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Seasonal resource use and niche breadth in an assemblage of coexisting grazers in a fenced Park

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ABSTRACT

Many small Parks in Kenya are being fenced to control human-wildlife conflict. Some of these Parks have a diversity of large herbivores which might increase in density in the wake of fencing and subsequent compression of their home ranges due to closure of their migratory routes. It is important to understand the consequences of such an increase on the structuring of insularised herbivore assemblages in such Parks. We studied seasonal resource segregation and niche breadth variation as mechanisms of coexistence in a high density grazer assemblage in Lake Nakuru National Park which is small and completely fenced. Diet composition and habitat use were considered as variables of resource use. We predicted that overlap in resource use and niche breadth would be the smallest among grazers with similar body weights in the dry season which is the most resource limiting for grazers in East Africa. Our results were contrary to the predictions because of lack of seasonal differentiation in the overlap of diet composition and habitat use, and in niche breadth. Overlaps in resource use were consistently high during both the wet and dry seasons, and niche breadth contraction during the dry season was not possible probably because of lack of species-specific niches during the dry season. Our results suggest that there might be competitive interactions in this grazer assemblage which is an important parameter to consider in the management of the Park.

Keywords: Niche Breadth; Diet Composition; Coexistence; Habitat Use; Overlap; Season; Grazer; Competitive Interactions

1. INTRODUCTION

The mechanisms by which coexistence of apparently many similar grazing ungulates is made possible have been a subject of study for some time [1-4]. A number of mechanisms have been identified by which resource segregation between large grazers become possible during coexistence. Among these mechanisms are physiological adaptations [5], interspecific differences in incisor arc width [6] and differences in body weight [4]. In case one or combinations of these mechanisms are not adhered to, then competitive interactions among grazers are expected to occur. Although competitive interactions in the field are hard to detect, a body of evidence [4,7,8] proves that these interactions play a role in the structuring and functioning of many large grazer assemblages.

Forage quantity of large grazers in East Africa varies with seasons, which are primarily defined by the amount of rainfall received in an area during a particular period in a year. Intra-annual rainfall in these areas is correlated with primary production [9,10]. 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 forage [11,12]. Therefore, both from the perspective of food availability and that of food quality, the dry season will generally be the most limiting in East Africa. It is expected that, in the dry season, resource segregation among coexisting grazers becomes more pronounced as they specialise in resource use to avoid interacting competitively with each other [8,13,14]. Their niche breadth in resource use also becomes smaller [15], while the reverse is expected during the non-limiting season when resources are abundant. It is also expected that during the non-limiting season, grazers in similar body weight classes will overlap more in resource use and have wider niche breadth in resource

use. These predictions have indeed been demonstrated in a number of grazer assemblages [16-19].

Studies in overlap of resource use and variation in niche breadth in dense assemblages of grazers in small fenced National Parks where there is no dry or wet season grazer migration have not been reported in literature. With this background we assessed overlap in seasonal diet composition and habitat use as major variables of overlap in resource use, and the implications of niche breadth in diet composition and habitat use on a high density assemblage of six coexisting large grazers of different body weights in Lake Nakuru National Park, Kenya which is a small Park (188 km^2) that has been completely fenced since 1977. The study hypothesised that, overlap in resource use between species in similar body weight classes, would be lowest in the dry season, and niche breadth in resource use would be smallest during the dry season.

2. MATERIALS AND METHODS

2.1. Description of the Study Area

Various types of vegetation communities utilised by grazers are found in Lake Nakuru National Park, the most dominant being *Cynodon nlemfuensis* grassland [20]. Other important grasslands which grazers utilise include *Chloris gayana*, *Sporobolus spicatus* and *Themeda triandra.* Lake shore vegetation comprising a mixture of *Cyperus laevigatus*, *Cynodon dactylon* and *Sporobolus spicatus* is also utilised. We distinguished eight physiognomic vegetation types within the above vegetation communities. In this study, these physiognomic vegetation types are classified as habitat types. They include the Lake shore vegetation which is dominated by *Cyperus laevigatus*, *Sporobolus spicatus* and *Cynodon dactylon*; Short open grassland ≈ below 30 cm tall; Medium open grassland ≈ 30 cm to 1m tall; Tall open grassland ≈ above 1 m tall; Swamp, flooded and riverine vegetation dominated by *Cyperus laevigatus* and *Typha domingensis*. Riverine vegetation is dominated by *Acacia xanthophloea* and *A. albida*; Open *Tarchonanthus* bush; Open *Acacia* woodland; and Woody vegetation comprising mainly of *Solanum* spp., *Ocimum* spp., *Aspilia* spp. and *Rhus natalensis* (**Figure 1**).

Rainfall pattern in the Park is bimodal, with a wet and a dry season occurring during the year. This study was conducted from the end of the long wet season of 1998 (late wet) with 171 mm, to the dry season of 1999 with 37 mm, and the early wet season of 1999 with 285 mm of rain.

2.2. Botanical Composition of Diet

Fresh dung samples belonging to African buffalo *Syncerus caffer* Sparrman, Burchell's zebra *Equus burchelli*, defassa waterbuck *Kobus defassa* Rüppell, warthog *Phacocoerus aethiopicus* Pallas, impala *Aepyceros melampus* Lichtenstein, and Grant's gazelle *Gazella granti* Brooke were collected during the study. Five pellets of fresh dung were collected from each individual. Dung samples collected in this manner from 15 individuals belonging to the same species were then composted into a single sample. Each composite sample was then air dried, ground and stored in an airtight polythene bag. Seasonal diet composition was determined by faecal analyses of the composite samples following a procedure described by [21].

2.3. Habitat Use

The area of the Park which the grazers utilise throughout the year was divided into five sites (**Figure 1**). In each site, a permanent road transect which traversed through the highest number of habitats was selected. Transect lengths were variable. Each transect was surveyed twice a month for one year from May 1998 to April 1999. An animal count was conducted during each survey. Morning counts started at 0600 h and ended at 0900 h, while afternoon counts started at 1600 h and ended at 1830 h when it started getting dark. These time periods coincided with active foraging of the grazers in the Park. During each count, the habitat types where animals were found foraging and number of animals counted on either side of the road were recorded.

2.4. Body Weight Classes

African buffalo (631 kg), Burchell's zebra (235 kg), defassa waterbuck (190 kg), warthog (73 kg), impala (52 kg), and Grant's gazelle (50 kg) were grouped into three body weight classes > 300 kg, 100 - 300 kg and 0 - 100 kg based on their mean live body weights obtained from [4,22,23].

2.5. Data Analyses

Overlap in diet composition and in habitat use were calculated using Pianka's index of resource overlap $\alpha = \sum P_{ij}P_{ik} \Big/ \sqrt{\left(\sum P_{ij}^2 \times \sum P_{ik}^2\right)}$, where P_{ij} and P_{ik} = proportion that resource category i contributes to the resource use of grazer j and k [24]. Overlap in resource use was computed as the product of overlap in diet composition and that in habitat use. Niche breadth for diet composition and habitat use was calculated using [25] index B: $B = 1 \Big/ \sum P_{ij}^2$, where P_{ij} = proportional use by animal species j of resource category i.

3. RESULTS

3.1. Overlap in Diet Composition

Seasonal overlap in diet composition between the

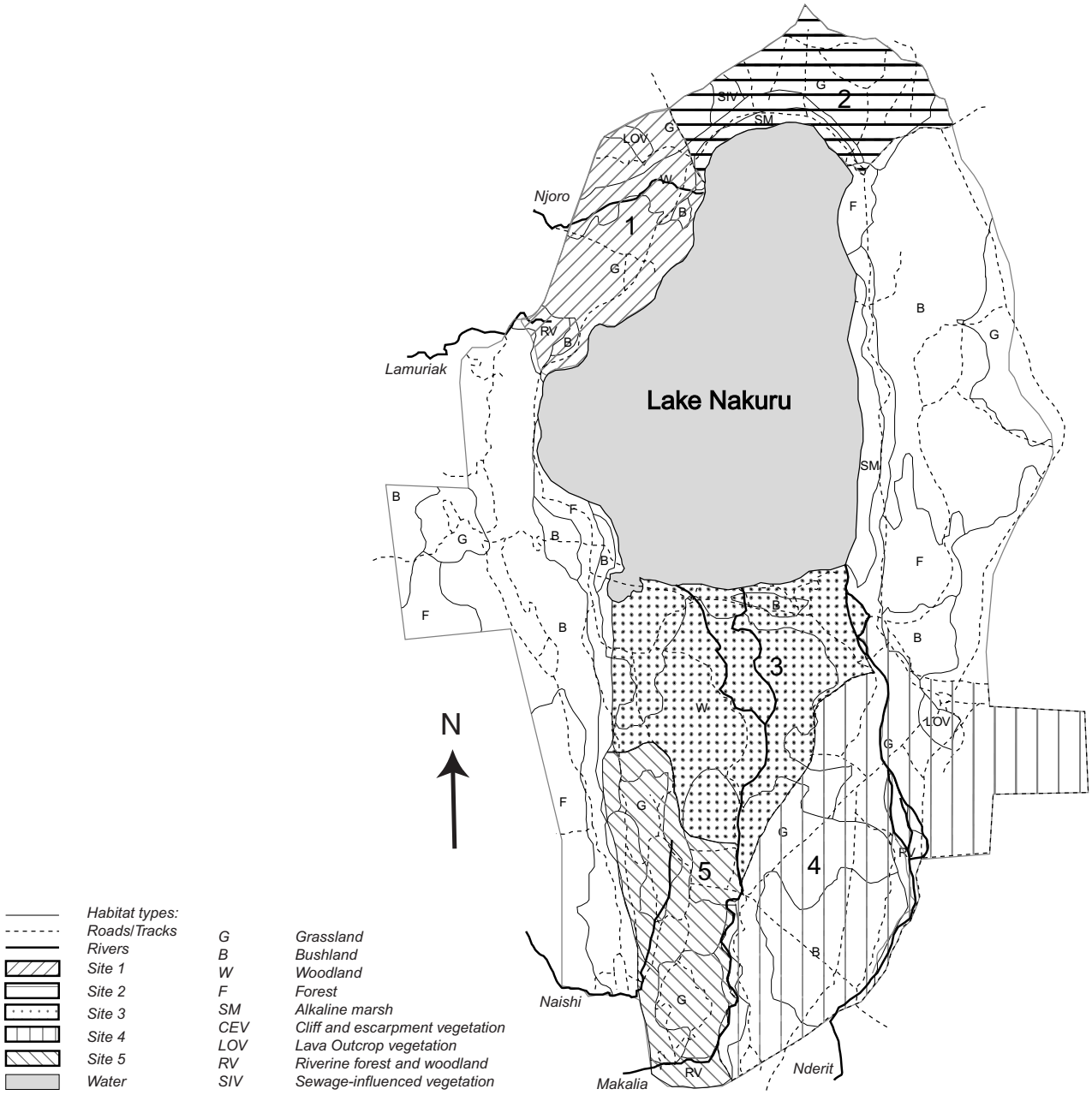

Figure 1. Map of Lake Nakuru National Park showing the location of study sites.

grazers was remarkable with the highest overlap, 0.94, observed during the early wet season between buffalo-zebra, and the lowest observed during the late wet season between buffalo-Grant's gazelle, 0.40. During the dry season, the highest overlap in diet composition, 0.87 was observed between zebra-warthog, while zebra-impala had the lowest overlap of 0.55 during this season. Grazers in similar body weight classes had their lowest overlap during the late wet season and highest during the early wet season: zebra-waterbuck, 0.56; warthog-impala, 0.6; warthog-Grant's gazelle, 0.7; and impala-Grant's gazelle, 0.64 (**Table 1**).

3.2. Overlap in Habitat Use

The highest overlap in habitat use, 0.99 was observed during the late wet season between Grant's gazelle-zebra, and the lowest, 0.79 between warthog-impala. During the dry season, waterbuck-zebra recorded the highest overlap, 0.97 and the lowest overlap, 0.79 was observed between warthog-impala, while in the early wet season, warthog-zebra overlapped most, 0.96, and warthog-impala overlapped the least, 0.48 in their habitat use. The lowest

Table 1. Indices of overlap in diet composition between grazers in Lake Nakuru National Park.

		Buffalo	Zebra	Waterbuck	Warthog	Impala
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
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
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

Table 2. Indices of overlap in habitat use between grazers in Lake Nakuru National Park.

		Buffalo	Zebra	Waterbuck	Warthog	Impala
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
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
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

seasonal overlap in habitat use was observed between warthog-impala and this was consistent during the three seasons. Only warthog-impala showed a remarkable change in overlap from 0.79 in both the late wet and dry season to 0.48 in the early wet season, and warthog-Grant's gazelle 0.91, in late wet season to 0.97 in dry season to 0.78 in early wet season (**Table 2**).

3.3. Overlap in Resource Use

Zebra-waterbuck, 0.73; warthog-impala, 0.50; warthog-Grant's gazelle, 0.78 and impala-Grant's gazelle, 0.68 had a higher overlap in resource use in the dry season. Lowest overlaps in resource use were observed during the early wet season with warthog-impala, 0.44; warthog-Grant's gazelle, 0.53; zebra-waterbuck, 0.75 not changing much from the dry season. For warthog-impala, warthog-Grant's gazelle and impala-Grant's gazelle, overlap in resource use increased slightly during the succeeding late wet season. However, for zebra-waterbuck the overlap decreased. The highest overlap in resource use, 0.82 between grazers in different body weight classes *i.e.*, zebra-warthog was recorded in the dry season (**Table 3**).

3.4. Niche Breadth

Niche breadth for diet composition was small (B_{max} = 12). The smallest niche breadth for buffalo, 5.34, zebra, 3.80 and waterbuck, 4.83 in diet composition were recorded during the dry season, while impala, 3.92 and Grant's gazelle, 4.9 had their smallest niche breadth for diet composition during the long wet season. Warthog had its smallest during the early wet season. Waterbuck had the highest shift in niche breadth from the dry to the early wet season, and also the largest niche breadth in diet composition, 8.30 compared to all other grazers. Niche breadth for habitat use was relatively small (B_{max} = 8) among the grazers. Like in diet composition, it was smallest in the long wet season, only warthog had its smallest niche breadth during the dry season (**Table 4**).

4. DISCUSSION

For species in similar body weight classes, the lowest overlap in diet composition was observed during the late wet season, probably because during this season which

Table 3. Indices of overlap in resource use (diet composition and habitat use) between grazers in Lake Nakuru National Park.

		Buffalo	Zebra	Waterbuck	Warthog	Impala
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
Dry season	Buffalo					
	Zebra	0.52				
	Waterbuck	0.72	0.73			
	Warthog	0.52	0.82	0.75		
	Impala	0.70	0.50	0.63	0.50	
	Grant's	0.45	0.71	0.65	0.78	0.68
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

Table 4. Niche breadth for diet composition and habitat use by grazers. LW, late wet season; D, dry season; EW, early wet season.

	Diet composition			Habitat use		
	LW	D	EW	LW	D	EW
Buffalo	5.45	5.34	5.69	2.05	2.46	3.46
Zebra	5.38	3.80	6.56	2.55	3.59	4.29
Waterbuck	6.77	4.83	8.30	2.28	2.72	2.77
Warthog	5.20	4.50	4.45	2.86	2.73	2.78
Impala	3.92	6.48	4.58	3.13	3.54	3.05
Grant's gazelle	4.90	6.09	7.18	2.34	3.99	4.05

succeeded the early wet season, most grasses which were the dominant forage items for the grazers [26], and liberally available in the Park during the early wet growing season had now become fibrous and senescent making the grazers experience a lesser forage choice. In the process they might have differently specialized on fewer forage species thus exhibiting the lowest overlap in diet composition. The dry season of 1999 received rainfall, which was abnormal because traditionally it doesn't receive any, and because of this, green standing crop biomass was still available during this season. In fact from field observations, perennial grasses were observed sprouting and new herbs growing during this season. This explains the lack of lowest overlap during this season as initially predicted since the grazers did not necessarily have to lower their overlap in diet composition because there was still adequate forage available.

There was lack of a discernible seasonal variation in overlap in habitat use between grazers in similar body weight classes among the three seasons. In fact overlap indices were consistently high during the seasons. This lack of a clear trend in overlap in habitat use and the fact that the overlaps between grazers within the same body weight classes were consistently high suggest that no reasonable change in seasonal habitat use occurred in the Park among the grazers contrary to what [27] found out. The habitats during the time of this study were more compressed with a higher population density of large grazers than when [27] conducted their field work five years earlier.

Coexisting grazers especially those in similar body weight classes are expected to segregate more in their resource use during period of resource limitation, and that their niche breadth becomes smaller [15]. Our results did not comply with this prediction since resource segregation and smallest niche breadth were not observed during the dry season which is traditionally the resource limiting period. This is explained by the fact that seasonal differences in overlap in resource use were not outspoken, and also that possibilities for niche "contraction" in the dry season were limited leaving the grazers with little chance to move to a species-specific niche in order to have the lowest niche breadth in diet composition and habitat use. If we consider a resource use overlap of 0.54 to be the critical limit to similarity for coexisting species [28,29], then our results indicate that overlap in resource use between grazers in similar body weight classes has exceeded this limit. This leaves no doubt that the grazers are competitively interacting with each other within the assemblage. The interactions are playing a critical role in the functioning and structuring of this assemblage, and should thus be considered central in the wildlife management of the Park.

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