru NP.

Several aspects of foraging by these co-existing grazers were investigated and results reported in **Chapter 4** and **Chapter 5**. **Chapter 4** examines diet overlap and combined resource (diet and habitat) overlap between the grazers in the Nakuru assemblage. In **Chapter 5**, the process by which some of these grazers acquire their food during the dry season is examined. In order to do so, foraging behaviour of two sympatric grazers, a ruminant and a non-ruminant occurring in Kenya Wildlife Service TI was studied. The effect of grass sward surface height, movement patterns and body weight on foraging behaviour of impala and zebra were determined. The results were used to provide insight into some aspects on how foraging by co-existing grazers actually occur in a wild, free ranging situation. So far most studies on foraging behaviour of grazers have focussed on captive or tame animals.

Chapter 6 provides a summary on how the results from the entire thesis can be used to provide an insight into grass-grazer and grazer-grazer interactions under conditions of high co-existing grazer biomass density. The management implications of this study are also discussed in this chapter.

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Chapter 2

The development of a grazer assemblage in Lake Nakuru National Park, Kenya, from 1976-1999

Shem M. Mwasi

with Sipke E. Van Wieren, Ignas M.A. Heitkönig, and Herbert H.T. Prins

Wageningen University
Department of Environmental Sciences
Tropical Nature Conservation and Vertebrate Ecology Group
Bornsesteeg 69
6708 PD, Wageningen
The Netherlands.

Abstract

We studied the development of the grazer assemblage in Lake Nakuru National Park after its enlargement to 188 km^2 and fencing in 1976, in the period 1976-1999. The assemblage consisted of species that were either of the grazer or of the mixed feeder type: defassa waterbuck (*Kobus defassa*), African buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), Grant's gazelle (*Gazella granti*), Thomson's gazelle (*Gazella thomsoni*), warthog (*Phacocoerus aethiopicus*), Burchell's zebra (*Equus burchelli*), eland (*Taurotragus oryx*), Chanler's reedbuck (*Redunca fulvorufula chanleri*), and Bohor reedbuck (*Redunca redunca*). Total biomass steadily increased over the years but total numbers appeared to stabilise after 15 years of growth. The assemblage shifted towards the smaller species (<100 kg) attaining highest population density and the larger species (>300 kg) attaining highest biomass density. Apart from a regular pattern in body weight distribution, no regular pattern could be detected in the population density distribution. This was due to the different species reacting very differently towards the new situation. Over the whole period Grant's gazelle, warthog, zebra, eland and buffalo showed high growth rates, impala and Thomson's gazelle moderate to low growth rates while Chanler's reedbuck, Bohor reedbuck and waterbuck declined. After 1990, Bohor reedbuck, warthog and waterbuck strongly declined. Of all the species that showed a lower than expected population response, Thomson's gazelle, warthog and waterbuck were possibly negatively affected from competition with other grazers, notably zebra and buffalo. After 24 years of undisturbed development, this grazer assemblage is now dominated by the impala in numbers and the African buffalo in biomass.

Keywords Biomass density · Body weight · Grazer assemblage · Population density

Introduction

The functioning and structuring principles of ungulate communities are still poorly understood. Nevertheless, the high diversity and high abundance of large herbivores in the savannas of Africa has puzzled the scientific community for quite some time (Bell 1971; Van Wieren 1996; Prins and Olff 1998; Ritchie and Olff 1999). In the past decades a number of key traits have been identified that have proved to be important in causing niche differentiation between large grazers. These are:

(i) *physiological adaptations*, leading to different digestive strategies (hindgut fermenters, browser-ruminants, grazer-ruminants and mixed grazer-ruminants) where each strategy is geared to exploiting a certain range of plant quality (Hofmann 1973; Van Wieren 1996; Iason and Van Wieren 1999)

(ii) *interspecific differences in incisor arc width* and other morphological features, leading to different strategies to exploit various sections of the quantitative food base (Illius and Gordon 1987; Gordon and Illius 1988; Schuette et al. 1998).

Recently body weight has been added as a possible explanatory variable as many ungulate communities can be characterised by a certain constancy in the body weight ratio of the species present (Van Wieren 1996; Prins and Olff 1998). It can be postulated that a certain optimal weight distance between two successive species exists whereby niche separation is maximal and interspecific competition is minimal.

Although progress is being made with relevance to these qualitative aspects of the make up of ungulate communities, very little is known about the quantitative aspects. Does a regular pattern in body weight distribution also lead to a regular pattern in the number distribution or the biomass distribution? How will different species interact at the population level? As it is generally recognised that population density (N km^{-2}) of mammals declines allometrically with body weight (Peters 1983), we hypothesise that, given a regular pattern in the body weight distribution of a community, the population density and the biomass density ((kg $km^{-2}(ha^{-1})$) distribution of this community will also show regularity. For herbivores, various exponents (of the allometric relationship $Y=aW^b$) have been suggested, ranging from b= -0.61 to -0.93 (Peters 1983). Here we use a relationship compiled by Peters (1983), using data from herbivores worldwide: $Y=103W^{-0.93}$; $r^2=0.71$. For biomass density we then expect: $Y=103W^{0.07}$.

In this paper we will analyse the population developments of the grazer assemblage of Lake Nakuru National Park, Kenya, after the Park had been enlarged, and fenced, substantially in 1976. From that time the grazer assemblage could spread freely into a large enclosed empty area, a natural experiment in the community development of ten interacting species.

Methods

Description of study site

Lake Nakuru NP lies between latitudes 0^0 18'S and 0^0 27'S; longitudes 36^0 1.5'E and 39^0 9.25'E on the floor of the East African Rift Valley. It is located about 160 km north west of Nairobi and 3 km south of Nakuru town. The Park receives a mean annual rainfall of 851 mm distributed in a bimodal pattern with rainfall peaks in the months of April and November. It has undergone one major change in size since it was gazetted in 1968. The original size was 63.5 km^2 of which 42 km^2 was occupied by Lake Nakuru and its shoreline (Vaucher 1973; Kutilek 1974). However, in 1973, the size was increased to the current 188 km^2 by the government in conjunction with World Wide Fund for Nature after buying adjacent land surrounding the entire former Park's perimeter which was mostly under livestock rearing and subsistence farming. After this expansion, large herbivores that were formerly confined to an original smaller area around the shoreline of Lake Nakuru had the opportunity to utilise a larger area. The Park was enclosed in 1976 along its perimeter by a chain link wire fence, which was later reinforced by a 74 km long electric fence in 1987. It thus became the first 'ecologically' isolated nature reserve in Kenya in 1976 when the fence largely curtailed movement of large herbivores into and outside the Park.

Species richness in Lake Nakuru NP is high. Of the ungulates, ten species belong to the grazer assemblage studied here, the species being either of the grazer or of the mixed feeder type: defassa waterbuck (*Kobus defassa* Rüppell), African buffalo (*Syncerus caffer* Sparrman), impala (*Aepyceros melampus* Lichtenstein), Grant's gazelle (*Gazella granti* Brooke), Thomson's gazelle (*Gazella thomsoni* Günther), warthog (*Phacocoerus aethiopicus* Pallas), Burchell's zebra (*Equus burchelli* Gray), eland (*Taurotragus oryx* Pallas), Chanler's reedbuck (*Redunca fulvorufula chanleri* Rothchild), and Bohor reedbuck (*Redunca redunca* Pallas). However, despite being a grazer, white rhinoceros (*Ceratotherium simum*) was not included in our study because of not being a resident of the Park in 1976 when it was enclosed. In fact, it was introduced recently in 1994 (Park records) and its biomass density is still low compared to most of the other grazers in the assemblage.

The Park is also host to a number of large carnivores that have been re-introduced over the years. A total of 40 leopards (*Panthera pardus*) and 6 lions (*Panthera leo*) have been translocated into the Park at different times between 1983 and 1993. Lion population stood at 35 in 1999 (Park records). Spotted hyaena (*Crocuta crocuta*) has also been translocated into the Park during different periods between 1989 and 1993 but its population size has not been well established. There are also other carnivores resident in the Park whose numbers have not been well documented. They include cheetah (*Acinonyx jubatus*), silver backed jackal (*Canis mesomelas*) and bat eared fox (*Octocyon megalotis*).

Census method

Our study made use of census data collected by the Park management between 1976 and 1999 (Park records). The Park has been divided into thirteen permanent counting blocks. Monthly censuses of animal species >5 kg are carried out in all the blocks as regularly as possible during the year. Each group of observers' traverse the entire block allocated to them by car although in some rare cases even on foot. The frequency of censuses varied between years with the minimum being one in 1986 and 1997, and a maximum of twelve in 1988. A sum for each monthly block count was computed per herbivore species. These were tallied for all the blocks to constitute a species monthly population size for the Park. In the case where only one monthly census was conducted in a year, a species monthly population size was used to represent its annual population size. However, in cases where there was more than one monthly census in a year, annual population size for a species was estimated as mean of the different censuses.

The census data could have some inherent sources of variation. These might have been due to a number of reasons:

(i) *inconsistency in use of same observer to count a particular block over years.* Change of observer mostly occurred due to transfer of Park personnel to other areas or retirement.

(ii) *irregularity in the number of censuses in a year.* The number of monthly censuses between years differed, with some years having more censuses than others.

Despite these limitations, we considered the census data to be reliable because they were collected using the same technique for many years. Mean live body weights were based on Prins and Olff (1998) and all densities were calculated from a land area of 146 km^2.

Assemblage structure

As it can be expected that species with similar body weights will negatively interact, species were grouped into three body weight classes to analyse the interaction of different body sizes through time. Three 'moments in time', to catch three different stages of development, were compared: the start (the average of the first three counts, (x(1-4)), the middle (x(11-13)) and the last period (x(22-24)) of the entire study period.

Results

Population developments

The results of the censuses are given in Table 2.1 while the general trend in numbers and biomass density is presented in Fig. 2.1. Fig. 2.1 shows that total biomass has steadily increased over the years ($y=520.6x+1125.6$; $r^2=0.917$) and after 24 years there are still no signs of a decrease. The trend in numbers is different: a rather strong increase till year 15 (1990), thereafter total numbers seem to stabilise. These trends demonstrate that the body weight pool of larger species grows faster than that of the smaller species.

Table 2.1 Censuses of grazing ungulates in Lake Nakuru National Park during 1976-1999 and exponential population growth rates during various periods. TG, Thomson's gazelle; CRb, Chanler's reedbuck; BRb, Bohor reedbuck; GG, Grant's gazelle; Im, impala; Wa, warthog; Wb, defassa waterbuck; Ze, Burchell's zebra; El, eland; Bu, African buffalo; BW, body weight in kg; Gr, grazer; IF, intermediate feeder

Species	TG	CRb	BRb	GG	Im	Wa	Wb	Ze	El	Bu
Type	Gr	Gr	Gr	IF	IF	Gr	Gr	Gr	IF	Gr
BW	20	30	45	50	52	73	190	235	471	631
1976	522	28	120	10	1225	27	1287	10	0	41
1978	281	3	43	8	900	23	1447	8	1	100
1979	93	5	49	9	559	18	1173	7	0	0
1986	124	0	27	57	1566	406	2759	93	63	248
1988	464	8	61	299	2946	751	3640	146	99	779
1990	409	40	51	196	4350	1214	4556	244	127	501
1991	371	7	49	213	3757	2291	2583	260	104	567
1992	530	3	20	217	3646	1782	1665	318	76	890
1993	714	5	17	212	3990	1712	1366	300	83	810
1994	629	4	15	211	4467	2453	1584	396	68	926
1995	568	4	11	252	5174	2319	1540	327	135	1309
1996	621	5	4	314	4384	2292	1247	555	81	1498
1997	588	6	3	232	3816	1135	1262	414	126	1975
1998	561	0	8	270	3270	815	954	575	40	2068
1999	610	0	0	358	3715	715	821	775	78	2189
$r_{(1-24)}$	0.050	-0.032	-0.118	0.174	0.079	0.206	-0.013	0.212	0.147	0.164
$r_{(1-15)}$	0.016	0.061	-0.035	0.266	0.109	0.320	0.096	0.270	0.410	0.182
$r_{(16-24)}$	0.029	0	-0.320	0.055	-0.008	-0.132	-0.130	0.119	-0.034	0.170

Large differences are apparent in species-specific exponential growth rates (Table 2.1). The growth rates have been calculated from the regression of numbers against year: $\ln N=rx+b$. As overall increase in animal numbers seems to come to a halt after 15 years, exponential growth rates have been calculated for the whole period ($r_{(1-}$

$_{24)}$), and for the two sub periods ($r_{(1\text{-}15}$, $r_{(16\text{-}24)}$). Zebra ($r_{(1\text{-}24)}$=0.212; r^2=0.94) and buffalo ($r_{(1\text{-}24)}$ =0.164; r^2=0.96) increased steadily and quite strongly over the whole period. In both species there might have been a lag phase as starting numbers were low. Grant's gazelle, warthog, and eland showed strong increase during the first 15 years and either

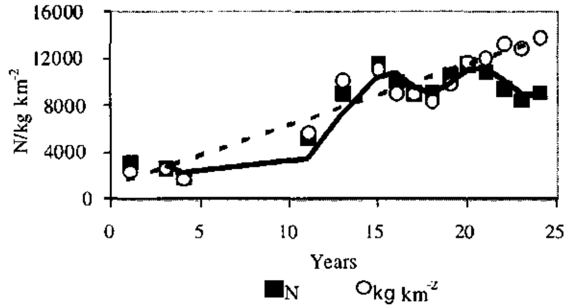

Fig. 2.1 Trend in total numbers (N) and total biomass density (kg km^{-2}) of the grazer assemblage in Lake Nakuru NP in the period 1976 (year 1)-1999 (year 24)

stabilised (Grant's gazelle and eland) or declined (warthog), ($r_{(16\text{-}24)}$ =-0.111; r^2=0.57). Impala and waterbuck had a moderate growth rate of 10% in the first period. Impala numbers stabilised in the second period (r=-0.008, r^2=0.03), but the waterbuck population declined steadily (r=-0.111, r^2=0.84). Chanler's reedbuck was present at low numbers throughout the whole period and little change was observed ($r_{(1\text{-}24)}$ =-0.032, r^2=0.08).

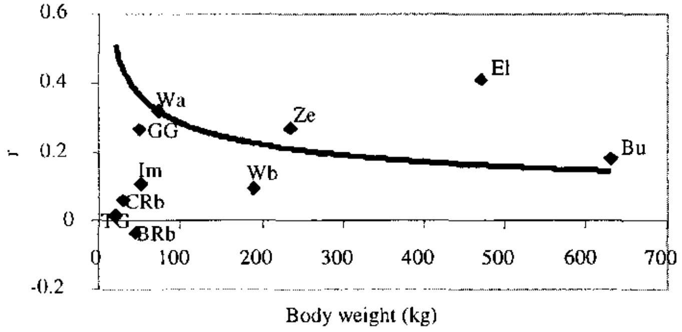

Fig. 2.2 Exponential growth rates of the grazer species of Lake Nakuru NP during year 1-15 (1976-1990), and a general relationship between r_{max} and body weight of herbivorous mammals: r_{max}=1.5W $^{-0.36}$ (Caughley and Krebs 1983). TG, Thomson's gazelle; CRb, Chanler's reedbuck; BRb, Bohor reedbuck; GG, Grant's gazelle; Im, impala; Wa, warthog; Wb, defassa waterbuck; Ze, Zebra; El, eland; Bu, African buffalo

The Thomson's gazelle population also changed very little over time while the Bohor reedbuck was the only species, which declined throughout the whole period. This decline was relatively low in the first period ($r_{(1-15)}$ =-0.035, r^2=0.18) but very high in the second ($r_{(16-24)}$ =-0.32, r^2=0.76).

Since the highest growth rates were generally found in the first 15 years, we compared these with a general allometric relationship between herbivore body weight and maximum growth rate ($r_{max}=1.5W^{-0.36}$)(weight in kg) (Caughley and Krebs 1983) (Fig. 2.2). Only a few species had growth rates close to expected (Grant's gazelle, warthog, zebra and buffalo). Growth rate of eland far exceeded the expected value while most of the smaller species performed very poorly (Bohor reedbuck, impala, Thomson's gazelle and Chanler's reedbuck).

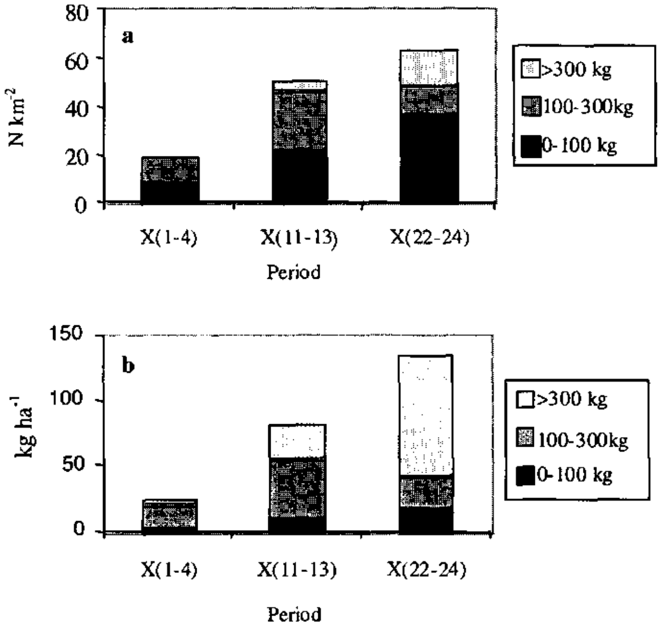

Fig. 2.3 Density (N km^{-2}, **a**), and biomass density (kg ha^{-1}, **b**) of grazers in three weight classes at three time steps during the study period. X(1-4)=mean of censuses of year 1-4; X(11-13)=mean of censuses of year 11-13; X(22-24)=mean of censuses of year 22-24. (X(1-4)=1976-1979; X(11-13)=1987-1989; X(22-24)=1997-1999)

Assemblage structure

The small sized species show a steady and strong increase in numbers while simultaneously exhibiting a less pronounced increase in biomass density compared to the medium and large sized species (Fig. 2.3). The medium sized species initially increase strongly both in population density and in biomass density but decrease strongly thereafter. Species from the largest weight class steadily increase in population density but do so very strongly in biomass density. In the last period, the small species' class is most abundant but the largest weight class outnumbers the medium sized ungulates. The large species dominate the total biomass.

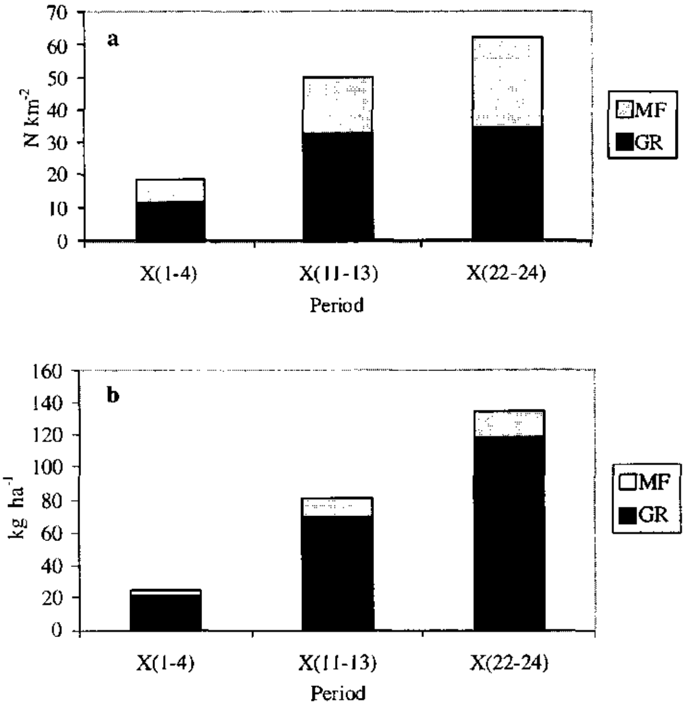

Fig. 2.4 Density (N km^{-2}, **a**), and biomass density (kg km^{-2}, **b**) of grazers in the two feeding type classes (MF, mixed feeders; GR, grazers) at three time steps during the study period. X(1-4)=mean of censuses of year 1-4; X(11-13)=mean of censuses of year 11-13; X(22-24)=mean of censuses of year 22-24. (X(1-4)=1976-1979; X(11-13)=1987-1989; X(22-24)=1997-1999)

Changes in species belonging to a certain feeding style are shown in Fig. 2.4. The trend in population density and biomass density is dissimilar. In the first 12 years, both grazers and intermediate feeders increase strongly in density but in the second period grazers population density remains the same while mixed feeder population density continues to increase. In the second period, the reverse trend is visible with respect to biomass density. The structure of the grazer assemblage was analysed using the most recent data (Table 2.2) since chances are high that the assemblage might have reached a more 'mature' state than would have been the case shortly after the closure of the Park. We thus compared this data with the expected densities derived from a general allometric relationship between density and body weight (Fig. 2.5). Fig. 2.5 makes it clear that in the grazer assemblage of Lake Nakuru NP no relationship exists between body weight and population density (and hence biomass density). No power function could be fitted through the data. The density of most species was (much) higher than expected and that of the buffalo exceeded by far all expectations.

Table 2.2 Population density (N km^{-2}) and biomass density (kg ha^{-1})of the grazer assemblage in Lake Nakuru Nakuru National Park in the period 1997-1999. BW, body weight in kg

Species	BW	N km^{-2}	kg ha^{-1}
Thomson gazelle	20	4.0	0.8
Chanler's reedbuck	30	0.0	0.0
Bohor reedbuck	45	0.1	0.0
Grant's gazelle	50	2.0	1.0
Impala	52	24.5	12.8
Warthog	73	6.1	4.4
Defassa waterbuck	190	6.9	13.2
Burchell's zebra	235	4.0	9.5
Eland	471	0.6	2.6
African buffalo	631	14.2	89.8

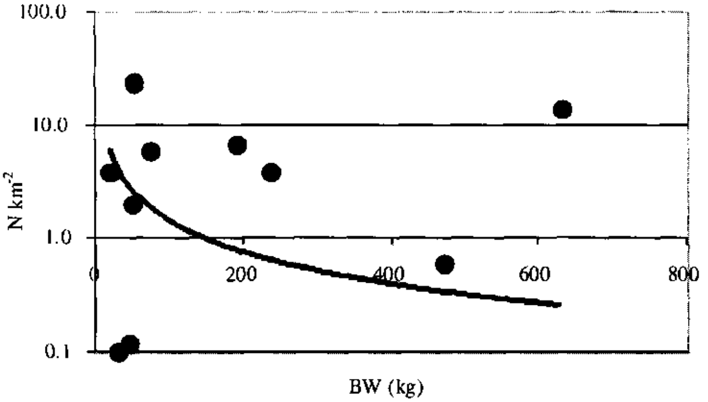

Fig. 2.5 Densities reached by the members of the grazer assemblage at the end of the study period (mean of 1997-1999) and a general allometric relationship between body weight and herbivore population density: $D=103W^{-0.93}$ (Peters 1983)

In Fig. 2.6, species were ranked according to body weight, population density and biomass density. The average weight ratio of this assemblage was 1.53 while the species packing was quite regular (r^2=0.956). The assemblage is not regularly structured with regard to population density (and biomass density) and distinct irregularities are apparent.

Discussion

Assemblage developments

From 1976 the study area was fenced, agricultural activities ceased, and the grazer assemblage had all the opportunity to expand. It did so and both population density and biomass density started to increase (Fig. 2.1). The fast initial growth was likely positively influenced by the elimination of diffuse competition from cattle, low predation, lack of poaching, stoppage of migration due to fencing and lack of major disease outbreaks. After 15 years, overall density stabilised while biomass density continued to increase. This indicates that the different members of the assemblage reacted differently to the changing situation and that the larger species became relatively more important at the expense of the smaller species. This could also be made clear when three weight classes were distinguished (Fig. 2.3). After the initial growth phase all three classes had increased both in population density and biomass density, but in the second period the medium sized species decreased while the large species increased strongly, especially in biomass density. On the whole, the population density of the grazers remained constant in the second period (Fig. 2.4) but biomass density kept increasing, indicating that a shift had occurred in favour of the larger species within the grazer feeding type. At all times, grazers were more prevalent than mixed feeders, and especially after 20 years, large grazers dominated the assemblage. This finding is in accord with the structure of other grazer assemblages on the rich volcanic soils of Eastern Africa (Prins and Douglas-Hamilton 1990; Caro 1999).

Density of most species was higher than expected from a general relationship developed by Peters (1983) (Fig. 2.5). The exponent of this function was -0.93; indicating that population density declines close to the inverse of body weight. A similar exponent (b=-1) was found by More (1947), but Damuth (1981) proposed that population density declines as $W^{-0.75}$. In Nakuru, no clear trend was observed, although the population density of the two reedbuck species may be considered outliers (see species discussion below). There is no reason to believe that the high buffalo population density is exceptional for the system under study (*cf.* Prins 1996; Caro 1999). Peters' allometric relationship was based on population densities of herbivores from four continents and in his data, obvious differences were apparent between temperate and tropical species: temperate herbivores are ten to twenty times more numerous per unit habitat, than tropical herbivores. This is most likely the result of a generally much higher species packing in tropical herbivores (Van Wieren 1996). Even so, on the rich soils of Eastern Africa, many herbivores can reach densities that match or exceed those of the temperate regions while at the same time species richness is much higher. The large intraspecific variation in population growth rates will have its repercussions on the pattern of the assemblage structure with regard to population density and biomass density (Fig. 2.6). With regard to weight ratio, the assemblage is regularly structured. The average weight ratio is 1.53 and this compares well with other 'grazer guilds' in Eastern Africa (Van Wieren 1996). With regard to biomass density no pattern is apparent and successive species can either be lower or higher in rank than adjacent species. We can not conclude yet that the lack of a regular pattern is either a unique feature of this particular assemblage or a common phenomenon of grazer assemblages because of lack of comparative data.

Population developments of species

The Thomson's gazelle population remained essentially constant throughout the whole period and the 'ultimate' density was 4 per km^2. Apparently this species was not facilitated by the large grazers as in the Serengeti (Gywnne and Bell 1968; Bell 1970;

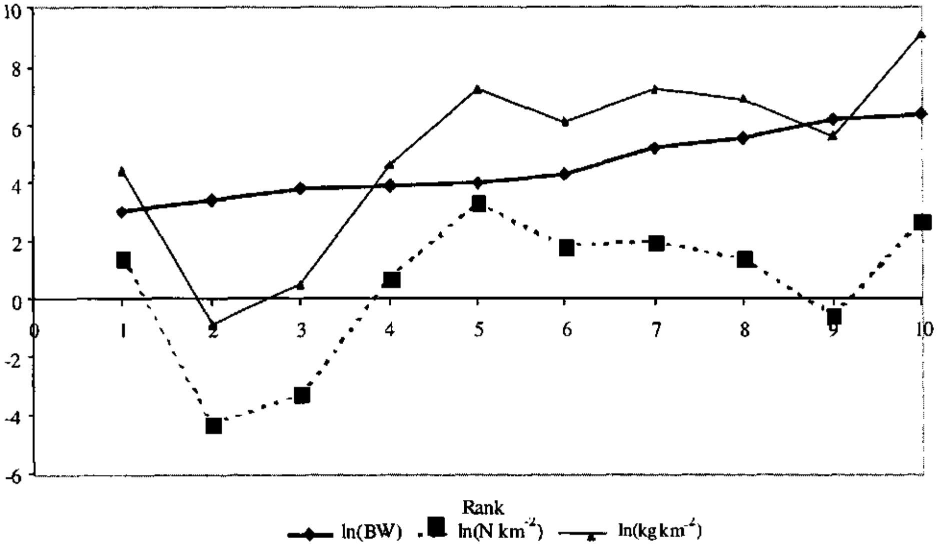

Fig. 2.6 Ranking of the species of the grazer assemblage (increasing body weight) according to body weight (BW), population density (N km^{-2}) and biomass density (kg km^{-2}). Population density and biomass density data are census means of the period 1997-1999

McNaughton 1976; Maddock 1979; Sinclair and Norton-Griffiths 1982) and the lack of an increase is puzzling. Essentially a specialist on the green flush (Stelfox and Hudson 1986), a substantial growth rate was thought possible. Competition with the reedbucks, closest in body weight, is unlikely as these species did not increase but a negative interaction with the other relatively small species: Grant's gazelle, impala and warthog, can not be ruled out as these species had already reached (or were close to) their highest density in 1990.

The two reedbuck species were only present at very low numbers in the mid-nineties, and then disappeared towards the late nineties (Table 2.1). The Chanler's reedbuck was always low in population density and apparently its suitable habitat, i.e., steep mountain slopes and dense habitat has always limited this species. Both species are dependent on water (floodplains) and the limited availability of this habitat probably has played a role too. In other similar areas, the density of reedbucks was also low (Katavi NP: 0.4 per km^2, Caro 1999), although in suitable areas, reedbuck population density can be as high as 79 per km^2 (Virunga NP, Muganga 1990). The Bohor reedbuck, however, decreased steadily after 1990 and rising numbers of the Grant's gazelle may have influenced this. Given a considerable diet overlap, both species prefer the same dense habitats with substantial cover (Estes 1991).

The fact that potential competitors, Thomson's gazelle, impala and warthog, either decreased or remained constant during the second period, does not presuppose the involvement of competition and this might be an indication that Grant's gazelle may have reached its 'carrying capacity' although 'final' density was not altogether high (Table 2.2).

Impala, a mixed feeder, is one of the most successful species in this assemblage. With a mean annual growth rate of about 8%, its numbers tripled. It attained a 'final' density of 24.5 per km^2 (Table 2.2) which was higher than 4 per km^2 recorded in Katavi NP (Caro 1999), but lower than 35 per km^2 recorded in Lake Manyara NP (Prins and Weyerhaeuser 1987). The fact that Maskall and Thornton (1989) found that 30% of the impala in Nakuru had blood copper levels below domestic normal levels does not seem to have limited impala density at all.

In the first period, the warthog increased at r_{max} (Fig. 2.2). The species was thus successfully expanding in its new range. In the second period, the species decreased by about 13% per year. The decline was especially severe after 1996 and this period coincided with strong increases of the zebra and buffalo populations and competitive displacement by these species is a likely explanation. The 'final' density of 6.1 per km^2 is, however, still high compared to similar areas (1 per km^2 in Lake Manyara NP, Prins 1987; 1.3 per km^2 in Katavi NP, Caro 1999).

Waterbuck density was the highest among the ungulate species and also the highest ever recorded (31 per km^2, Kutilek 1974) before enlargement of the Park. This was attributed to the high percentage of favourable habitat available. After enlargement, the waterbuck population grew by a moderate 10% per year till 1990 followed by a collapse in two years (from 4556 animals in 1990 to 1665 in 1992). After that the decline continued less dramatically. This collapse is not easy to explain as neither of the other members of the assemblage changed substantially during that period. The sudden decrease suggests some disease (possibly parasites) which probably went unnoticed. Its further decrease might have been due to competitive interactions with the other large grazers, notably buffalo and, to a lesser extent, zebra. As a species dependent on water, cover and open grasslands (Estes 1991), it can be expected that waterbuck has a limited and patchy distribution. But strangely enough Mwangi and Western (1998) found in a study carried out in 1991/1992 in Nakuru that it preferred the widest ranges of habitats and this is contrary to results of most other studies (Lamprey 1963; Hanks et al. 1969; Spinage 1970). It is likely that waterbuck were able to occupy sub-optimal habitats when overall density of the large grazers reached high levels, thus their utilisation of a wide range of habitats. Asymmetric competition for resources has also been suggested as the cause of population decline in the waterbuck in Umfolozi Game Reserve, South Africa (Melton 1987). Despite its decline in the nineties, waterbuck density is still high in Lake Nakuru NP (7 per km^2) compared to other areas (Tarangire Game Reserve, 2.6 per km^2, Lamprey 1963; Ruwenzori NP, 2.1 per km^2, Spinage 1970; Katavi NP, 4.4 per km^2, Caro 1999).

Zebra increased rapidly in the first period and kept increasing in the second albeit at a lower rate. Intraspecific density dependent effects can explain this lower growth rate but some displacement by the buffalo can not be ruled out. The 'final' density of zebra is comparable with another similar area (Katavi NP, Caro 1999).

The eland population increased strongly in the first period but slightly decreased in the second. Census data during the second period fluctuated widely. Being an adaptive mixed feeder, competitive interactions with other members of the assemblage do not seem likely. It is, however, possible that the fence negatively impacts on the eland. The species is known to be one of the most mobile antelopes and female home ranges are at least 174-422 km^2 (Hillman 1988), hence the fence might be limiting eland movements. Although low, the density found in Nakuru is in accord with the finding of Hillman (1988) that the overall density of eland is generally less than 1 per km^2.

The remark by Estes (1991) that buffalo is 'one of the most successful African mammals in terms of geographical range, abundance and biomass' seems to apply to the buffalo of Nakuru as well. It grew with r_{max} almost throughout the whole study period and finally reaches a high population density, and by far dominating the assemblage in terms of biomass density (Table 2.2). Even higher buffalo population densities have been recorded by Prins (1996) for Lake Manyara NP, Tanzania (20 per km^2) and Caro (1999) for Katavi NP, Tanzania (21.6 per km^2).

In conclusion, the structure of this assemblage changed during its development after enlargement of the Park. A shift was observed towards domination in numbers by the small species and domination in biomass by the large species. Apart from a regular pattern in body weight distribution, no such pattern could be detected in the population density distribution. This could be due to the different species reacting very differently towards the new situation. A number of the species showed unexpected population responses in the first period or declined in the second. Of these Bohor reedbuck, warthog and waterbuck were possibly negatively affected by other grazers, presumably buffalo and zebra.

The relatively poor performance of most of the smaller species indicates that, contrary to the hypothesis of Prins and Olff (1998), smaller grazers are not necessarily facilitated by the larger ones and that competition apparently can occur across a wide range of body weights. At present, the assemblage is dominated by two very successful species: the versatile small mixed feeder, the impala, and the large generalist grazer, the African buffalo.

Acknowledgements

The authors wish to thank Kenya Wildlife Service, through the management of Lake Nakuru National Park for the census data. This research was funded by the Netherlands Organisation for International Co-operation in Higher Education, to which we are grateful.

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Chapter 3

Habitat use by a dense grazer assemblage in Lake Nakuru National Park, Kenya: facilitation, competition or habitat segregation?

Shem M. Mwasi

with Ignas M.A. Heitkönig, Sipke E. Van Wieren, and Herbert H.T. Prins

Wageningen University
Department of Environmental Sciences
Tropical Nature Conservation and Vertebrate Ecology Group
Bornsesteeg 69
6708 PD, Wageningen
The Netherlands.

Abstract

We studied habitat utilisation by an assemblage of co-existing grazers in Kenya's Lake Nakuru National Park: Thomson's gazelle (*Gazella thomsoni*), Grant's gazelle (*Gazella granti*), impala (*Aepyceros melampus*), warthog (*Phacocoerus aethiopicus*), defassa waterbuck (*Kobus defassa*), Burchell's zebra (*Equus burchelli*) and African buffalo (*Synceros caffer*). Grass forms a common resource to these grazers, and sharing it is expected to lead to niche differentiation among them. According to the ideal free distribution theory, subordinate individuals within a population are forced to occupy low quality habitat by despotic individuals which, by extension to a multi-species assemblage, implies that subordinate species are forced to occupy lower quality habitats and may even get displaced. We assumed that the larger grazers in the Lake Nakuru NP assemblage were dominant over the smaller ones based on findings that large herbivore species in the Dutch Oostvaardersplassen area are dominant over smaller ones. We also used the predictions of the multi-specific facilitation theory whereby, larger grazers are expected to crop the taller fibrous grass tufts leaving the lower grass sward levels for the smaller grazers. Frequency of seasonal habitat occupancy on the short and medium open grasslands, which were the most utilised habitats by large- and small-bodied grazers appear to be similar, contrary to the predictions of the ideal free distribution theory. Furthermore waterbuck, warthog and Thomson's gazelle were more restrained in their habitat choice than other grazers because they had a high degree of habitat overlap with other grazers (larger or smaller). They were, however, not displaced by the larger grazers as expected but instead seem to use the same resources. This might imply that the larger grazers were facilitating waterbuck, warthog and Thomson's gazelle. However, we found out that this was not the case, because Mantel test results did not provide a clear positive correlation between similarity in habitat use and similarity in body weight in the early- and late-wet season when grass regrowth, which is good for smaller species, is expected to occur. However, the weak negative correlation calculated for the late wet season suggests a possibility of competition among the grazers during this season. We therefore conclude that competitive interactions among grazers in Nakuru are apparent through directional habitat use overlap indices, and might have been the cause of the negative population growth rates in waterbuck and warthog.

Introduction

We observed an increase in grazer densities in Lake Nakuru National Park from 1976 onwards, and we recorded a development towards high numbers and biomass values for many grazer species (Chapter 2). The high numbers totalling *ca.* 60 individuals per km^2 (0.6 individuals per ha), with a total biomass of *ca.* 13400 kg km^{-2} (134 kg ha^{-1}) excluding the recently introduced white rhinoceros (*Ceratotherium simum*) suggest that resource limitation might take place. Before 1974, a similarly high density of about 60 individuals per km^2 was observed when the Park boundaries were limited to a small zone surrounding Lake Nakuru, but the grazer biomass density stood considerably lower then at *ca.* 63 kg ha^{-1} (Kutilek 1974). Park extension from *ca.* 46 to *ca.* 188 km^2 terrestrial surface in 1974 lowered the grazer number and biomass density to approximately 15 individuals per km^2 (0.15 individuals per ha) and 1540 kg km^{-2} (15.4 kg ha^{-1}) respectively at that time (calculated from Kutilek 1974).

The animals in this grazer assemblage share grass as a common resource. Sharing a common resource is expected to lead to spatial and/or temporal measures of niche differentiation in order to avoid competition and to retain fitness. We do not know of a theory that adequately explains habitat use by species assemblages, so we explore the possible consequences of the mono-specific animal distribution theory and of the multi-specific competition/facilitation theory to develop hypotheses on this issue for our study. Prins (2000) reviewed the evidence for competition among wildlife species, and between wildlife and livestock.

Different grazer species prefer different types of habitat (Hirst 1975), especially when food supply and/or food quality is poor. The ideal free distribution, designed to predict habitat use for a single species, suggests that all high quality habitat is preferentially used until the moment that species density is so high that low quality habitat becomes at least as attractive (Fretwell 1972). If all species were equal, this would suggest that the highest densities of all species would occur in prime habitat, and lower densities of all species in poor habitat. However, species are obviously not equal, and differences in body mass and mouth morphology have led to biomass and morphological based explanations for differential habitat use (Murray and Brown 1993; Chapter 2). In particular, larger grazers are expected to use moderate and low quality swards with high productivity, which tend to be of moderate or low quality, and smaller grazers are expected to use low productive swards, which tend to be of moderate or high quality (Wilmshurst et al. 2000). If the ideal free distribution is operational, the densities of large and small grazers are accordingly different over high and low production swards.

The ideal despotic distribution predicts that subordinate individuals within a single species are forced to occupy low quality habitat by despotic individuals (Fretwell 1972). Translated to multi-species assemblages this suggests that subordinate species will be forced to occupy lower quality habitat. They may even become displaced, avoiding resource overlap with the dominant species. In geese (*Anser* spp.), larger species are dominant over smaller species, and large herbivores in the Dutch Oostvaardersplassen area are dominant over smaller herbivores (Van Wieren, pers. obs.). For the purpose of this study, and due to a lack of information to the contrary, we therefore consider the larger grazers in the Lake Nakuru NP assemblage to be dominant over smaller species.

Niche differentiation may be enhanced through resource competition, or counteracted through facilitation. In a direct way, larger grazer species crop the taller, fibrous grass tufts in the sward, making the lower sward levels available for smaller herbivores. In a dynamic process, larger grazer species crop the sward, which responds with leaf regrowth in the wet season, and which in turn again can be cropped by either the same large, or other smaller grazers. When regrowth does not take place, for instance in the ensuing dry season, this dynamic facilitation is expected to stop.

We hypothesise that subordinate species will be forced into lower quality habitat once prime habitat has become saturated. This process of habitat displacement is expected to take place mainly during the dry season, when grass regrowth has stopped and resource availability is therefore further reduced. We furthermore hypothesise that the current, dense grazer assemblage at Lake Nakuru NP operates through facilitation of smaller species by larger species. This process involves regrowth of grasses, which will only be possible during the wet season.

We tested these hypotheses by first calculating habitat use and habitat overlap for each of the seven predominantly grazing species in contrasting seasons, and then by comparing figures of habitat overlap with body weight ratios between pairs of species across the seasons. We furthermore drew on the population development of the species in the grazer assemblage in the past period to corroborate our results.

Methods

We measured habitat use by scoring the occurrence of seven predominantly grazing species, namely Thomson's gazelle (*Gazella thomsoni* Günther), Grant's gazelle (*Gazella granti* Brooke), impala (*Aepyceros melampus* Lichtenstein), warthog (*Phacocoerus aethiopicus* Pallas), defassa waterbuck (*Kobus defassa* Rüppell), Burchell's zebra (*Equus burchelli* Gray), and African buffalo (*Syncerus caffer* Sparrman) along fixed car transects throughout Lake Nakuru NP, covering all parts of the Park twice monthly from May 1998 until March 1999, and allocating the position of individuals or groups to one of eight physiognomic vegetation units:

(1) Lake shore vegetation, dominated by *Cyprerus laevigatus* and *Sporobolus spicatus*
(2) short open grassland ≈ below 30 cm tall
(3) medium open grassland ≈ 30 cm to 1 m tall
(4) tall open grassland ≈ above 1 m tall
(5) swamp vegetation, including mud/pond/riverine vegetation/flooded area
(6) open *Tarchonanthus* bush
(7) open *Acacia* woodland
(8) woody vegetation comprising other scrub species, including *Solanum* spp.

Since 1998 was a very wet year with 1121 mm of precipitation, and with at least 44 mm of rain during each month, the functional seasons distinguished here deviate somewhat from the more commonly used long and short wet and dry seasons. In our case, the period May-June 1998 represents the early growing season, with lush green grass. The October-December period is characterised by tall, fibrous swards and represents the late wet season. The dry season in our case is January-March 1999, when the swards turned yellow and regrowth stopped.

Data analyses

The animal data from the bi-weekly transect surveys were summed for each season, and summarised as fractions for each habitat, where each species sums to 1.00 across all habitats. It was of particular interest in this study to assess the extent to which species *k* overlaps on each of the other species, rather than to assess an average value for the overlap of species *k* in species *j* and of species *j* on species *k*. Hence, we used the directional MacArthur and Levins (1967) index of niche overlap for this purpose, substituting physiognomic vegetation units for niche: $O_{jk}=\Sigma p_{ij}\, p_{ik} / \Sigma p^2_{ij}$

Where:

O_{jk} = MacArthur and Levins vegetation unit overlap of species *k* on species *j*, furthermore called the habitat index or index of habitat overlap

p_{ij} = proportion of vegetation unit *i* of the total vegetation units used by species *j*

p_{ik} = proportion of vegetation unit *i* of the total vegetation units used by species *k*

Substituting *k* for *j* and *j* for *k* in this formula, we were also able to calculate the overlap of species *j* on species *k*.

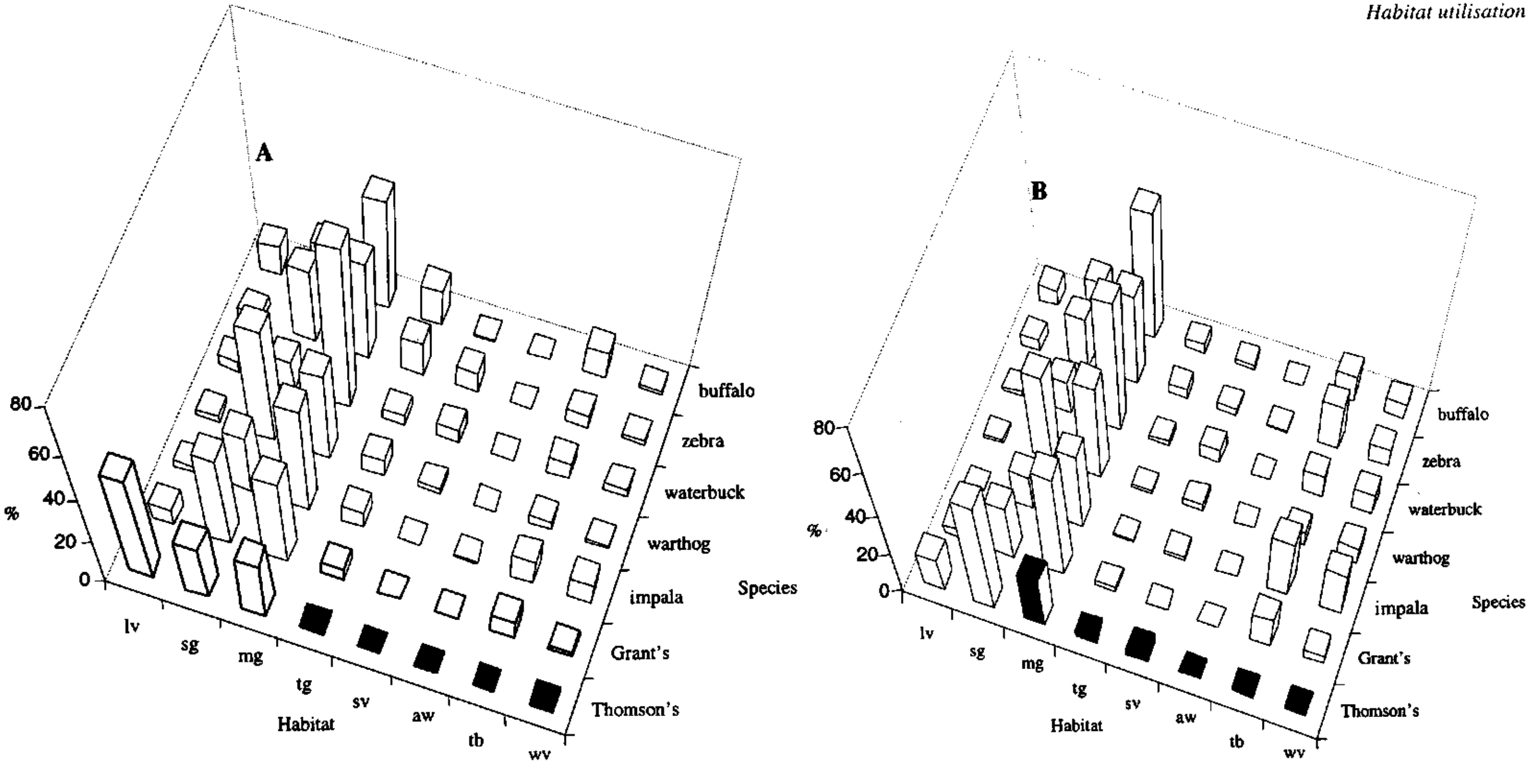
In order to assess whether the similarity in habitat use was correlated with similarity in body weight for each pair of species, we first calculated the difference between the pairs of niche overlap values associated with each of two species pairs, for each season. More specifically, we subtracted the index overlap value of species *j* on species *k* from the index overlap value of species *k* on species *j*. This provided three distance matrices, one for each season. These were correlated with a distance matrix of body weight ratios. The body weight ratios in the latter matrix were calculated as ln(1+ body weight), with body weight in kg. This calculation and transformation provided values between 0 and 1. The correlations with habitat similarity were calculated using Mantel tests on the species-species distance matrices, followed by 999 Monte Carlo permutation tests to estimate the significance (P) of each seasonal correlation (R) between similarity in habitat use and similarity in body weight. We created an impression of the correlation between body weight similarity and similarity in habitat use by producing seasonal scatter graphs, based on the data from the distance matrices.

Results

Description of seasonally changing habitat use by each of the seven species is given in 3 dimensional figures (Fig. 3.1, A-C). Many species have similar habitat uses, with high occurrences in short and medium open grasslands. Tall open grasslands are not much used, even by the largest grazers, nor are the riverine vegetation and marshland. Woody areas become more used from the late wet season onwards. Thomson's gazelle seems to prefer Lake shore vegetation more than other species. Most prominent changes across the species are from early wet to late wet season (Fig. 3.1, A-B), rather than from late wet to dry season (Fig. 3.1, B-C).

MacArthur and Levins indices of habitat overlap for each of the three seasons suggest that zebra habitat use was consistently broader than the other species in all seasons, while that of impala and buffalo were mostly broader (Table 3.1). Habitats for waterbuck, warthog and Thomson's gazelle were mostly subsets of the other species, especially in the early wet and late wet seasons. The measures of habitat overlap for each of the three seasons suggest that the largest dissimilarities in habitat use occur between the species pairs: waterbuck-buffalo, waterbuck-zebra, waterbuck-impala, warthog-buffalo and waterbuck-zebra in the early wet season, waterbuck-zebra, waterbuck-impala and warthog-zebra in the late wet season, and between waterbuck-zebra, warthog-zebra and Thomson's gazelle-zebra in the dry season (Table 3.2). Both waterbuck and warthog feature prominently here, in combination with zebra and buffalo.

Mantel test results indicate very low levels of correlation among similarity in habitat use and similarity in body weight in the early wet season ($R=0.054$, $P=0.424$), the late wet season ($R=-0.239$, $P=0.211$) and in the dry season ($R=-0.091$, $P=0.421$). Inspection of the scatter graphs (Fig. 2, A-C) confirms the absence of clear trends regarding the influence of body weight similarity on habitat use similarity. It is apparent that species pairs with extreme or medium differences in body weight and thus with low body weight ratios, have similarly divergent patterns in habitat use as species with small body weight differences.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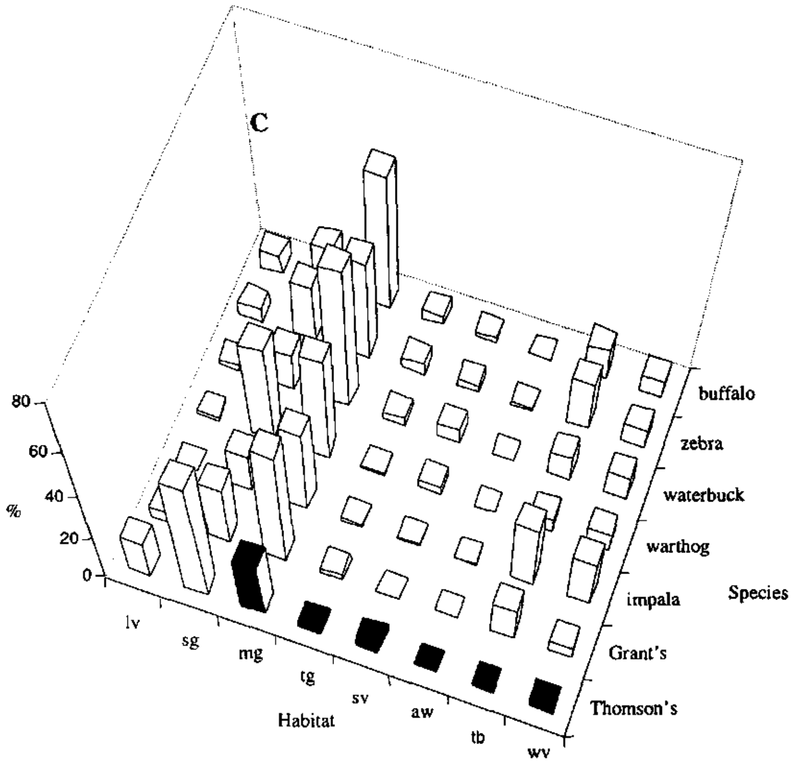

Fig. 3.1 Frequency of habitat occupancy by seven grazer species in Lake Nakuru National Park, Kenya, for three periods throughout a wet year: early part of a long wet season (**A**; May-July 1998), last part of a long wet season (**B**; October-December 1998), and the ensuing short dry season (**C**; January-March 1999). Animal species are arranged in ascending order of body weight (see Chapter 2, Table 2.1). Habitat lv: Lake shore vegetation, sg: short open grassland (< 300 mm tall), mg: medium open grassland (300-1000 mm tall), tg: tall open grassland (>1000 mm tall), sv: riverine and marsh vegetation, aw: open *Acacia* woodland, tb: open *Tarchonanthus* bush, wv: other shrub vegetation. The most prominent change in habitat occupancy appears to take place from early wet to late wet season, when woody areas increase in favour for most species.

Discussion

The observations were carried out in an extremely wet year, with monthly rainfall averaging 93 mm, and exceeding 44 mm in any one month from May to December 1998. In fact, rains started two months before our detailed field observations, so the total rainfall over that period has exceptionally enhanced grass production. In other words, if facilitation would occur, it would most likely have been visible in this particular period of observation. Nevertheless we did not find any evidence for this process.

Evidence for habitat segregation

In contrast to a study by Mwangi and Western (1998) in the same study area, our results indicate that there is a high degree of habitat overlap among the seven large grazer species in Lake Nakuru NP, that habitat segregation in general is very limited, and that waterbuck in particular uses a smaller habitat spectrum than other species in almost all seasons. All grazers use the short and the medium open grasslands to a high degree, and all species appear to use the tallest swards to a very limited degree only. Hence, the densities of large and small grazers appear to be similar, rather than different over high and low productive swards. This suggests that the ideal free distribution adapted for multi-species assemblages is not operational here.

Table 3.1 *Index of habitat overlap of species k in column heading on species j in rows.* A positive (+) sign means that the MacArthur and Levins index of habitat overlap of species *k* on species *j* is larger than the overlap of species *j* on species *k*. A negative (-) sign means that the opposite is the case

	Thomson's	Grant's	impala	warthog	waterbuck	zebra	buffalo
Early wet season							
Thomson's		-	-	+	+	-	-
Grant's	+		-	+	+	-	-
impala	+	+		+	+	-	-
warthog	-	-	-		+	-	-
waterbuck	-	-	-	-		-	-
zebra	+	+	+	+	+		+
buffalo	+	+	+	+	+	-	
Late wet season							
Thomson's		-	-	-	+	-	-
Grant's	+		-	+	+	-	-
impala	+	+		+	+	-	+
warthog	+	-	-		+	-	-
waterbuck	-	-	-	-		-	-
zebra	+	+	+	+	+		+
buffalo	+	+	-	+	+	-	
Dry season							
Thomson's		-	-	-	-	-	-
Grant's	+		+	+	+	-	+
impala	+	-		+	+	-	+
warthog	+	-	-		+	-	-
waterbuck	+	-	-	-		-	-
zebra	+	+	+	+	+		+
buffalo	+	-	-	+	+	-	

Waterbuck, Thomson's gazelle and warthog have mostly + signs in their respective columns, which suggests that the way in which they are distributed over the habitats forms a subset of the way in which other species: zebra, buffalo, impala, and Grant's gazelle are distributed over the habitats.

Are subordinate species forced to occupy lower quality habitat? And are they even displaced, avoiding resource overlap with the dominant species? The high degree of habitat overlap of waterbuck, warthog and Thomson's gazelle on other species (+ signs in Table 3.1) suggests that they are more restrained in their habitat choice than the other

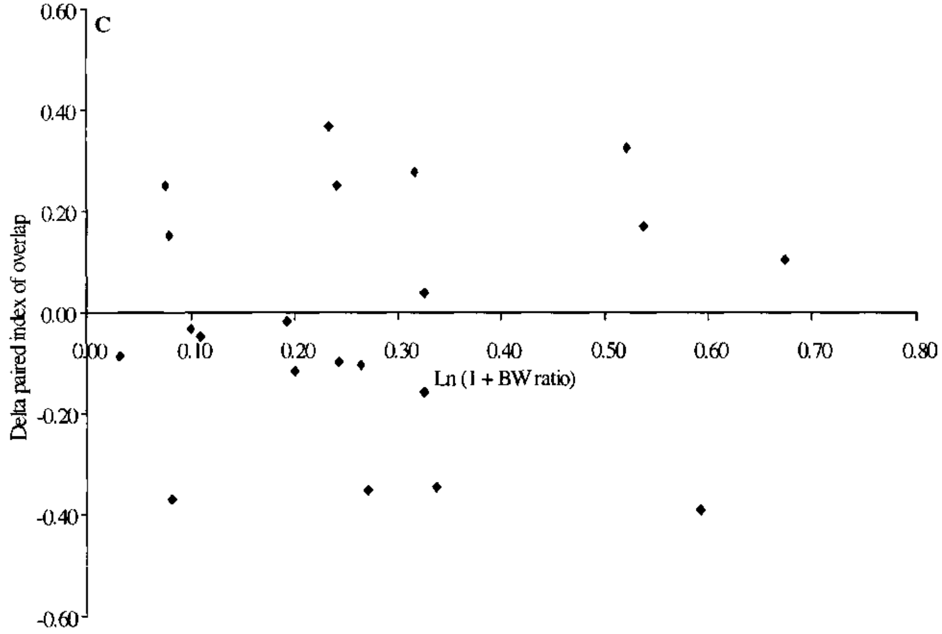

Fig. 3.2 Scatter diagrams of the difference in MacArthur and Levins species-paired habitat overlap indices *versus* the natural logarithm of the body weight ratio of the animal species pairs, by season: **A** early wet season, **B** late wet season, **C** dry season. The scatters are not correlation diagrams *per se*, but purport to visualise the outcome of the Mantel tests between the difference in paired habitat overlap indices (i.e., the overlap index of species *k* on species *j* minus the overlap index of species *j* on species *k*) and the paired body weight ratio of each of the species combinations. Mantel test R values are close to zero, ranging from -0.239 to +0.054 (P>0.21), suggesting that the extent of habitat overlap is independent of the body weight ratio of the grazers in each season.

matrix correlations, with further graphical support from the scatter diagrams (Fig. 3.2). However, the absence of any clear, positive correlation between these variables in the early wet and late wet seasons, suggests that facilitation does not take place, or at least not according to the mechanism, which we expected it to operate. Detailed analysis of diet overlap could shed more light on this issue. Contrary to our hypothesis, a weak negative correlation in the late wet season suggests that competition takes place during that period. If competition takes place, the outcome should be visible in terms of a fitness parameter like population growth rate. Indeed, waterbuck and warthog both show declining population sizes in Lake Nakuru NP, whereas the population sizes of other species increase or remain constant (see Chapter 2, Table 2.1). Therefore, we reject our hypotheses on facilitation and species displacement or habitat segregation to occur in Lake Nakuru NP. Instead, the large overlap in habitat use and subsequent loss of fitness in those species with the most restrained habitat choice suggest that competition for food resources takes place, even in the wet season. We suggest that the high degree of habitat overlap is associated with negative growth rates in several large grazer species. In years of average or even low rainfall, resource limitation is expected to be even more severe, leading to more intensive competition, and further declines in species numbers. We foresee further negative effects on warthog and waterbuck, especially now that white rhinoceros has been introduced into the Park.

Conclusion

The Lake Nakuru grazer assemblage consists of seven species, ranging in body weight from 20 to well over 600 kg. The species occur in large densities, and show a high degree of habitat overlap in a particularly wet year, with associated high biomass production. We did not find indications for facilitation to occur, but competition was apparent through the directional habitat overlap indices. The two species with the highest degree of habitat overlap (waterbuck and warthog) also showed negative population growth rates (Chapter 2), confirming our analysis of resource competition. We expect this interaction among the herbivores to be even stronger in years with average or below average rainfall. It appears that the current policy on introducing large herbivores like white rhinoceros to Lake Nakuru NP needs to be re-examined.

Acknowledgements

We wish to thank the Netherlands Organisation for International Co-operation in Higher Education for financially supporting this research and the Kenya Wildlife Service for allowing the research to be conducted in Lake Nakuru National Park. We are also grateful to Charudutt Mishra for helping us shape our thoughts on the data analyses.

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Chapter 4

The potential for competition within the grazer assemblage of Lake Nakuru National Park, Kenya

Shem M. Mwasi

with Sipke E. Van Wieren, Ignas M.A. Heitkönig, and Herbert H.T. Prins

Wageningen University
Department of Environmental Sciences
Tropical Nature Conservation and Vertebrate Ecology Group
Bornsesteeg 69
6708 PD, Wageningen
The Netherlands.

Abstract

We studied resource use and resource overlap of a grazer assemblage of Lake Nakuru National Park at the end of a long wet, during a short dry and in the early long wet season in the period 1998-1999. Diet composition was estimated by means of faecal analysis of epidermal fragments and habitat use by direct observation. Because of large variations in population developments of the members of the assemblage and because of a high animal density, we predicted that overall resource overlap would be substantial, that niche breadth and overlap would be smallest in the dry season and overlap would be greatest between species with similar body weights. Both diet composition and habitat use were very similar for all species across seasons. Niche breadth of diet and habitat was narrow in all seasons. As expected, niche breadth for diet was smallest in the dry season for almost all species, but this was not the case for habitat use. Overlap in diet composition and habitat use was high between all pairs of species across all seasons. Similar sized species had higher dietary overlap in the short wet season and the short dry season than species whose body weights differed widely; with habitat overlap no differences were found. Indices of combined overlap showed that in the majority of cases a critical limit to similarity for co-existence was exceeded, indicating that competitive interactions are occurring at present. No conclusions could be drawn on how the various species are affected by these interactions. Further work is needed to unravel the precise mechanisms and directions of the competitive forces.

Keywords Combined overlap · Competitive interactions· Niche breadth

Introduction

The savannas of East Africa are well known for their high diversity and abundance of ungulate species. Contributing to this richness most likely is the presence of rich volcanic soils that permit a high primary productivity and a high mineral content of important forage plants (Field 1972; Wrench et al. 1997; Voeten 1999). The mechanisms by which co-existence of so many (apparently) similar species is made possible have been subjects of study for quite some time (Lamprey 1963; Bell 1971; Field 1972; Hofmann 1973; Prins and Olff 1998). A number of key traits have been identified by means of which resource segregation between large herbivores becomes possible. Among these traits are *physiological adaptations*, leading to different digestive strategies (hindgut fermenters, browser-ruminants, grazer-ruminants and mixed grazer-ruminants) where each strategy is geared towards exploiting a certain range of plant quality (Hofmann 1973; Van Wieren 1996), and *interspecific differences in incisor arc width*, leading to different strategies to exploit various sections of the quantitative food base (Gordon and Illius 1988; Schuette et al. 1998), while also *body weight* is considered a differentiating factor (Van Wieren 1996; Prins and Olff 1998). Nevertheless, it has also been speculated that competitive interactions can be expected especially when species become 'too' similar (Van Wieren 1996; Prins and Olff 1998) or when species are being reintroduced in their former range (Prins and Olff 1998). Although competition in the field is very hard to detect, evidence that it might be playing a role within grazer-communities has been reported (Field 1972; De Boer and Prins 1990; Fritz et al. 1996; Prins and Olff 1998). It is expected that during the season when resources are most limiting, resource separation among animals become more pronounced as they specialise to avoid competition. This phenomenon has been reported in a number of instances (Field 1972; Gordon and Illius 1989; Dekker et al. 1996; Fritz et al. 1996).

Forage quality of wild grazing ungulates in East Africa varies with seasons, which are primarily defined by amount of rainfall received in an area during a particular period. Using this criterion, two broad categories of seasons characterise areas where large concentrations of wild grazing ungulates are found: wet and dry. Intra-annual rainfall in these areas is correlated with primary production (Phillipson 1975; Sinclair 1975). During a dry season with little or no rainfall, above ground green standing crop biomass might be relatively low, while a wet season is characterised by a high green standing crop biomass. An increase in green standing crop biomass is generally associated with improved quality of the forage (Wrench et al. 1997; Voeten 1999). Hence, both from the perspective of food availability and that of food quality, the dry season will generally be the most limiting in East Africa, although fluctuations in quality are probably of more importance than those in biomass (Field 1975; Sinclair 1975; Prins 1996).

We have evidence that, at present, competitive interactions are taking place between members of the grazer assemblage in Lake Nakuru National Park, Kenya, and that competition actually is one of the factors shaping this community. Earlier we described population developments of the grazer assemblage in this Park after its enlargement to 188 km^2 in 1976 (Chapter 2). During the subsequent 24 years, the different species reacted very differently to the new situation. Some showed a steady or large increase in biomass throughout this whole period (buffalo, zebra), while others did well in an early phase but poorly (remaining constant or decreasing) in a second phase, after 15 years (waterbuck, Grant's gazelle, impala, warthog) (Chapter 2). These differential developments suggest that the smaller grazers are negatively affected by the larger ones. One of the prerequisites for competition is resource overlap and in this paper we will study diet choice, habitat use and indices of resource overlap of the main members of the grazer assemblage in Lake Nakuru NP during 1998-1999. We hypothesise that, within the assemblage,

1. *resource overlap will be substantial in all seasons but least in the dry season, and*
2. *resource overlap will be greatest between species with similar body weights.*

Materials and methods

Study area

Lake Nakuru NP is situated about 160 km north west of Nairobi (Kenya). The Park is enclosed by a perimeter electric fence. Its area is 188 km^2 in which Lake Nakuru occupies about 42 km^2. Various types of vegetation are observed in the Park, the most dominant being grassland (Fig. 4.1). A detailed description of the habitat types found in the Park is given by Mutangah (1994).

We distinguished eight different physiognomic vegetation units whose correspondence with the habitat types from Fig. 4.1 is indicated in Table 4.1. Grasslands are found throughout the Park. They are dominated by *Cynodon nlemfuensis* (Mutangah 1994). Other important forage plants for the grazers include *Chloris gayana*, *Sporobolus spicatus*, *Themeda triandra* and *Cyperus laevigatus*.

Rainfall pattern in the Park is bimodal, whereby two wet and two dry seasons occur during the year. The first wet season starts in October and ends in December (short wet), while the second starts in March and ends in June (long wet). In between are two dry seasons: January to February (short dry) and July to September (long dry). The data were collected at the end of an abnormally long wet season of 1998 (late wet) with 171 mm, the short dry season of 1999 with 37 mm, and the early long wet season of 1999 with 285 mm of rain. No data collection was possible during a long dry season because substantial rainfall characterised the potential long dry season during the study period.

Table 4.1 Physiognomic vegetation units and corresponding habitat types of Lake Nakuru National Park. G, grassland comprising mainly of *Cynodon nlemfuensis*, *Themeda triandra*, *Chloris gayana*, *Sporobolus spicatus* and *Digitaria abyssinica* (see Mutangah 1994); SM, alkaline marsh; RV, riverine vegetation; B, bushland; W, woodland

Unit	Description	Habitat
LSV	Lake shore vegetation, dominated by *Cyperus laevigatus*, *Sporobolus spicatus* and *Cynodon dactylon*	SM
SOG	Short open grassland ≈ below 30 cm tall	G
MOG	Medium open grassland ≈ 30 cm to 1m tall	G
TOG	Tall open grassland ≈ above 1m tall	G
SW/V	Swamp, flooded and riverine vegetation dominated by *Cyperus laevigatus*, *Typha domingensis*. River banks are dominated by *Acacia xanthophloea* and *A. albida*	RV
OTB	Open *Tarchonanthus* bush	B
OAW	Open *Acacia* woodland	W
WV	Vegetation comprising mainly of *Solanum* spp., *Ocimum* spp., *Aspilia* spp. and *Rhus natalensis* mixed with grassland	G

Forage quality

To determine possible inter-seasonal differences in plant quality, samples of the most important forage plants in Lake Nakuru NP were collected from patches within grasslands where repeated heavy grazing by ungulates occurred. Total nitrogen content of leaf and stem was used as an indicator of forage quality. Forage plants included *Chloris gayana*, *Sporobolus spicatus*, *Cynodon nlemfuensis* and *Themeda triandra.* Grass samples were clipped at ground level during the late wet season of 1998, short dry season of 1999 and early long wet season of 1999. After clipping each sample was separated into portions of green leaves and stems, and sun dried. Nitrogen content was then determined from ground portions of each plant part using the Kjeldahl procedure. Data on nitrogen content of *Cyperus laevigatus* which is also an important forage plant for the Nakuru grazers were taken from Prins (1996) on work done in Lake Manyara NP (Tanzania) whose soil characteristics and rainfall patterns are relatively similar to those of Lake Nakuru NP.

Botanical composition of diet

Data on diet were collected from an area of the Park where grazers are always encountered throughout the year. The area mainly includes the northern and north-western, central and southern parts of the Park (Fig. 4.1).

Fresh dung samples (where nitrogen had not leached out yet) belonging to defassa waterbuck *Kobus defassa* Rüppell, African buffalo (*Syncerus caffer* Sparrman), impala (*Aepyceros melampus* Lichtenstein), warthog (*Phacocoerus aethiopicus* Pallas), Grant's gazelle (*Gazella granti* Brooke), and Burchell's zebra (*Equus burchelli* Gray) were collected during the study periods mentioned above. About 5 g (or 5 pellets) of fresh dung was collected from each individual. Dung samples collected in this manner from 15 individuals belonging to the same species in a particular block were then composted into a single sample. Each composite sample was then air dried, ground and stored in a watertight polythene bag. Composite samples were then used for determination of diet composition.

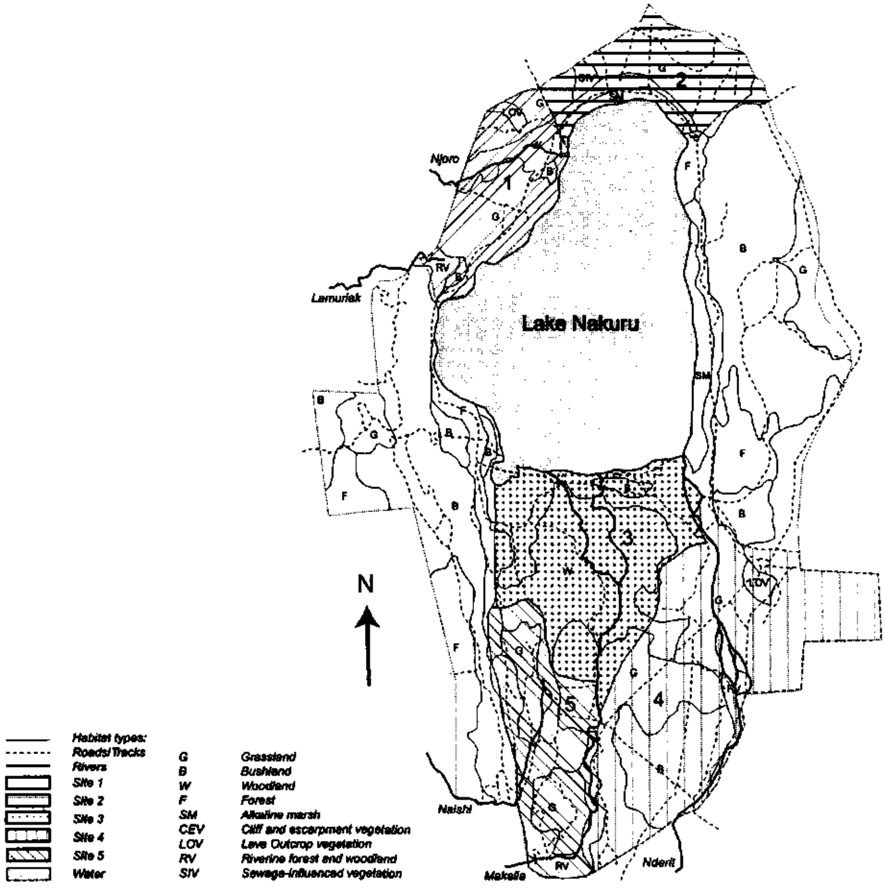

Fig. 4.1 Study sites and vegetation units in Lake Nakuru National Park

Prior to the beginning of microhistological analyses of faeces, reference slides of various parts (i.e., adaxial and abaxial leaf sides, stem, inflorescence and leaf sheath) of common grass species found in Lake Nakuru NP were prepared. Microphotographs of these slides were then taken, and later compared with unknown epidermal fragments from the dung during microhistological analyses, for positive identification if they matched them. The procedure for microhistological analyses of faeces was adopted from De Jong et al. (1995).

Habitat use

The area of the Park which grazers utilise throughout the year was subdivided into five sites (Fig. 4.1). In each site, a permanent transect (road) which traverses through the highest number of physiognomic vegetation units (Table 4.1) was selected. Transect lengths were variable. Each transect was surveyed twice a month from May 1998 to April 1999. An animal count was conducted during each survey. Morning counts started at 0700 h and ended at 0900 h, while afternoon counts started at 1600 h and ended at 1800 h. These time periods coincided with active grazing of the herbivores in the Park. During each count, the vegetation units where animals were found grazing and number of animals counted on either side of the road were recorded.

Data analyses

Diet and habitat overlap was calculated using Pianka's index of resource overlap $\alpha = \Sigma P_{ij} P_{ik} / \sqrt{(\Sigma P^2_{ij} * \Sigma P^2_{ik})}$, where P_{ij} and P_{ik}=proportion that resource category i contributes to the resource use of herbivore j and k (Pianka 1973). The combined overlap is the product of both overlap indices. Niche breadth was calculated using Levins (1968) index B: $B = 1/\Sigma P^2_{ij}$, where P_{ij}=proportional use by animal species j of resource category i.

Results

Seasonal differences in diet quality

The period 1998-1999 was very wet with much rain in even the 'long dry' season. The short dry season of 1999 had lowest rainfall (37 mm).

Table 4.2 Crude protein content (% dry matter; 6.25 * nitrogen content) of leaf and stem of important forage plants for grazers in Lake Nakuru National Park

	Early wet season	Late wet season	Short dry season
Cynodon nlemfuensis			
Green leaves	19.5	16.6	11.9
Green stem	10.4	8.8	6.8
Sporobolus spicatus			
Green leaves	9.4	8.7	8.3
Green stem	7.2	7.8	7.0
Chloris gayana			
Green leaves	7.3	6.8	5.9
Green stem	4.5	4.8	3.5
Themeda triandra			
Green leaves	6.0	5.6	4.3
Green stem	5.4	4.7	3.5
*Cyperus laevigatus**	6.8	6.8	6.8

*Data from Lake Manyara NP (Prins 1987)

Table 4.3 Percentage botanical composition of diet, based on faecal analysis, of grazers in Lake Nakuru National Park. LW, late wet season; SD, short dry season; EW, early wet season; Grant's, Grant's gazelle. Number in brackets after spp. indicate number of plant species included in that particular genus

	Buffalo			Zebra			Waterbuck			Warthog			Impala			Grant's		
	LW	SD	EW	LW	SD	EW	LW	SD	EW	LW	SD	EW	LW	SD	EW	LW	SD	EW
Monocots																		
Cynodon spp. (2)	11.9	24.5	10	3.8	1.9	8	13.8	28.3	10.2	14.2	6.8	10	11.5	20	5.9	25.5	9.6	11
Sporobolus spicatus	0	11.1	13	4.3	11.1	14	19.5	0	0	17.8	7.4	6.3	22.3	22	5.7	34.1	7.1	4.7
Chloris spp. (2)	19.8	0	32	36	26.3	27	6.6	24	20.3	12.3	13	12	42.5	11	26	9.5	26.4	23
Themeda triandra	8	23.9	14	7.2	12.9	13	19.8	14.2	10.1	0	0	0	0	7.2	3.4	3.8	0	0
Cyperus laevigatus	34.6	19.9	11	11	40.5	15	16	21.9	18.3	31.1	41	43	7.9	11	37	6.2	18.8	14
Aristida spp.	6.1	10.4	11	7.1	0	3.4	8.3	3.1	6.8	1.1	11	6.5	0	15	1.7	6.6	17.5	20
Cenchrus ciliaris	0	0	0	8.9	2.6	0	0	0	3.8	0	2.2	2	3.4	0	3.8	0	0	0
Cymbopogon spp.	0	0	0	0	0	0	0	0	1.5	0	8.2	7.7	0	0	2	0	0	0
Enneapogon cenchroides	0	0	0	0	0	0	0	0	0	0	0	5.2	0	0	2.2	0	0	0
Eragrostis spp. .	1.8	8.6	0	15	0	11	12.3	0	13.8	16.9	9.2	5	0	12	3.2	9.2	12	12
Hyparrhenia spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.4	0	0	0
Panicum maximum	0	0	0	5.4	0	0	0	0	0	0	0	1.4	6.5	0	2	0	0	0
Unidentified monocots	6.1	0.8	0	1.7	3.1	4.6	1.5	4	4.8	1.5	0	0	6	0	0	1.1	5	8
Dicots	4.6	0	0	0	2.3	0	2.4	3.1	10.4	2.8	0	0	0	0	2.1	3.9	3.5	5.7
Unknown cuticle	7.1	0.8	0	0	1.9	1.3	0	1.4	0	2.3	0.6	0.5	0	1.6	0	0	0.2	2.9

Crude protein concentration of leaf and stem of the five most important food plants are presented in Table 4.2. Green leaves have generally higher crude protein levels than green stem but the differences in *Sporobolus spicatus* and *Themeda triandra* are small. *Cynodon nlemfuensis* is by far the best food plant. Seasonal effects could not be analysed statistically, but rank correlation revealed that protein levels were highest in the early wet season and lowest in the short dry season. Except for *Cynodon*, seasonal differences in crude protein levels were quite small, however.

Table 4.4 Percentage seasonal habitat use of the grazer assemblage in Lake Nakuru National Park. For description of habitats see Table 1. LW, late wet season; SD, short dry season; EW, early wet season; Grant's, Grant's gazelle

	Buffalo			Zebra			Waterbuck			Warthog			Impala			Grant's		
Habitat	LW	SD	EW	LW	SD	EW	LW	SD	EW	LW	SD	EW	LW	SD	EW	LW	SD	EW
LSV	0	0	2	6	0	4	2	3	1	2	2	1	0	0	0	4	4	2
SOG	11	11	11	3	20	36	6	11	21	33	38	53	5	12	8	11	31	23
MOG	68	58	26	59	45	25	64	57	54	48	47	23	45	39	22	62	35	27
TOG	12	3	3	6	7	7	4	4	3	1	1	0	2	2	0	4	4	0
SW/V	2	0	0	1	4	3	6	0	0	1	1	2	0	0	1	0	1	0
OTB	0	2	1	0	3	0	0	0	0	0	0	0	0	0	0	0	3	0
OAW	1	2	14	18	15	15	9	16	16	8	6	11	21	28	48	16	16	29
WV	6	23	44	7	5	10	8	10	5	6	5	9	27	18	20	2	6	19

Diet composition

In all seasons monocots were by far the most important type of forage for all species (Table 4.3), including the typical mixed feeders considered, i.e., impala and Grant's gazelle. Across all herbivores, *Chloris* and *Cyperus* were the most dominant food plants in the diet. Seasonal differences within species were generally small. Some differences between species can be noted. The most nutritious food plant, *Cynodon*, takes up some 10-25% of the diet of most species, except for zebra that takes only small amounts of *Cynodon*. *Themeda* takes up a much greater proportion of the diet of the larger species than of the smaller ones.

Table 4.5 Niche breadth for diet and habitat use of grazers in Lake Nakuru National Park. LW, late wet season; SD, short dry season; EW, early wet season; Grant's, Grant's gazelle

	Diet				Habitat			
	LW	SD	EW	Mean	LW	SD	EW	Mean
Buffalo	5.45	5.34	5.69	5.49	2.05	2.46	3.46	2.66
Zebra	5.38	3.80	6.56	5.25	2.55	3.59	4.29	3.48
Waterbuck	6.77	4.83	8.30	6.63	2.28	2.72	2.77	2.59
Warthog	5.20	4.50	4.45	4.72	2.86	2.73	2.78	2.79
Impala	3.92	6.48	4.58	5.00	3.13	3.54	3.05	3.24
Grant's	4.90	6.09	7.18	6.02	2.34	3.99	4.05	3.46
Mean	5.25	5.17	6.12		2.54	3.17	3.40	

Table 4.6 Indices of diet overlap between members of the grazer community in Lake Nakuru National Park. Grant's, Grant's gazelle

		Buffalo	Zebra	Waterbuck	Warthog	Impala	Grant's
Late wet season	Buffalo						
	Zebra	0.68					
	Waterbuck	0.65	0.56				
	Warthog	0.81	0.62	0.67			
	Impala	0.58	0.83	0.51	0.6		
	Grant's	0.4	0.44	0.81	0.7	0.64	
	Mean	0.62	0.63	0.64	0.68	0.63	0.6
Short dry season	Buffalo						
	Zebra	0.58					
	Waterbuck	0.76	0.75				
	Warthog	0.62	0.87	0.79			
	Impala	0.81	0.55	0.68	0.63		
	Grant's	0.55	0.75	0.74	0.8	0.78	
	Mean	0.66	0.7	0.74	0.74	0.69	0.72
Early wet season	Buffalo						
	Zebra	0.94					
	Waterbuck	0.81	0.9				
	Warthog	0.57	0.66	0.84			
	Impala	0.75	0.82	0.85	0.93		
	Grant's	0.82	0.81	0.87	0.68	0.73	
	Mean	0.78	0.83	0.85	0.74	0.82	0.78

Habitat use

Seasonal habitat use is shown in Table 4.4. For most species in all seasons, the medium open grassland is the most important habitat, especially in the late wet season, but less in the early wet season. The short open grassland is the second most important habitat, especially in the early wet season. In the early wet season, a number of habitat types become more equally important when compared to the other seasons (medium open grassland, short open grassland, open *Acacia* woodland, woody vegetation). The short open grasslands are most preferred by zebra, warthog and Grant's gazelle. The open *Acacia* woodland and other woody vegetation are being utilised substantially by impala, especially in the early wet season. Of the other species, these woodlands are also being utilised by buffalo and Grant's gazelle, most notably in the early wet season.

Niche breadth

Niche breadth values for diet composition and habitat use are given in Table 4.5. Niche breadth for diet was generally quite narrow (B_{max}=12). For almost all species, it was broadest in the early wet season and for three out of six it was most narrow in the short dry season. Dietary niche breadth varied little across seasons in buffalo and zebra but the variation was greater in the other species. Waterbuck had the greatest shift in niche breadth from the short dry to the early wet season, and also had the highest niche breadth, 8.3, in the early wet season. Niche breadth for habitat generally was very small (B_{max}=8) across species and seasons. Like in diet, it was broadest in the early wet season

Table 4.7 Indices of habitat overlap between members of the grazer community in Lake Nakuru National Park. Grant's, Grant's gazelle

		Buffalo	Zebra	Waterbuck	Warthog	Impala	Grant's
Late wet season	Buffalo						
	Zebra	0.95					
	Waterbuck	0.98	0.99				
	Warthog	0.89	0.85	0.89			
	Impala	0.83	0.92	0.89	0.79		
	Grant's	0.96	0.99	0.98	0.91	0.87	
	Mean	0.92	0.94	0.95	0.87	0.86	0.94
Short dry season	Buffalo						
	Zebra	0.9					
	Waterbuck	0.95	0.97				
	Warthog	0.85	0.94	0.94			
	Impala	0.86	0.91	0.93	0.79		
	Grant's	0.8	0.96	0.87	0.97	0.87	
	Mean	0.87	0.94	0.93	0.9	0.87	0.89
Early wet season	Buffalo						
	Zebra	0.66					
	Waterbuck	0.64	0.83				
	Warthog	0.54	0.96	0.69			
	Impala	0.71	0.64	0.65	0.48		
	Grant's	0.82	0.89	0.83	0.78	0.9	
	Mean	0.67	0.8	0.73	0.69	0.68	0.84

but not lowest in the short dry season. Niche breadth for habitat was smallest in waterbuck, and largest in zebra.

Resource overlap

Indices of overlap between species in diet, habitat use and combined (diet + habitat use) are given in Tables 4.6-4.9. Diet overlap between all pairs of species in all seasons was high (Table 4.6), with hardly any exceptions. Grand average overlap was highest in the early wet season and lowest in the late wet season (Table 4.9). Similar sized species had higher overlap in the late wet season and the short dry season than species with widely differing body weights, except in the long dry season when overlap was highest (Table 4.9).

Habitat overlap between species was extremely high in the late wet and the short dry season but low in the early wet season (Table 4.7, 4.9). There appears to be no difference in habitat overlap between species of similar weights and species of different weights (Table 4.9).

Being the product of the indices of diet and habitat overlap, combined overlaps can be seen to be reduced (Table 4.8, 4.9). If we consider a combined overlap of 0.54 to be the critical limit to similarity for co-existing species (MacArthur and Levins 1967; Putman 1994), then results in Table 4.8 makes it very clear that combined resource overlap between many pairs of species has exceeded this critical level. On average, overlap in the short dry season was highest while overlap between species with different body weight was lower than that between similar sized species in the late wet and the short dry season but not in the early wet season.

Table 4.8 Indices of combined overlap between members of the grazer community in Lake Nakuru National Park. Grant's, Grant's gazelle

		Buffalo	Zebra	Waterbuck	Warthog	Impala	Grant's
Late wet season	Buffalo						
	Zebra	0.64					
	Waterbuck	0.64	0.55				
	Warthog	0.72	0.53	0.6			
	Impala	0.48	0.76	0.46	0.47		
	Grant's	0.39	0.43	0.79	0.65	0.56	
	Mean	0.57	0.58	0.61	0.59	0.55	0.56
Short dry season	Buffalo						
	Zebra	0.52					
	Waterbuck	0.72	0.73				
	Warthog	0.52	0.82	0.75			
	Impala	0.7	0.5	0.63	0.5		
	Grant's	0.45	0.71	0.65	0.78	0.68	
	Mean	0.58	0.66	0.7	0.67	0.6	0.65
Early wet season	Buffalo						
	Zebra	0.62					
	Waterbuck	0.52	0.75				
	Warthog	0.31	0.52	0.58			
	Impala	0.54	0.52	0.55	0.44		
	Grant's	0.67	0.72	0.72	0.53	0.66	
	Mean	0.53	0.63	0.62	0.48	0.54	0.66

Discussion

Seasonal differences were small because during the year 1998 mean annual rainfall was above average. The short dry and long dry seasons of that year received more rainfall than they normally do. Above annual average rainfall occur in Nakuru area after every 9-10 years. Also protein levels did not vary much between seasons for most forage plants although small differences were consistent. In the early wet season values were highest and in the short dry season lowest. Differences were most pronounced in the important forage plant, *Cynodon nlemfuensis*. Because of the consistency of the differences, the short dry season is considered the most limiting season. Although a detailed analysis of diet composition and habitat use will be given elsewhere, a few remarks will be made here. It is clear that all species considered behaved like true grazers including those which are normally classified as typical intermediate feeders, e.g., impala and Grant's gazelle (Table 4.3). In other studies, grass dominated in impala's diet in the rainy season but browse was most important in the dry seasons (Dunham 1980; Meissner et al. 1996). Because there is ample browse available in the Park, impala and Grant's gazelle probably prefer grass and it has been shown in impala that diet quality is positively related to the percentage grass in the diet (Dunham 1980). All species strongly preferred open grasslands of short to medium height (Table 4.4). For most species this preference was found in all seasons, except for impala and buffalo who preferred woodland vegetation to grassland in the early wet season.

It can be expected that competing species tend to segregate more in their resource use during periods of resource limitation, and that their niche breadth then become smaller (Begon et al. 1996). The reverse can be expected in the non-limiting season when resources are abundant. This pattern has indeed be found in a number of grazer communities, both in savanna systems and elsewhere (Field 1972; Gordon and Illius 1989; Dekker et al. 1996; Fritz et al. 1996). Our data comply largely with this prediction. We also found that niche breadth, both for diet and habitat, is broadest in the early wet season and smallest, for diet, in the short dry season. Both for habitat and diet, however, the seasonal differences in niche breadth were small. This could be due to the fact that seasonal differences were not very outspoken but it is also very likely that possibilities for niche 'contraction' in the dry season were limited and that species had little room to move to a species-specific niche. If this is true then high overlap in resource use can be expected and this is what was found. Diet overlap between all

Table 4.9 Grand mean seasonal resource overlap and mean resource overlap of selected groups of member species of the grazer community in Lake Nakuru National Park. Bu, buffalo; Ze, zebra; Wb, waterbuck; Im, impala; Gg, Grant's gazelle; Wa, warthog; LW, late wet season; SD, short dry season; EW, early wet season; Grant's, Grant's gazelle

	Diet			Habitat			Combined		
	LW	SD	EW	LW	SD	EW	LW	SD	EW
Grand mean	0.63	0.71	0.8	0.91	0.9	0.74	0.58	0.64	0.58
Bu-Ze-Wb	0.63	0.7	0.88	0.97	0.94	0.71	0.61	0.66	0.63
Im-Gg-Wa	0.65	0.74	0.78	0.86	0.88	0.72	0.56	0.65	0.54
Im-Gg-Bu-Ze	0.56	0.67	0.8	0.93	0.88	0.77	0.52	0.59	0.61

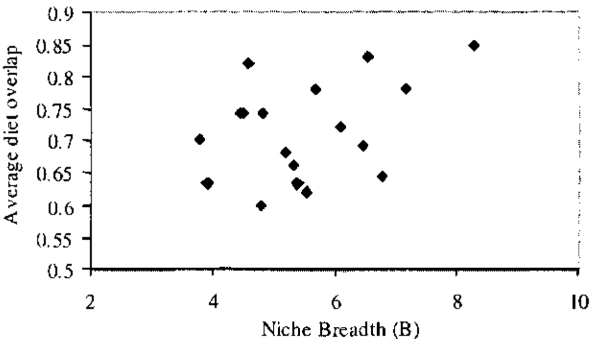

Fig. 4.2 The relationship between dietary niche breadth of each species and the average diet overlap between that species and all other species considered

species across all seasons was high and for habitat, overlap was extremely high. Even the intermediate feeders, impala and Grant's gazelle, while using the woodland habitats more in the early wet season but not in the dry season, kept eating grass in the dry season. Like with niche breadth, and related to it, it can be expected that resource overlap is smallest in the dry season. Neither for diet nor for habitat or for the combined overlap this was found. It was also expected that differences between similar sized species should be smaller than between species with widely different body weights. This was indeed found in the diet data in two seasons (the late wet and the short dry) but not in the habitat data. With the diet and habitat data combined, it was found in all three seasons but, again, the differences were small. The combined data give the best insight in overlap in resource use. If a combined overlap of 0.54 is indeed a critical limit to similarity for co-existing species (MacArthur and Levins 1967; Putman 1994), then of all pairs of species that have been compared, competitive interactions should be occurring in 25 out of 45 combinations studied, while many other overlaps are close to this level. All this leaves little doubt that all species are heavily interacting with at least a number of the other members of the assemblage in all seasons. Although there are very few studies to compare with, the combined indices of overlap found here are among the highest ever reported (Putman 1994; Fritz et al. 1996; Grootbruinderink et al. 1999).

In light of so much overlap in resource use, it can be expected that species try to do their best to specialise so as to reduce competition (Begon et al. 1996), but apparently this is not possible in this system. The overall density in Lake Nakuru NP is very high (*ca.* 60 animals per km^2) and, given the strong preferences for only a few habitat types, the effective density on the grasslands will be even much higher. This implies that not only interspecific competition is operating but that intraspecific competition might be playing an important role as well. Both processes have opposing effects on resource utilisation: intraspecific competition tends to lead to an increase in niche breadth while interspecific competition tends to lead to a decrease in niche breadth (May 1973; Begon et al. 1996). A larger niche breadth should lead to a larger overlap in resource use and vice versa. Our data suggest that for diet, such a relationship might indeed exist (Fig. 4.2) although the amount of variation explained is small and no such relationship was found for habitat use. Even while trying hard, the occupied niches are apparently the best trade-offs between interspecific and intraspecific competition.

It can be concluded that the overlap in resource use among the members of the grazer community in Lake Nakuru NP at present is very high. This suggests that competitive interactions are taking place between many species. As resource overlap is only one of the prerequisites for competition, our data do not prove that competition is really operating let alone that it can be made out which species are the winners or which ones are the losers. For this, it is necessary to know if resources are limiting and which species are negatively affected by resource limitation. Although we know that the larger grazers (buffalo and zebra) are doing better that the smaller ones, to detect the real mechanisms behind the differential population developments, more detailed work is still needed.

Acknowledgements

Permission to conduct research in Lake Nakuru National Park was given by Kenya Wildlife Service to which we are grateful. We wish to thank the former Park Warden, Mr. Daniel Kilonzo and his entire staff for their invaluable support especially in logistics and the Netherlands Organisation for International Co-operation in Higher Education for funding the research.

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Chapter 5

Foraging behaviour of impala and zebra in relation to grass sward height in a small nature reserve in Naivasha, Kenya

Shem M. Mwasi

with Ignas M.A. Heitkönig, Sipke E. Van Wieren, and Herbert H.T. Prins
(Journal of Tropical Ecology, *in press*)

Wageningen University
Department of Environmental Sciences
Tropical Nature Conservation and Vertebrate Ecology Group
Bornsesteeg 69
6708 PD, Wageningen
The Netherlands.

Abstract

We studied the effect of grass sward height on foraging behaviour and local movement among patches of free ranging sympatric wild impala (*Aepyceros melampus*) and Burchell's zebra (*Equus burchelli*) by testing hypotheses based on predictions from the body weight-fibre tolerance/sward quality/sward height interaction. From this interaction we expect that since small-bodied herbivores have a high metabolic requirements/gut capacity ratio and consequently a shorter gut retention time, they tend to have a higher specific mass intake rate than their large-bodied counterparts while feeding on patches of similar quantity and quality. By extension, in order for small-bodied herbivores to fulfil their daily metabolic requirements, they have to consume highly digestible forage that can readily be obtained from short swards. Our results on the effect of sward height on specific mass intake rate in impala did not support the predictions from the body weight-fibre tolerance/sward quality/sward height interaction. We suggest that forage biomass on short swards might have been inadequate for maintenance of the smaller species and sex, thus making them utilise tall swards to a great extent. Sward height in combination with sex was found to have a profound effect on specific mass intake rate in impala. Zebra had a longer feeding station interval and lower stepping rate on tall swards compared to impala suggesting that it might have been restricted by bite depth on short swards. This, in turn, could have made it exhibit a high intake rate on tall swards. The fact that impala and zebra utilised similar tall swards during the dry season suggests that they ate different parts of the shared resource and in the process might have avoided competitive interactions between them.

Key words Metabolic weight · Intake rate · Feeding station interval

Introduction

Foraging behaviour is an important ecological process that relates a herbivore population to the plant community. Among wild ungulates, it is a dominant activity consuming about 40-60% of their daily time (Owen-Smith 1982; Beekman and Prins 1989). Therefore, understanding the mechanisms of foraging behaviour is important to provide relevant information for managing herbivore populations and their habitats.

Foraging behaviour can be described in terms of its two basic components: functional response and movement pattern. Holling's (1959) 'disc model' describes the typical, type II functional response, i.e., the relationship between the per capita prey consumption by a predator and the density of prey available. Although designed for predators, Holling's 'disc model' also forms a basis for understanding the process of foraging in herbivores. During foraging, a herbivore walks a number of steps during the search phase and once it locates a food item, it stops and then starts feeding at the new feeding station. Novellie (1978) used step-sets (number of steps an animal takes while foraging, whereby one step-set consists of two steps) and feeding station interval (time interval in seconds between successive step-sets spent foraging), as basic movement variables to explain the differences in food selection between blesbok (*Damaliscus dorcus*) and springbok (*Antidorcas marsupialis*).

Since it is difficult to experiment with free ranging animals, most often tame or captive animals have been studied to determine type II functional response relationships for large grazers (Owen-Smith and Novellie 1982; Illius and Gordon 1987; Spalinger et al. 1988; Gross et al. 1993; Parsons et al. 1994). The difficulties might have contributed to the few studies (Dunham 1980; Bradbury et al. 1996; Wilmshurst et al. 1999; Murray and Illius 2000) that have recently been conducted on foraging behaviour of large African wild grazers. In grazers, intake rate has been found to be a function of bite size (Stobbs 1973; Chacon and Stobbs 1976; Black and Kenny 1984; Wickstrom et al. 1984), which in turn is influenced by sward characteristics (e.g., height, bulk density, biomass, grass nutritional status, age, spinousness and fibrousness) and an animal's own anatomy (e.g., body weight, digestive capacity, jaw dimensions). The relationship between intake rate and bite size has been shown to be asymptotic and conform to a type II functional response in mammalian herbivores (Allden and Whittaker 1970; Spalinger et al. 1988; Spalinger and Hobbs 1992; Gross et al. 1993).

The profound effects of sward characteristics on bite size have been used by researchers to explain variation in the foraging process. Sward height has been suggested as an important parameter, which influences intake rate through its effect on bite size. Bite size on short swards is usually small (Black and Kenny 1984), but tends to increase with sward height (Black and Kenny 1984; Laca et al. 1992 Gross et al. 1993). Illius and Gordon (1987) predicted that the increase in bite size with sward height continues until a point is reached when the amount of grass that can be cropped in a single bite exceeds the animal's mouth dimensions. Intake rate at this point is limited by the rate at which swallowing competes with chewing (Spalinger and Hobbs 1992). Bradbury et al. (1996) found that height in short to medium savanna grass swards tends to influence bite size of grazing ungulates.

Short grass swards that are continuously grazed often have more leaves and fewer stems than taller ones (McNaughton 1984). Therefore, they are generally less fibrous and have a higher proportion of highly digestible parts compared to tall swards. Fibrousness in grass is a function of age and height, with short young grass having less fibre (low cell wall content) and consequently a higher metabolic constituents/structural constituents ratio than tall mature grass.

Demment and Van Soest (1985) showed that there is an isometric relationship between gut capacity and body weight (W) in herbivores and that a decreasing non-linear relationship between metabolic requirements and metabolic weight ($W^{0.75}$) exists. They therefore predicted that large-bodied herbivores have a lower metabolic requirement/gut capacity ratio and longer gut retention time than small ones supporting the hypothesis that large grazers are capable of tolerating poor quality forage (very fibrous food) compared to small grazers. Since total metabolic requirements of herbivores (kJ d^{-1}) increase with body weight in a decreasing rate, large herbivores require more gross daily energy than small ones. However, small herbivores need more energy per unit body weight than large ones and by extension the specific mass intake rate (intake rate per unit metabolic weight) of small herbivores is expected to be higher than that of large herbivores when these two are feeding on patches with similar quality (energy content and digestibility) and quantity of forage.

Illius and Gordon (1987) developed a model on the grazing mechanics of ruminants to explain the relationship between sward height and body weight. They argued that large grazers could not subsist on short swards because the size of food items in the grazed sward horizon (layer of grass removed by biting) would be too small to fulfil their daily energy needs. Illius and Gordon (1987) used the incisor breadth model, to explain why larger grazers select taller swards, which in most cases are of lower quality when forage biomass on short swards decline.

We used Demment and Van Soest's (1985) body weight-fibre tolerance relationship in conjunction with the sward height-sward quality relationship and Illius and Gordon's (1987) body weight-sward height relationship (Fig. 5.1) and Novellie's (1978) propositions on movement pattern to investigate the foraging behaviour of sympatric wild impala (*Aepyceros melampus* Lichtenstein) and Burchell's zebra (*Equus burchelli* Gray) in a grassland found at the Kenya Wildlife Service Training Institute by direct observations. For us to be able to conduct this investigation, we quantified the effect of sward height on functional response and movement pattern of impala and zebra. On the basis of the complex interaction between body weight and fibre tolerance/sward quality/sward height (Fig. 5.1), we expect that impala (sexes taken together) should have the highest specific mass intake rate on short swards, while zebra (sexes taken together) should have its highest specific mass intake rate on tall swards. We also expect a higher specific mass intake rate on short swards by female impala, while male impala exhibit a higher specific mass intake rate on tall swards. Given sexual dimorphism in impala, and the differences in sward heights within our study site, we hypothesised that specific mass intake rate for female and male impala differs in relation to sward height.

However, due to the absence of observed sexual dimorphism in zebra in our study area, we could not compare their specific mass intake rates. Similarly, because of differences in digestive strategies between impala and zebra, we could not compare their specific mass intake rates. Differences in their gut morphology influence their intake rates in unique ways, which might cause errors in interpretation of results if functional responses between these two grazers are compared. However, we compared their movement patterns to try and gain some insight into how they utilised similar sward height classes. This we did by hypothesising that impala should have a shorter feeding station interval and higher stepping rate than zebra on tall swards.

Methods

Study area

The study area, Kenya Wildlife Service TI is located about 3 km east of Naivasha town and 90 km north west of the city of Nairobi, Kenya. It is composed of three adjacent land units: Main campus (*ca.* 2 km^2), Annex (*ca.* 0.2 km^2) and Game farm (*ca.* 4 km^2). A wire mesh fence that has five wildlife passages to allow movement of wild ungulates to the Game farm and Annex surround the entire perimeter of Main campus where this study was conducted. Vegetation communities found within the study area can broadly be grouped as follows:

(i) *Tarchonanthus* bush
(ii) *Euphorbia* and cliff vegetation
(iii) Open savanna grassland.

A diversity of wild ungulates utilises the Main campus for foraging. They include impala, zebra, eland (*Taurotragus oryx*), warthog (*Phacochoerus aethiopicus*) and dikdik (*Rhynchotragus kirkii*). Masai giraffe (*Giraffa camelopardalis tippelskirchi*), African buffalo (*Syncerus caffer*), Coke's hartebeest or kongoni (*Alcelaphus buselaphus cokii*), and defassa waterbuck (*Kobus defassa*) are infrequent visitors to Main campus.

A nearly square shaped study site measuring *ca.* 1 ha was selected in the middle of the open grassland where there was consistent foraging by impala and zebra. These two sympatric species were the most common grazers found in the study area. Grass swards within the study site were dominated by *Cynodon* spp. and *Eragrostis* spp.

Observations

The study was conducted during the dry season (January 1999 to March 1999). Observations were made from 0700 h to 1100 h in the morning and 1400 h to 1800 h in the afternoon. These time periods coincided with daytime peak feeding activity of impala and zebra on the site. No observations were conducted during the night. A single adult male or female of either species was selected at random and its foraging behaviour observed for a maximum period of 5 min. One person made the observations while another recorded.

The following activities were recorded while an animal foraged on patches found in each of the three pre-determined sward height classes (short: 1-5 cm, medium: 5-15 cm and tall: ≥ 15 cm):

(i) *Number of bites*: a bite occurred when movement of the head of an animal was observed while cropping some grass
(ii) *Number of chews*: conspicuous jaw movements after biting indicated chewing
(iii) *Number of steps*: an animal took a step when one of its forelegs moved forward
(iv) *Feeding station interval.*

Other auxiliary information that was recorded include date and time of the day, local weather conditions, sex and species of individual and grass sward height. Number of bites, steps and chews were then converted to foraging behaviour variables (mean rates of each activity) for easier interpretation. Two types of foraging behaviour variables were distinguished: functional response variables (bite rate, chewing rate, gross and specific mass intake rate) and movement pattern variables (stepping rate and feeding station interval).

Intake rate

Ginnett and Demment's (1995) mechanistic model, which describes a type II functional response, was used to estimate instantaneous intake rate of impala and zebra. It is a modification of an earlier model by Spalinger and Hobbs (1992); Gross et al. (1993). The underlying principle behind this model is that mean dry matter intake rate of a herbivore is a function of its mean bite size. Accordingly, intake rate approaches an asymptotic maximum as bite rate increases (*cf.* Michaelis-Menten function) and that biting and chewing are mutually exclusive activities. The model also divides a herbivore's per bite handling time into chewing and biting parameters that are independent of bite size.

$$\text{The model}: \mathrm{IIR} = \frac{S}{(h + cES)}$$

Where:

IIR=instantaneous intake rate (g min^{-1})
S=mean bite size (g)
h=mean time required to crop a bite from the patch (min per bite)
c=mean time of one chewing motion (min per chew)

E=mean number of chews allocated to each gram forage (chews g^{-1}).

Specific mass intake rate (g min^{-1} per $W^{0.75}$) was obtained by dividing mean instantaneous intake rate of female and male impala or zebra by their respective metabolic weights. Metabolic weights of 17.4 kg and 21.3 kg for female and male impala respectively and 60 kg for zebra were calculated from mean live body weight of 45 kg and 59 kg for female and male impala respectively (Haltenorth and Diller 1980; Skinner and Smithers 1990) and 235 kg for zebra (Prins and Olff 1998). We indirectly determined bite size, i.e., the mass in grams of plant tissue that is cropped at a single instant by a herbivore (Spalinger and Hobbs 1992) by use of Parsons et al. (1994) mechanistic model which proposes that bite size is a product of bulk density of grazed sward horizon and bite volume. An experiment was conducted in the field to determine bulk density of the grazed horizon (Parsons et al. 1994). Square shaped grass patches belonging to each of the three sward height classes were selected. These had to be as homogenous as possible in structure, height and species composition. Each patch was divided into two equal parts, in one, pre-grazed forage volume above 1 cm (assume ungrazable horizon below 1 cm height; Ungar and Noy-Meir 1988) was determined and all standing crop above this height clipped, dried and weighed. This served as the pre-grazed biomass. After a single grazing event by an individual on the unclipped twin patch, bite depth (cm) was calculated by measuring the difference between initial sward surface height and new sward surface height after grazing (Edwards et al. 1995). The volume of forage left after a single grazing event (post-grazed volume) was also determined. After that, all the standing crop above 1 cm in the grazed patch was clipped, dried and weighed (post-grazed biomass). Mean bulk density of the grazed horizon of each sward height class was then computed as:

$$BD = \left(\frac{b_i - b_f}{v_i - v_f}\right)$$

Where:

BD=bulk density in g cm^{-3}

b_i=initial forage biomass (pre-grazed) in g

b_f=final forage biomass (post-grazed) in g

v_i=initial forage volume (pre-grazed) in cm^3

v_f=final forage volume (post-grazed) in cm^3.

Bite volume was estimated as the product of bite area and bite depth (Parsons et al. 1994). Bite area was computed as the square of incisor breadth from skulls of each species from Naturalis, Leiden, the Netherlands and the Transvaal Museum, Pretoria, South Africa (Heitkönig, unpubl. data).

Grazing time for comparison with other findings

The estimated time a grazer spends actively feeding in a day was determined as:

$$T_g = \left(\frac{\text{DDMI}}{\text{IIR} \times 60}\right)1000$$

Where:

T_g=grazing time (h)

DDMI=daily dry matter intake (kg d^{-1})$= 0.025 \times W$ (Van Soest 1982; Van Wijngaarden 1985)

W=mean adult live body weight (kg)

IIR=instantaneous intake rate (estimated).

Statistical analyses

All foraging behaviour variables were found to have come from a normally distributed population. However, some of them had unequal variances that had to be homogenised for purposes of employing parametric data analyses techniques. One-factor analyses of variance was used to test for differences in foraging behaviour variables between short, medium and tall sward height classes for impala and zebra separately, and also for the effect of sward height on movement pattern variables between impala and zebra. Differences in foraging behaviour variables between female and male impala, in relation to sward height were tested using two-factor analyses of variance. All the analyses were performed on transformed data with the aid of SPSS version 8.0. statistical package.

Data reliability

Observations on foraging behaviour of free ranging grazers on natural grasslands are difficult to conduct. Errors may arise due to difficulties in ascertaining the structure and composition of sward while observing an animal feeding from a distance or from inability to accurately observe the real activity an animal is engaged in while its head is held low and muzzle close to the ground, e.g., when an animal chews at the same time continues to crop. Chewing in this case can easily be confused with cropping, and hence recorded as the latter by an observer. However, in this study we tried to minimise such errors as much as possible, for example, by placing marked stakes adjacent to swards of pre-determined height, we were able to ascertain the exact sward height from a distance. An observation platform, 3 m high, was constructed to facilitate, with minimal animal disturbance, accurate direct observations on activities related to foraging behaviour. The platform also enabled observations on animals grazing behind small bushes and grass clumps.

In our study, all the methods used for measuring foraging behaviour variables borrowed heavily from models tested only on captive animals. Bite size determination in the study site posed the greatest challenge to us because direct measurements were impossible to conduct. However, we resorted to an indirect method of estimating bite size based on the mechanistic model of Parsons et al. (1994).

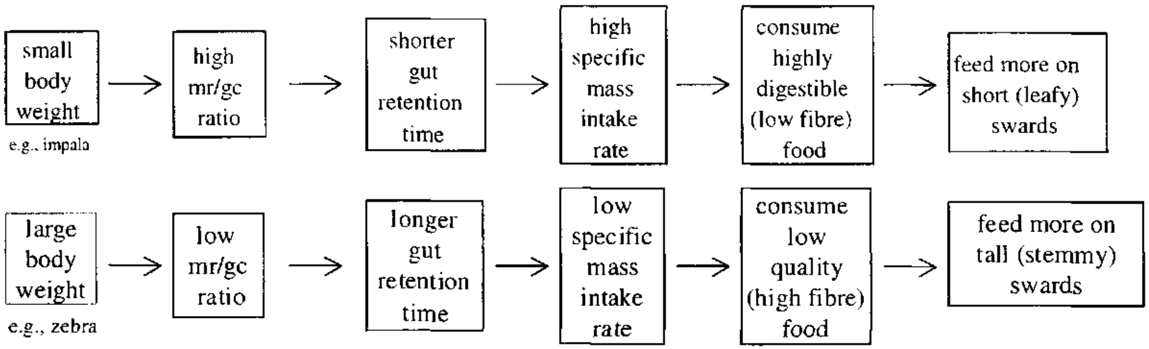

Fig. 5.1 An illustration showing the body weight-fibre tolerance/sward quality/sward height interaction. mr is the metabolic requirements and gc is the gut capacity

Results

Bite size

Estimated bite size increased with sward height in both impala and zebra. It increased from short (0.14 g) to tall (0.27 g) in female impala, 0.15-0.3 g in male impala, and from 0.68-1.8 g for zebra (Table 5.1). Zebra had approximately four- and five-fold larger bite sizes compared to impala on short and tall swards respectively. Both herbivores had their largest bite sizes while foraging on tall swards (Table 5.1).

Effect of sward height on foraging behaviour variables in impala and zebra

The results of analyses of effect of sward height on foraging behaviour variables in impala are summarised in Table 5.2 (a). Bite rate decreased with sward height from 25 bites min^{-1} on short swards to 17.6 bites min^{-1} on tall swards. Chewing rate on the other hand, increased from 23 chews min^{-1} on short swards to 40 chews min^{-1} on tall swards, estimated instantaneous intake rate from 1.8 g min^{-1} on short swards to 2.7 g min^{-1} on tall swards, and specific mass intake rate from 0.06 g min^{-1} per $W^{0.75}$ on short swards to 0.16 g min^{-1} per $W^{0.75}$ on tall swards. Bite rate, chewing rate, instantaneous intake rate, and specific mass intake rate differed significantly among the three sward height classes in impala.

In zebra, bite rate decreased from tall (20.3 bites min^{-1}) to short (10.6 bites min^{-1}) swards and differed significantly among the three sward height classes (Table 5.2 (b)). A significant increase from short to tall swards in instantaneous intake rate (7-9.7 g min^{-1}), and specific mass intake rate (0.12-0.16 g min^{-1} per $W^{0.75}$) respectively was observed in zebra.

The results of analyses for differences in movement pattern variables between impala and zebra are summarised in Table 5.3. Impala had a significantly higher stepping rate (4.1 steps min^{-1} on short to 3.6 steps min^{-1} on tall swards) compared to zebra (2.7 steps min^{-1} on short swards to 1.8 steps min^{-1} on tall swards), while feeding station interval in zebra was significantly longer (43.4 s on short to 54.9 s on tall swards) than in impala (20.5 s on short to 33.2 s on tall swards).

Effect of sward height and sex on foraging behaviour variables in impala

The results of analyses for effect of sward height and sex on foraging behaviour variables in impala are summarised in Table 5.4. Female impala had a higher chewing rate on short swards (27.1 chews min^{-1}) compared to male (16.8 chews min^{-1}), while on medium and tall swards, males exhibited a higher chewing rate. Both sward height and sex significantly affected chewing rate. Specific mass intake rate increased with sward height in both sexes, with female having a lower specific mass intake rate (0.05 g min^{-1} per $W^{0.75}$) than male (0.09 g min^{-1} per $W^{0.75}$) on short swards, while the situation reversed on tall swards where female had a higher specific mass intake rate (0.18 g min^{-1} per $W^{0.75}$) compared to male (0.12 g min^{-1} per $W^{0.75}$). Both sward height and sex in impala significantly affected specific mass intake rate.

Stepping rate in female impala increased from short (3.3 steps min^{-1}) to tall swards (3.7 steps min^{-1}), while in males it decreased from short (5.4 steps min^{-1}) to tall swards (3.2 steps min^{-1}). The effect of both sex and sward height on stepping rate in impala was significant.

Table 5.1 Estimates of mean bite size using Parsons et al. 1994 mechanistic model

Species	Sward	Mean bulk density ($g\ cm^{-3}$)	Mean incisor breadth (cm)	Mean bite area (cm^2)	Mean bite depth (cm)	Estimated bite volume (cm^3)	Estimated bite size (g)
Female impala	short	0.0015	3.03	9.18	1	9.18	0.14
	medium	0.0038			6	55.08	0.21
	tall	0.002			15	137.7	0.27
Male impala	short	0.0013	3.34	11.16	1	11.16	0.15
	medium	0.003			8	89.28	0.27
	tall	0.002			16	178.56	0.3
Zebra	short	0.0086	6.3	39.69	2	79.38	0.68
	medium	0.003			11	436.59	1.3
	tall	0.0023			20	793.8	1.8

In female, feeding station interval increased with sward height from short (24.1 s) to medium swards (31.8 s) but decreased on tall swards (19.6 s), while in male it decreased from short (14.8 s) to medium swards (11.2 s) but increased on tall swards (55.1 s). The effect of both sward height and sex on feeding station interval was significant.

Grazing time

Estimated maximum grazing time for female and male impala, and zebra decreased with sward height and estimated instantaneous intake rate. Zebra had a higher grazing time than both sexes in impala on all sward height classes (Table 5.5).

Discussion

Foraging behaviour variables

This study is unique in that we measured bite rate, chewing rate, stepping rate and feeding station interval for free ranging impala or zebra. Most previous studies use captive animals and may not be representative of what really happens in nature. For example using tame impala feeding on a wide range of woody browse species, Dunham (1980) obtained a maximum bite size and instantaneous intake rate of 0.47 g and 7.5 g min^{-1} respectively, while our study estimated a maximum bite size and instantaneous intake rate of 0.3 g and 2.9 g min^{-1} respectively in male impala. In our case, male impala had a larger bite size and instantaneous intake rate than female impala on all sward height classes.

Although our estimates and those of Dunham (1980) were based on completely different feeding conditions (browsing vs. grazing), Dunham's results suggest that if an impala was to feed only on *Diospyros lycioides* where it attained its maximum instantaneous intake rate, then it would need to browse for about 3 hours to obtain adequate forage for daily maintenance. However, our study predicts a maximum of 8.5 hours per day if male impala maintained its highest instantaneous intake rate while grazing, which is more realistic considering that most ruminants graze for about 8-9 hours a day (Arnold and Dudzinski 1978; Beekman and Prins 1989).

It is not possible to compare bite size and instantaneous intake rate of zebra from our study with results or predictions from other studies on zebra because they were not available in literature. However, our computed maximum daily grazing time for zebra, 14.1 hours, conform with the findings of Beekman and Prins (1989) that zebra grazes for between 13-21 hours daily.

Specific mass intake rates and grass sward height

Our results did not support the hypothesis that impala had the highest specific mass intake rate on short swards, in fact its highest specific mass intake rate was observed on tall swards contrary to the predictions from the body weight-fibre tolerance/sward quality/sward height interaction. Low specific mass intake rate observed on short swards could be attributed to the swards possibly having low biomass, thus unable to provide impala with adequate forage for their daily maintenance. Therefore, impala seem to practice a feeding strategy that maximises intake on tall swards that are of comparatively lower quality but of higher biomass than short swards. We suggest that feeding by impala on tall swards might have been more rewarding than on shorter swards as the former might have offered optimal returns both in quality and quantity by the end of the day. Considering the fact that our investigations were conducted during the dry season, when there was hardly any precipitation and hence low grass production, short swards despite being of higher quality than tall ones, might generally not have had adequate biomass to meet impala daily energy requirements. Wilmshurst et al. (1999) study on Thomson's gazelle (*Gazella thomsoni*) postulated that since in the dry season there is generally no grass regrowth in the savanna, grass biomass and quality are not inversely related and essentially digestibility ceases to be a function of grass height. Therefore, selective ruminants such as Thomson's gazelle must utilise tall grass patches to maximise their energy intake. This further supports our findings that impala had a higher specific mass intake rate on tall swards. The ability of the small muzzle of impala to select highly digestible grass parts as food might have helped it choose leafy parts and avoid the more fibrous stemmy parts while feeding on tall swards (Jarman and Sinclair 1979).

A similar effect of sward height on specific mass intake rate was exhibited by zebra having a significantly higher specific mass intake rate on tall than on shorter swards. This supported our hypothesis that zebra had the highest specific mass intake

Table 5.2 (a) Variation in foraging behaviour variables of impala (sexes taken together) grazing on short, medium and tall swards

Variable	Short sward mean ± CI	Medium sward mean ± CI	Tall sward mean ± CI	F-ratio
bites min^{-1}	25 ± 2.4 (45)	20.4 ± 0.89 (105)	17.6 ± 1.1 (66)	11.08^{***}
chews min^{-1}	23 ± 5.3 (45)	39.8 ± 3.1 (100)	40 ± 3.1 (64)	29.56^{***}
IIR	1.8 ± 0.18 (45)	2.4 ± 0.12 (100)	2.7 ± 0.16 (64)	28.11^{***}
SMIR	0.06 ± 0.008 (45)	0.12 ± 0.006 (100)	0.16 ± 0.01 (64)	79.73^{***}
steps min^{-1}	4.1 ± 0.82 (45)	3.7 ± 0.47 (105)	3.6 ± 0.69 (66)	0.7^{ns}
FSI	20.5 ± 6.4 (31)	23.9 ± 9 (26)	33.2 ± 10.7 (34)	3.08^{ns}

IIR, instantaneous intake rate (g min^{-1}); SMIR, specific mass intake rate (g min^{-1} per $W^{0.75}$); FSI, feeding station interval in seconds; CI=95% confidence interval; number of observations in parenthesis. Values of mean and confidence interval presented in the table were calculated from untransformed dry season data.

Table 5.2 (b) Variation in foraging behaviour variables of zebra (sexes taken together) grazing on short, medium and tall swards

Variable	Short sward mean ± CI	Medium sward mean ± CI	Tall sward mean ± CI	F-ratio
bites min^{-1}	20.3 ± 1.8 (38)	12.7 ± 0.5 (121)	10.6 ± 0.54 (108)	107.75^{***}
chews min^{-1}	43.7 ± 6.7 (38)	48.5 ± 1.3 (121)	48.6 ± 1.5 (108)	0.52^{ns}
IIR	7 ± 0.6 (38)	8.3 ± 0.34 (121)	9.7 ± 0.5 (108)	3.9^{*}
SMIR	0.12 ± 0.01 (38)	0.14 ± 0.01 (121)	0.16 ± 0.01 (108)	3.8^{*}
steps min^{-1}	2.7 ± 0.44 (38)	1.9 ± 0.25 (120)	1.8 ± 0.21 (108)	1.76^{ns}
FSI	43.3 ± 9.5 (26)	41.1 ± 6.3 (26)	54.9 ± 9.9 (49)	0.05^{ns}

IIR, instantaneous intake rate (g min^{-1}); SMIR, specific mass intake rate (g min^{-1} per $W^{0.75}$); FSI, feeding station interval in seconds; CI, 95% confidence interval; number of observations in parenthesis. Values of mean and confidence interval presented in the table were calculated from untransformed dry season data.

Table 5.3 One-factor analyses of variance test for differences in movement pattern variables between impala and zebra grazing on short, medium and tall swards. Sexes were taken together

Sward	Variable	Impala mean ± CI	Zebra mean ± CI	F-ratio
Short	steps min^{-1}	4.1 ± 0.82 (45)	2.7 ± 0.44 (38)	52.82^{***}
	FSI	20.5 ± 6.4 (31)	43.4 ± 9.5 (26)	347.35^{***}
Medium	steps min^{-1}	3.7 ± 0.47 (105)	1.9 ± 0.25 (120)	174.84^{***}
	FSI	23.9 ± 9 (26)	41.1 ± 6.3 (26)	393.03^{***}
Tall	steps min^{-1}	3.6 ± 0.69 (66)	1.8 ± 0.21 (108)	117.74^{***}
	FSI	33.2 ± 10.7 (34)	54.9 ± 9.8 (49)	799.11^{***}

FSI, feeding station interval in seconds; CI, 95% confidence interval; number of observations in parenthesis. The mean and confidence interval values presented in the table were calculated from untransformed dry season data.

rate on tall swards, and thus agreed well with the prediction that large grazers (e.g., zebra) might be more restricted by bite depth on short grass swards than small grazers (e.g., impala) (Illius and Gordon 1987). Zebra being hind gut fermenters are capable of tolerating more fibrous forage than ruminants because of their high gut throughput and lack of a sieving mechanism for large food particles that delays food passage through the gut as in ruminants (Van Soest et al. 1983). Thus they can tolerate decreased forage conditions which might be encountered on tall swards.

Table 5.4 Two-factor analyses of variance test for differences in foraging behaviour variables between male and female impala grazing on short, medium and tall swards

Variable	Sward	Female mean ± CI	Male mean ± CI	F-ratio $_h$	$_s$	$_{hs}$
bites min^{-1}	short	24.1± 2.8 (27)	26.4 ± 4.7 (18)	14.29^{***}	10.11^{**}	1.61^{ns}
	medium	21.6 ± 1.1 (65)	18.5 ± 1.3 (40)			
	tall	19 ± 1.4 (45)	14.6 ± 1.1 (21)			
chews min^{-1}	short	27.1 ± 8.5 (27)	16.8 ± 3.4 (18)	31.93^{***}	0.01^{ns}	3.12^{*}
	medium	37.1 ± 3.9 (65)	44.7 ± 4.6 (35)			
	tall	40 ± 3.4 (43)	40.3 ± 6.9 (21)			
IIR	short	1.6 ± 0.19 (27)	2 ± 0.35 (18)	29.69^{***}	15.92^{***}	0.54^{ns}
	medium	2.3 ± 0.12 (65)	2.7 ± 0.23 (35)			
	tall	2.6 ± 0.2 (43)	2.9 ± 0.21 (21)			
SMIR	short	0.05 ± 0.01 (27)	0.09 ± 0.01 (18)	66.81^{***}	2.41^{ns}	24.56^{***}
	medium	0.12 ± 0.01 (65)	0.12 ± 0.01 (35)			
	tall	0.18 ± 0.01 (43)	0.12 ± 0.02 (21)			
steps min^{-1}	short	3.3 ± 0.88 (27)	5.4 ± 1.5 (18)	1.47^{ns}	2.69^{ns}	3.17^{*}
	medium	3.6 ± 0.63 (65)	3.9 ± 0.7 (40)			
	tall	3.7 ± 0.82 (45)	3.2 ± 1.4 (21)			
FSI	short	24.1 ± 9.9 (19)	14.8 ± 6.1 (12)	7.71^{**}	0.23^{ns}	12.79^{***}
	medium	31.8 ± 13.6 (16)	11.2 ± 2.4 (10)			
	tall	19.6 ± 4.5 (22)	55.1 ± 25 (12)			

IIR, instantaneous intake rate (g min^{-1}); SMIR, specific mass intake rate (g min^{-1} per $W^{0.75}$); $_h$, sward height; $_s$, sex; $_{hs}$, interaction; FSI, feeding station interval in seconds; CI, 95% confidence interval; number of observations in parenthesis. The mean and confidence interval values presented in the table were calculated from untransformed dry season data.

Table 5.5 Maximum estimated daily grazing time of adult impala and zebra based on estimated instantaneous intake rates. Compare with observed daily grazing time for ruminants, e.g., impala: 8-9 h (Arnold and Dudzinski 1978; Beekman and Prins 1989) and zebra: 13-21 h (Beekman and Prins 1989)

	Sward	IIR (g min^{-1})	DDMI (kg d^{-1})	T_g (h)
Female impala	short		1.13	11.79
	medium			8.15
	tall	3.07		7.16
Male impala	short			12.41
	medium			9.04
	tall	2.93	1.48	8.45
Zebra	short			14.1
	medium			11.8
	tall	9.71	5.88	10

IIR, instantaneous intake rate; DDMI, daily dry matter intake; T_g, grazing time.

Effect of sward height and sex on specific mass intake rate in impala

Our results supported the hypothesis that specific mass intake rates for female and male impala differ in relation to sward height. Specific mass intake rate in both sexes increased with sward height, but differed with sex. Male impala had higher specific mass intake rate than females on short swards. However, both sexes had their highest specific mass intake rate on tall swards, supporting our earlier argument that tall swards provided maximum returns in terms of forage quality and quantity in our study site during the dry season. Females had higher specific mass intake rate on tall swards than males, supporting the prediction that small-bodied herbivores have a higher metabolic requirement/gut capacity ratio than larger ones with similar digestive strategies.

The pattern in which female and male impala move within patches while foraging can be used to some extent to explain differences in their specific mass intake rate on tall swards where both sexes exhibited their highest intake rates. Male impala had lower stepping rate and consequently a longer feeding station interval than females. Female impala on the other hand wandered more within different patches on tall swards, suggesting that they were feeding more selectively within patches than males. Despite more movement within patches, female impala exhibited a higher specific mass intake rate than males on tall swards implying that their metabolic requirements were higher than their male (larger) counterparts. This conforms to our predictions.

Feeding station interval and stepping rate between impala and zebra

Zebra had a significantly longer feeding station interval and lower stepping rate on tall swards compared to impala. This conforms to the body weight hypothesis. Higher feeding station interval and lower stepping rate coupled with highest specific mass intake rate on tall swards for both impala and zebra suggest that these sympatric species utilised to a great degree the same sward heights during the dry season. This led us to speculate that these two species overlap in resource use during the dry season, when in theory, food resources are low and probably limiting in the savanna. The potential for competition between impala and zebra might have been high considering that both species exhibited their highest specific mass intake rate on tall swards. However, zebra capable of feeding on more fibrous forage, could utilise stems and upper mature parts of grass, while impala utilised the less fibrous parts found below which they select using their slender mouths, probably reducing competitive interactions. Furthermore, there is evidence (see Chapter 4) that the lowest combined resource overlap between impala and zebra (Pianka's index=0.5) occurs during the dry season, suggesting that competitive interactions between these species might actually be less during this season.

Acknowledgements

We thank Mr. Frank Litondo, the former principal of Kenya Wildlife Service Training Institute (KWSTI) and his staff for their logistical support. The invaluable help of Alison Bartlett and Michael van Hasselt during fieldwork is highly appreciated. This research was funded by the Netherlands Organisation for International Co-operation in Higher Education and Wageningen University. Kenya Wildlife Service granted permission for fieldwork to be conducted at KWSTI. To all these organisations we are very grateful.

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Chapter 6

Co-existence in compressed nature: a synthesis

Shem M. Mwasi

'The real challenge for future research is to go beyond documenting that species interact, and determine exactly how different species co-exist in the presence of these interactions'

Linnell and Strand (2000)

An overview

In the recent past, many researchers have suggested several explanations behind the high diversity of grazers in the East African savannas. These range from a constancy in body weight ratios between successive herbivore species when ranked from lightest to heaviest in an assemblage (Prins and Olff 1998), differences in their metabolic requirements (Demment and Van Soest 1985), differences in their gut morphology (Hoffman 1973; Van Soest 1982; Van Wieren 1996; Iason and Van Wieren 1999), differences in their feeding styles (Van Wieren 1996) and variation in their incisor arc width (Illius and Gordon 1987; Schuette et al. 1998). These differences are thought to allow maximal niche separation and greatest resource partitioning among grazers thus lowering the intensity of competitive interactions among them.

The diverse grazer species, which inhabit the savannas of East Africa, have for a long time had expansive habitats to utilise annually. Large scale movement of wildlife is, however, becoming increasingly difficult nowadays because of the ever expanding human population whose associated activities (increased human settlements, farms, fences, livestock and habitat destruction) exert varied pressure on wildlife. Recent studies suggest that livestock is a potential competitor with wildlife (Prins 1992; Voeten 1999; Mishra 2001) and fencing is one of the causes of closure of wildlife migratory routes (Borner 1985). Settlements and farming activities are directly responsible for fragmentation, isolation and the subsequent compression of wildlife habitats, which eventually leads to reduction in home range sizes of large herbivores, stoppage of their migration and an increase in their biomass densities.

The way things stand, is that human occupation in the savannas will continue to grow and in the process require more land to settle, in most cases this will be wildlife habitats. This has led to the emergency of a new strategy of wildlife conservation in some parts of the savanna, whereby new wildlife reserves are established in already fragmented areas. Such areas would not have been given any serious consideration as vital conservation areas until the late 1960s in Kenya, because expansive wildlife habitats were still available. In order for successful wildlife conservation to take place in these newly created reserves, wildlife biologists need to understand the dynamics of the herbivore populations in their new habitat conditions, i.e., smaller home ranges, increased herbivore densities, introduction of new herbivore species or re-introduction of those species which used to live in these areas in the past, and/or removal of livestock and other forms of human activity such as burning, subsistence hunting and cultivation.

In this thesis, I made an attempt to address some of the crucial issues on how the grazer-plant sub-system might be functioning in the wake of isolation. I expect that with isolation and the subsequent increase in biomass of local grazer assemblages, competitive interactions among co-existing grazers get exacerbated.

In Chapter 1 of this thesis, I raised two important questions: first, *does a decline in a grazer species biomass in an isolated small reserve due to an increase in biomass* *of other co-existing grazers?* and second, *does a high resource overlap exist among co-existing grazers in an isolated small reserve?* To get answers to these questions, I focused on the grazer assemblage (comprising of ten co-existing grazers (Table 2.2 in Chapter 2)) of Lake Nakuru NP, an example of a small isolated nature reserve in Kenya. In Chapter 2, we examined the way in which population size of the different members of the grazer assemblage in Lake Nakuru NP changed over a 24-year period from the time the Park became isolated in 1976 and consequently started getting compressed to 1999. We found out that as total numbers of species in the assemblage became constant, the species in the small body weight class (Table 2.2 in Chapter 2) were more in total numbers but lower in total biomass compared to species of the large body weight class, whose total numbers also increased but to a lower extent. This led us to conclude that there might be competitive interactions among grazers in this assemblage. To find out the mechanisms behind these interactions, we examined the nature of habitat (physiognomic vegetation unit) utilisation by the grazers in Chapter 3. Here we estimated a high habitat overlap among the grazers throughout the year. These results lead us to examine even in more detail how these grazers utilise their resources (food and habitat). This we did by determining resource (combined food and habitat) overlap between pairs of grazers (Chapter 4). We found out that dietary overlap was high between all pairs of grazers during all seasons, that there was no effect of body weight similarity on diet divergence, and that the combined resource overlap between grazers was also high. A major question that arises from these findings so far: Do these grazers partition their resources at all, as is expected among co-existing species? We attempted to answer this question by investigating the foraging behaviour of sympatric impala (*Aepyceros melampus* Lichtenstein) and Burchell's zebra (*Equus burchelli* Gray) on a short open grassland during the dry season, when forage quality (nutrients, energy content and digestibility) and biomass are expected to be low in the savanna. We discussed that differential use of the same food resource might explain the use of similar feeding sites between these two species (Chapter 5). Indeed, despite sharing the same habitat and same grass species, impala and zebra did show feeding differences at plant structure (leaf, stem or flowering stalk) level, which can be attributed to mouth morphology and body mass differences between the two species.

Habitat compression and co-existence

Co-existence of potential competitors might be possible if their population densities are maintained below levels where resources are limiting by external factors (biotic or abiotic) (Putman 1996). However, this might not necessarily be the case in some small isolated reserves, e.g., in Lake Nakuru NP, where there is a high grazer population and a possibility of resource limitation, two things might happen to warrant co-existence in such a case. The first being that there could be compensatory mortality between species within the same herbivore guild and secondly, there could be differential use of similar forage resources by the co-existing species.

Chances of potential competitive interactions in Lake Nakuru NP among the grazers are high considering their high biomass densities in a fixed size habitat where no emigration or immigration is impossible. At the end of the 24-year study period in 1999, defassa waterbuck (*Kobus defassa* Rüppell), warthog (*Phacocoerus aethiopicus* Pallas) and eland (*Taurotragus oryx* Pallas) whose growth rate initially increased during the first 15 years, was observed to have declined. Impala, Chanler's reebuck (*Redunca fulvorufula chanleri* Rothchild) and Thomson's gazelle (*Gazella thomsoni* Gunther) showed constant growth rates during the study period, while growth rates of zebra and African buffalo (*Syncerus caffer* Sparrman) increased (Chapter 2, Table 2.1). It seems therefore, that waterbuck and warthog might have negatively been affected probably by the other large grazers, while impala and Chanler's reedbuck do not seem to be affected. The growth rate of Bohor reedbuck (*Redunca redunca* Pallas) declined especially after 1990, probably due to a rise in the population of Grant's gazelle (*Gazella granti* Brooke) whose body weight is similar to that of Bohor reedbuck. The decline in growth rate of eland after 1990 might be attributed to the fence serving as a barrier to its movements since it is the most mobile antelope in the savanna (see Hillman 1988).

In the Nakuru grazer assemblage, there might be fewer species-specific niches available due to habitat compression and a high total grazer biomass leading to the observed high resource overlap. If resources were not limiting, then I would expect all the grazer growth rates to continue to increase, largely because there has been no cases of major disease outbreaks in Lake Nakuru NP between 1976 and 1999, which could have attributed to the decline in waterbuck, warthog and eland especially after 1994. However, the sharp drop in biomass density of waterbuck between 1990 and 1993, is difficult to explain from my findings. The fact that growth rates of grazers have varied so much in this assemblage over the 24-year study period, where for some species they have increased, others have remained constant, while a sharp decline was observed for others, suggests that resource limitation might be occurring in the assemblage especially after 1990.

Implications of the findings

It has been suggested that interspecific competition might be responsible for structuring grazer assemblages (Sinclair and Norton-Griffiths 1982; Putman 1996). Chapter 2 provides some evidence that the structuring of the grazer assemblage in Lake Nakuru NP might have been due to competitive interactions among its members. We highlighted the fact that there were abundant resources after human activities were eliminated from the Park through fencing in 1976, making some grazer species populations grow exponentially until 1990, when these rates seemed to have reached their 'peak' (Chapter 2). Thereafter, we suspect that competitive interactions might have been responsible for the assemblage shifting towards the small-bodied grazers attaining highest population density, while the large bodied grazers attaining highest biomass density. On specific grazer-grazer interactions, the strong decline in growth rate in Bohor reedbuck after 1990 might be attributed to competition with Grant's gazelle while the decline in Thomson's gazelle, warthog and waterbuck towards the late 1990s might have been due to the negative influence by zebra and buffalo, which is inconsistent with the hypothesis of Prins and Olff (1998) that larger grazers facilitate smaller ones and that competition occurs only across a close range of body weights. In my study, competition seems to have occurred across a wide range of body weights.

It is evident from this study that there was a high degree of habitat overlap between different pairs of co-existing grazers throughout the year. There was a high degree of habitat overlap of waterbuck and warthog on other grazers' habitat (Chapter 3), suggesting that waterbuck and warthog may be more restricted in their habitat choice than the larger bodied species in the assemblage. However, waterbuck and warthog were not clearly displaced by the large bodied species as might be expected from (Fretwell 1972) but seem to share the large bodied grazers' habitat instead. This suggests that competition runs at least in part at the habitat level. We attributed the high habitat overlap to resource limitation which manifested itself in fitness loss among the smaller bodied grazers which utilised the most restrained habitat, e.g., in waterbuck and warthog which have exhibited a decline in growth rate since early 1990s (Chapter 2).

Since competition is a complex process which might not adequately be inferred by just examining values of overlaps between pairs of species utilising a single resource (in this case habitat), in Chapter 4 we examined competitive interactions among grazers in the Nakuru assemblage by evaluating broader resource overlap values. This helped us to get an even better insight into what might be going on in the Nakuru grazer assemblage as far as competitive interactions between pairs of grazers are concerned. Seasonal diet overlap between all pairs of grazers was high compared to the low habitat overlap observed between them at the same time. Combined overlap between pairs of grazers was in most cases high regardless of season. In fact, in many cases higher than 0.54, which is considered a critical limit for similarity of co-existence between species (MacArthur and Levins 1967; Putman 1994). This suggests that many possibilities of competitive interaction exist among grazers in Lake Nakuru NP.

One is now left wondering why competitive displacement has not been observed in this assemblage so far considering such a high potential for competition, the possible lack of facilitation by large bodied grazers on smaller ones and the apparent inability of the grazers to specialise in resource use due to a high total biomass density (134 kg ha^{-1}). Our study on the effect of grass sward height on foraging behaviour of impala and zebra in a savanna grassland site under high grazing pressure (impala, 15 kg ha^{-1}; zebra, 40 kg ha^{-1} in 1999 *cf.* impala and zebra in Chapter 2, Table 2.2) during the dry season, revealed that both species had their highest specific mass intake rate on taller swards within the short open grassland (Chapter 5). The fact that both impala and zebra had their highest specific mass intake rate on taller swards during the dry season, suggests that they might possibly be using the same feeding sites to a large extent and that their co-existence might have been due to utilisation of different parts of the shared resource, e.g., zebra capable of feeding on more fibrous forage could utilise stems and upper mature parts of grass, while impala utilise less fibrous parts found below which it can select using its slender mouth. Sward heterogeneity in this case is apparently important in allowing two species to share the same resource. This differential use of the same resource by co-existing grazers might be assumed to occur between other grazers in the assemblage, although documentary evidence is yet to be obtained to support this. Differential use might have been a way to ease the intensity of competitive interactions among the grazers in Nakuru.

The findings of this study support the first hypothesis of this thesis that there is a high resource overlap among co-existing grazers in isolated small reserves. High resource overlap was observed between pairs of grazers in Nakuru during all seasons of the year. Most studies on co-existing grazers show high resource overlap between pairs of species at least during part of the year especially when resources are abundant (e.g., red deer (*Cervus elaphus*)-cattle, Gordon and Illius 1989; cattle-pony, Putman 1996;

cattle-wildebeest (*Connochaetus taurinus*) and wildebeest-zebra, Voeten 1999). Only in a few instances, e.g. between zebra and wildebeest in Lake Manyara NP (De Boer and Prins 1990) have cases of high resource overlap all year round been observed among co-existing grazers. I suggest that the high resource overlap observed in my case is probably due to habitat compression.

My second hypothesis that a decline in biomass of some grazer species in small isolated reserves is a consequence of an increase in biomass of the other co-existing grazers was partly supported by the fact that with waterbuck biomass density decline after 1990, other grazers' biomass densities especially those of zebra and buffalo continued to rise. Similarly, a decline in warthog biomass density from 1995 occurred at a time when that of buffalo and zebra continued to increase. On the other hand, the decline in biomass density of Bohor reedbuck might have been due to competitively interacting with Grant's gazelle whose biomass density continued to increase in the 1990s in Lake Nakuru NP. There might have been compensatory mortality occurring among species in the Nakuru grazer assemblage, a phenomenon which is normally associated with assemblage stability, e.g., in Lake Manyara NP, Tanzania (Prins and Douglas-Hamilton 1990) which is similar to Lake Nakuru NP. However, it is difficult to ascertain whether the Nakuru assemblage is stable yet since total biomass density has continued to increase, albeit slowly.

Areas for further research

Going back to the opening statement, my study tried to examine the interactions among co-existing grazers in conditions of high biomass density. Apart from providing insight into how co-existence occurs in an assemblage composed of competitively interacting species, my study also raised questions that need to be further addressed. Despite attempts in this study to investigate differences in foraging behaviour, weight ratios, resource use overlap and local herbivore movements, parameters which are thought to be key to co-existence in grazers, there is still need in future to examine in more detail the foraging behaviour of other members of the assemblage apart from impala and zebra which were considered in my study. It will also be important to investigate the effect of diseases especially on the poor performing species, e.g., waterbuck, warthog and Bohor reedbuck. However, this will only be possible if specialised research programmes are implemented in small isolated nature reserves. Modelling forage parameters (biomass and quality), off-take, rainfall, edaphic factors, and population dynamics of the grazers might give even more insight into the nature of various ecological processes occurring between grazers and within the plant-grazer sub-system. These processes can then be compared between open and closed reserves to further understand the impact of short-term ecological isolation on grazer-grazer and grass-grazer interactions. The fact that some results from my study were contrary to expectations from current ecological predictions calls for further research especially on the principle of facilitation, ideal free distribution and seasonal resource partitioning in compressed habitats.

The future

The future of the Nakuru grazer assemblage might be influenced by the perturbations that take place in the Park especially the introduction and re-introduction of new species, e.g., the white rhinoceros (*Ceratotherium simum*) in 1994, lion (*Panthera leo*) and leopard (*Panthera pardus*) during different times in the 1980s and 1990s. These perturbations may induce conditions that either enhance or reduce competitive interactions in the grazer assemblage. For example, the introduced white rhinoceros, a large bodied grazer, might compete with 'native' large grazers for resources.

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Summary

Small nature reserves have recently become focal points of wildlife conservation in many parts of East Africa. They are mostly found in the savannas where the diversity of co-existing wild grazing ungulates is exceptionally high. An increasing threat to the future of these reserves is the expanding human population in their periphery, which has made them, become increasingly ecologically isolated and consequently compressed. This may lead to an increase in the population and biomass densities of large grazers, which are the dominant herbivores in these reserves, and in intensity of competitive interactions between them. Therefore, there is need to understand the functioning of the grass-grazer sub-system in these reserves in the wake of habitat compression so as to provide ecological information that is significant for conservation of the grazers.

Lake Nakuru National Park serves as an important small nature reserve for purposes of this study because it was the first to become ecologically isolated in Kenya in the mid-1970s. It has intrigued many biologists due to its ability to support a high total biomass density of grazers (*ca.* 134 kg ha^{-1} excluding the recently introduced white rhinoceros *Ceratotherium simum*), probably one of the highest ever recorded for a grazer assemblage in East Africa. In order to understand the functioning of the grazer-grass sub-system, I studied the grass-grazer and grazer-grazer interactions in the Lake Nakuru NP grazer assemblage.

This assemblage has experienced an increase in total biomass since it became completely isolated in 1976. Its structure has also changed during the period: 1976-1999 whereby, total biomass is now dominated by species in the large weight class (>300 kg) consisting of the African buffalo (*Syncerus caffer*) and the eland (*Taurotragus oryx*), unlike during the first 13 years after isolation when species of the middle weight class (100-300 kg) consisting of defassa waterbuck (*Kobus defassa*) and Burchell's zebra (*Equus burchelli*) dominated in total biomass. The small weight class (0-100 kg) comprising of warthog (*Phacocoerus aethiopicus*), impala (*Aepyceros melampus*), Grant's gazelle (*Gazella granti*), Bohor reedbuck (*Redunca redunca*) Chanler's reedbuck (*Redunca fulvorufula chanleri*) and Thomson's gazelle (*Gazella thomsoni*) increased during the period: 1976-1999, albeit at a much slower rate compared to the large body weight class. The change in the structure of the assemblage may be attributed to the poor performance by Bohor reedbuck, waterbuck and warthog and the success of buffalo, zebra and Grant's gazelle in the 1991-1999 period. Buffalo with a growth rate of 17% and zebra with 12%, might have had a negative impact on warthog and waterbuck, while the sharp decline in Bohor reedbuck may be attributed to the increase in Grant's gazelle (6%) which belong to the same weight class and prefer similar habitats.

In Nakuru, grazers utilise to a large extent (≥30%) the short and medium open grasslands across all seasons during the year. Niche breadth for both diet and habitat use was largest during the early wet season, and for diet it was smallest during the dry season as expected. However, seasonal differences in niche breadth were small, probably because seasonal differences were not pronounced or maybe because the possibilities of niche 'contraction' during the dry season were limited. Average diet overlap index between all pairs of grazers across all seasons was high: >0.6, while that of habitat use overlap was even higher: >0.7. Some of the poorly performing species (waterbuck and warthog) were found to be more restrained in their habitat choice by having a high degree of overlap on other species' (smaller or larger) habitats. They were, however, not displaced from the larger species habitats but instead they shared it. There was no evidence of facilitation in the grazer assemblage but the large overlap in habitat use and negative population growth rate exhibited by waterbuck and warthog suggest that competition for food resources might be occurring. In fact, indices of seasonal combined (diet + habitat use) overlap between pairs of grazers, e.g., late wet season for: impala-zebra (0.76), impala-buffalo (0.48), impala-waterbuck (0.46); dry season for: impala-zebra (0.5), impala-buffalo (0.7), impala-waterbuck (0.63); early wet season for: impala-zebra (0.52), impala-buffalo (0.54), impala-waterbuck (0.55) in most cases exceeded the critical limit to co-existence (0.54), suggesting that there might be competitive interactions among the grazers.

So far, despite these interactions, no competitive displacement within the assemblage has been observed, probably due to the differential utilisation of the same feeding sites exhibited by the grazers. A study on the foraging behaviour of impala and zebra found out that they both had their highest specific mass intake rate on tall grass swards (≥15 cm high) within the short open grasslands (0-30 cm high). Therefore, in essence they utilised similar feeding sites but zebra, capable of feeding on more fibrous forage than impala, might crop flowering stalks, stems and upper parts of grass, while impala feed on less fibrous parts, e.g., leaves found below mature stalks which it can select using its slender mouth. This differentiation at feeding level might probably reduce competitive interactions between grazers. The functioning of the Nakuru-grazer sub-system seems to be influenced by competitive interactions operating at the habitat, diet and plant structure (leaf/stem/flowering stalk) level, and these are expected to be intense during years of average or below average rainfall.

Samenvatting

De aandacht van het natuurbeheer in grote delen van Oost Afrika richt zich de laatste tijd op kleine natuurreservaten. Die komen vooral voor in de savannes, waar een uitzonderlijke grote variatie aan samenlevende wilde grazende hoefdiersoorten aanwezig is. De toekomst van die reservaten wordt in toenemende mate bedreigd door de uitdijende omringende menselijke populatie, waardoor ze reeds in het verleden steeds meer werden geïsoleerd en daardoor ook werden samengedrukt. Dit proces kan leiden tot een groeiende populatie en biomassadichtheid van grote grazers, die de dominante herbivoren in deze systemen zijn, en tot meer intense concurrentie tussen de soorten. Het is derhalve van belang om de gras - grazer trofische relaties te begrijpen, met het oog op habitatcompressie, zodat met behulp van die ecologische informatie de bescherming van de grote grazers kan verbeteren.

Het Lake Nakuru Nationale Park (LNNP) in doet dienst als studiegebied voor het onderhavige onderzoek. Het is het eerste Keniaanse Park dat door middel van een omheining ecologisch geïsoleerd kwam te liggen in het midden van de jaren '70. Veel biologen zijn geïntrigeerd door de hoge dichtheid aan grazerbiomassa in dit Park, dat met ca. 134 kg ha^{-1} (met uitzondering van de recent gereïntroduceerde witte neurhoorn *Ceratotherium simum*) waarschijnlijk een van de hoogst beschreven dichtheden voor een gemeenschap van grote grazers in Oost-Afrika kent. Om het functioneren van het gras-grazer subsysteem beter te begrijpen heb ik de de interacties tussen grassen en grazers, en tussen grazersoorten onderling bestudeerd in de grazergemeenschap van het Lake Nakuru Nationale Park.

Deze gemeenschap raakte geïsoleerd van omliggende populaties in 1976 en kende een groei in biomassa, die in de eerste 13 jaar gedomineerd werd door diersoorten van middelmatig lichaamsgewicht (100-300 kg), zoals de defassa waterbok (*Kobus defassa*) en Burchell's zebra (*Equus burchelli*). In de laatste tien jaar tot 1999 domineerden de meer dan 300 kg wegende buffel (*Syncerus caffer*) en de elandantiloop (*Taurotragus oryx*) de gemeenschap. De kleinere soorten (<100 kg) gaven een wisselend populatieverloop tussen 1976 en 1999: wrattenzwijn (*Phacocoerus aethiopicus*), impala (*Aepyceros melampus*), Grant's gazelle (*Gazella granti*), Bohor rietbok (*Redunca redunca*), Chanler's rietbok (*Redunca fulvorufula chanleri*), en Thomson's gazelle (*Gazella thomsoni*). Het lokaal uitsterven van de Bohor rietbok is wellicht toe te schrijven aan de groei van de Grant's gazelle populatie (6%); beide soorten behoren tot dezelfde gewichtsklasse en hebben eenzelfde habitatvoorkeur. De achteruitgang van waterbok en wrattenzwijn in de laatste negen jaar lijkt in verband te staan met de sterke groei van de buffel (17%) en de zebra (12%).

De grazers in LNNP maken veel gebruik van de korte en halflange open graslanden gedurende elk seizoen. De nichebreedte voor zowel diëet als habitatgebruik was het grootst gedurende de vroege natte tijd, en nichebreedte van het diëet was het kleinst in de droge tijd, conform de verwachting. Seizoensverschillen tussen nichebreedtes waren echter gering, mogelijk vanwege het gebrek aan duidelijke verschillen tussen seizoenen waarin de observaties werden uitgevoerd, of vanwege de beperkte mogelijkheden tot 'nichecontractie' in de droge tijd. De gemiddelde index van diëetoverlap tussen alle paren van grazersoorten over alle seizoenen was hoog (>0.6), en de index van habitatoverlap was nog hoger (>0.7). Sommige van de nu zwak reproducerende soorten (waterbok en wrattenzwijn) vertoonden een grote mate van overlap in habitatgebruik met beter reproducerende grotere of kleinere soorten. Ze werden echter niet uitgesloten van het habitat van de grotere soorten, maar deelden het. Er waren geen aanwijzingen voor facilitatie in de grazergemeenschap. De grote mate van habitatoverlap en de negatieve populatiegroeisnelheden van waterbok en wrattenzwijn suggereren dat er sprake kan zijn van concurrentie om voedselbronnen. Seizoenale indices van gecombineerd habitat- en diëetoverlap tussen paren van grazers overschrijden in de meeste gevallen de limiet van co-existentie (0.54). Dit betreft in de natte tijd in het bijzonder de grazerparen impala-zebra (0.76), impala-buffel (0.48) en impala-waterbok (0.46); in de droge tijd impala-zebra (0.5), impala-buffel (0.7) en impala-waterbok (0.63); in het vroege natte seizoen impala-zebra (0.52), impala-buffel (0.54) en impala-waterbok (0.55). Deze hoge waarden suggereren dat er concurrentie tussen de grazers kan optreden.

Ondanks de gesuggereerde interacties hebben we echter geen uitsluiting van soorten op basis van concurrentie ('competitive displacement') kunnen waarnemen. Dit is mogelijk toe te schrijven aan het verschillend gebruik van dezelfde voedselplanten door verschillende grazersoorten. Een studie naar het foerageergedrag van impala en zebra maakte duidelijk dat beide soorten de hoogste voedselopnamesnelheden bereikten op plaatsen met hoog gras (≥ 15 cm) binnen zogenaamde korte open graslanden (0-30 cm hoogte). Bij het exploiteren van dezelfde voedselplanten is zebra in staat om meer vezelrijk materiaal te eten, zoals bloeiwijzen, stengels en hogere grasdelen, terwijl impala vezelarmer materiaal verorbert, zoals bladeren onder aan de stengels, die het met zijn smalle bek kan bereiken. Deze differentiatie op het nivo van voedselplanten kan de concurrentie tussen grazersoorten waarschijnlijk reduceren. Het functioneren van het Nakuru-grazer subsysteem lijkt te worden beinvloed door concurrentie die zich afspeelt op habitat-, diëet-, en plantendeel- (blad/stengel/bloeiwijze) nivo. Deze is naar verwachting het sterkst gedurende jaren van gemiddelde of lage regenval.

Curriculum vitae

Shem Mwawaka Mwasi was born on 7th January 1967 in Mombasa, Kenya. He undertook his secondary and high school studies in Shimo la Tewa School, Kenyatta High School and Dr. Aggrey High School in the Coast province of Kenya between 1981 and 1987. In 1988, he was admitted to Moi University, Kenya, for a BSc (Wildlife Management) degree programme, which he completed and graduated with an upper second class honours in 1991 and soon after during that same year, he was awarded a Kenya Government scholarship to undertake an Mphil (Environmental Biology) degree programme at Moi University where he investigated the population regulation mechanism of waterbuck in Lake Nakuru National Park, Kenya, for his research project and graduated in 1994. Upon graduation, he was employed as an assistant lecturer in the Department of zoology at Jomo Kenyatta University of Agriculture and Technology in Kenya until February 1996 when he resigned and joined Moi University, School of Environmental Studies in the same capacity. In June 1996, he was awarded a scholarship by the Netherlands Organisation for International Co-operation in Higher Education to pursue a PhD degree programme in the Tropical Nature Conservation and Vertebrate Ecology Group, in the Department of Environmental Science, Wageningen University, the Netherlands. He specialised in community ecology of large wild grazers of the savanna. Prof. Herbert Prins and Dr. Ignas Heitkonig supervised his PhD project. He is married to Catherine Mbala, whom they have two children, Beryl Anaga (11 years old) and Ronald Tunji (8 years old).

This study was financially supported by the Netherlands Organisation for International Co-operation in Higher Education (NUFFIC).

Cover design: Willemien Schouten

Cover photo: Shem M. Mwasi