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Habitat selection by large herbivores in Lake Nakuru National Park, Kenya

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The overall density of 17 large herbivore species encountered during the study differed among species and habitat types, but not between seasons. There were clear seasonal patterns of association among species, which were more pronounced during wet than dry seasons, suggesting greater habitat selectivity and increased ecological separation. The defassa waterbuck (*Kobus ellypsiprymnus defassa* Ruppel) showed ecological separation from other species, possibly because it competitively displaced them.

Keywords: Nakuru; herbivores; populations; habitat; seasons.

Introduction

For wildlife managers, both the number of species and time spent occupying a given habitat are important in determining the conservation value of such habitats. Many management activities aim to maintain populations in an area without detriment to either habitat or animals. Achievement of this goal depends on a clear insight into the habitat needs, habitat use and potential interspecific competition among the animal species (Scogings *et al.*, 1990). This paper presents the findings of a study to quantify habitat use in an ecologically isolated large herbivore community.

The study was carried out in Lake Nakuru National Park, the first of Kenya's protected areas to be fully fenced. It lies between the longitudes 36° 03′ and 36° 07′ E, and latitudes 0° 18′ and 0° 30′ S. Rainfall is bimodal, with two wet seasons from March to May and October to December, separated by two dry seasons from June to September and January to March. The completion of the electric perimeter fence in 1987 stopped all cross-border large mammal movements, except translocations into or out of the park.

Methods

Data for animal density and distribution were collected by driving along a series of transects laid along the existing road and track network. Prior to the study, transects were selected along roads traversing the main habitat types occupied by large herbivores. The samples were distributed so as to ensure as much spatial representation as possible.

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All counts were conducted by two observers, one serving as a driver and the other as a recorder, beginning between 6.30 and 7.00 a.m. The species and number of all large herbivores found within a predetermined strip width on either side of the road were recorded. Whenever a new habitat type was encountered, the current transect was terminated and a new one begun.

Distances covered along transects were measured by recording the vehicle's odometer reading at the start and end of each transect. Transects located within two distinct regions of the park were surveyed in four consecutive days within the first week of every month for one year and thereafter every other month for another year, starting from March 1991.

The numbers counted for each species in each habitat type were expressed as densities for each sampling session. The density of each species in each habitat type was expressed as a proportion of overall total for that sampling session. The density distribution provided a measure of relative abundance coded according to species, season and habitat. The resulting matrices were subjected to detrended correspondence analysis (DCA) (Hill, 1979) to generate scattergrams depicting ecological association where the samples represented the various habitat types by season.

Results

The overall herbivore density for 17 species recorded in this study differed significantly among species and habitat types (3-way ANOVA, $F_{16,4,7} = 109.993^{***}$, 21.661^{***} for species and habitat types, respectively), but not among seasons. Only nine species were encountered in all transect surveys. A comparison of their occupancy in different seasons and habitat types is presented in Table 1. Density differed significantly among habitat types, except for the buffalo (*Syncerus caffer* Sparrmann) and eland (*Taurotragus oryx* Pallas). No species except the eland showed a seasonal change in distribution. The interaction between the effects of season and habitat type was significant only for the waterbuck and warthog (*Phacochoerus aethiopicus* Pallas).

Figure 1 presents the results of DCA on relative abundance of 17 herbivore species in the five major habitat types and eight seasons covered in the study. Two distinct clusters resulted, one grouping the eland. Grant's gazelle (*Gazella granti* Brooke), black rhinoceros (*Diceros bicornis* L.), buffalo, zebra (*Equus burchelli* Gray), impala (*Aepyceros melampus* Lichtenstein) and Rothschild's giraffe (*Giraffa camelopardalis rothschildi* Lydekker), all of which are either large-bodied, bulk of mixed feeders. A second cluster grouped together two predominantly smaller-bodied grazer species, the Thomson's gazelle (*Gazella thomsoni* Gunther) and warthog.

When wet season samples were considered separately, the larger cluster remained relatively unchanged, as did the second one comprising the Thomson's gazelle and warthog. DCA on dry season samples resulted in much less clustering of species. The waterbuck data showed no tendency to cluster with any other species, either in the wet or dry seasons.

DCA based on habitat by seasons samples resulted in four distinct clusters. The grassland, woodland and shoreline grassland samples formed a cluster each, irrespective of season. The fourth cluster grouped together wooded and bushed grassland samples (Fig. 2). The same pattern was found when wet seasons were considered separately, while dry season analysis showed a tendency for grassland and shoreline grassland samples to fall in one cluster.

Table 1. Herbivore population densities (No. km^{-2}, mean ± SE) in different seasons and habitat types

Year	Season	Grassland	Woodland	Shoreline grassland	Bushed grassland	Wooded grassland
(a) Buffalo						
1991	long dry	5.9 ± 2.3	1.1 ± 0.8	2.6 ± 1.5	143.5 ± 107.5	6.8 ± 2.3
	long rains	6.9 ± 4.4	0.9 ± 0.6	4.8 ± 3.3	6.1 ± 3.7	11.9 ± 7.2
	short dry	7.1 ± 5.0	0.3 ± 0.3	0.6 ± 0.5	13.4 ± 7.7	15.5 ± 8.4
	short rains	10.2 ± 6.3	0.3 ± 0.3	4.9 ± 2.9	15.0 ± 15.0	2.6 ± 2.6
1992	long dry	6.9 ± 3.4	9.1 ± 2.9	2.5 ± 1.3	10.3 ± 4.5	10.4 ± 4.6
	long rains	5.1 ± 3.4	0.2 ± 0.2	3.7 ± 1.7	8.4 ± 5.6	7.6 ± 5.6
	short dry	16.8 ± 16.3	2.3 ± 2.3	13.5 ± 13.5	12.3 ± 12.3	7.2 ± 4.9
	short rains	11.1 ± 10.2	3.4 ± 2.1	6.2 ± 3.8	6.2 ± 5.6	1.6 ± 1.3
F value		(7,82) 0.343 NS	(7,64) 2.662*	(7,64) 1.135 NS	(7,82) 1.64 NS	(7,136) 0.424 NS
(b) Eland						
1991	long dry	–	2.4 ± 2.4	–	–	3.3 ± 2.6
	long rains	20.0 ± 13.9	–	–	–	6.3 ± 6.3
	short dry	0.3 ± 0.3	–	–	–	4.6 ± 4.2
	short rains	3.7 ± 3.7	–	–	–	–
1992	long dry	0.2 ± 0.2	0.6 ± 0.6	–	0.3 ± 0.3	1.3 ± 0.8
	long rains	0.5 ± 0.5	–	–	1.2 ± 1.2	0.4 ± 0.3
	short dry	–	–	–	–	–
	short rains	–	–	–	–	–
F value		(7,82) 2.273*	(7,64) 0.538 NS	(7,64) –	(7,82) 0.555 NS	(7,136) 0.664 NS
(c) Giraffe						
1991	long dry	–	–	0.2 ± 0.2	–	0.3 ± 0.3
	long rains	25.4 ± 25.5	–	0.9 ± 0.6	–	–
	short dry	–	0.1 ± 0.1	2.1 ± 2.1	0.6 ± 0.6	–
	short rains	–	–	–	0.3 ± 0.3	–
1992	long dry	–	2.0 ± 1.7	–	–	–
	long rains	0.3 ± 0.3	–	–	–	–
	short dry	–	0.3 ± 0.3	–	–	0.3 ± 0.3
	short rains	–	–	0.3 ± 0.3	–	–
F value		(7,82) 1.153 NS	(7,64) 0.47 NS	(7,64) 0.81 NS	(7,82) 0.748 NS	(7,136) 1.248 NS
(d) Grant's gazelle						
1991	long dry	4.8 ± 2.8	–	–	–	4.7 ± 2.0
	long rains	12.4 ± 6.7	–	–	–	2.8 ± 1.5
	short dry	2.9 ± 1.6	–	–	2.8 ± 2.8	3.8 ± 2.2
	short rains	5.5 ± 4.0	–	–	–	11.2 ± 6.5
1992	long dry	5.4 ± 2.0	0.5 ± 0.4	0.8 ± 0.8	1.5 ± 1.5	9.1 ± 3.6
	long rains	2.5 ± 1.1	–	0.8 ± 0.5	–	6.5 ± 3.7

Table 1 (*Continued*)

Year	Season	Grassland	Woodland	Shoreline grassland	Bushed grassland	Wooded grassland
	short dry	7.2 ± 4.5	–	–	–	2.8 ± 1.9
	short rains	6.6 ± 6.6	–	0.3 ± 0.3	–	2.6 ± 2.6
F value		(7,82) 0.808 NS	(7,64) 0.677 NS	(7,64) 0.355 NS	(7,82) 0.525 NS	(7,136) 0.584 NS
(e) Impala						
1991	long dry	84.7 ± 36.3	76.3 ± 18.5	21.7 ± 8.9	29.5 ± 15.8	150.6 ± 26.2
	long rains	103.3 ± 30.8	23.0 ± 12.6	25.0 ± 10.3	21.4 ± 19.4	180.8 ± 27.7
	short dry	27.8 ± 10.6	42.3 ± 23.4	11.9 ± 8.4	62.1 ± 52.0	188.4 ± 40.6
	short rains	114.0 ± 46.2	31.2 ± 17.7	5.6 ± 1.9	40.0 ± 40.0	278.3 ± 81.2
1992	long dry	73.8 ± 19.7	105.7 ± 33.0	54.9 ± 15.2	55.0 ± 15.7	105.0 ± 22.3
	long rains	113.7 ± 36.1	42.2 ± 11.3	16.2 ± 7.4	18.7 ± 6.6	222.4 ± 49.8
	short dry	70.4 ± 41.1	5.8 ± 5.0	54.7 ± 46.0	12.6 ± 7.8	236.7 ± 100.7
	short rains	98.0 ± 65.4	18.6 ± 10.8	16.3 ± 13.9	13.1 ± 7.4	208.8 ± 102.9
F value		(7,82) 0.648 NS	(7,64) 1.473 NS	(7,64) 1.535 NS	(7,82) 0.643 NS	(7,136) 1.645 NS
(f) Thomson's gazelle						
1991	long dry	10.2 ± 4.3	–	6.7 ± 4.0	–	11.7 ± 3.9
	long rains	14.4 ± 13.4	–	4.0 ± 3.3	–	4.9 ± 2.7
	short dry	17.4 ± 11.8	0.5 ± 0.5	7.2 ± 4.8	–	7.4 ± 3.8
	short rains	17.4 ± 17.4	–	8.5 ± 8.5	–	4.4 ± 3.1
1992	long dry	11.1 ± 4.9	–	8.6 ± 2.5	–	5.4 ± 1.5
	long rains	11.4 ± 8.5	–	10.4 ± 5.5	–	7.5 ± 4.1
	short dry	4.1 ± 4.1	–	10.2 ± 6.9	–	6.6 ± 6.6
	short rains	–	–	5.0 ± 5	–	0.1 ± 0.1
F value		(7,82) 0.267 NS	(7,64) 1.161 NS	(7,64) 1.213 NS	(7,82) –	(7,136) 0.747 NS
(g) Waterbuck						
1991	long dry	79.7 ± 26.7	76.7 ± 33.5	111.7 ± 44.5	8.2 ± 4.1	66.9 ± 17.0
	long rains	102.2 ± 46.4	35.8 ± 15.6	76.5 ± 23.8	2.1 ± 1.5	116.8 ± 54.0
	short dry	27.2 ± 9.0	35.0 ± 15.0	192.1 ± 47.8	5.2 ± 3.2	75.4 ± 17.9
	short rains	79.9 ± 25.2	43.3 ± 33.1	242.9 ± 48.9	0.3 ± 0.3	80.8 ± 20.4
1992	long dry	43.3 ± 13.1	76.2 ± 13.5	107.5 ± 26.8	6.6 ± 2.6	15.0 ± 3.5
	long rains	47.8 ± 18.9	56.2 ± 24.4	77.0 ± 34.1	4.6 ± 2.7	34.8 ± 15.7
	short dry	38.4 ± 30.7	9.6 ± 6.8	176.1 ± 81.9	10.9 ± 10.9	5.1 ± 3.6
	short rains	13.8 ± 9.7	98.8 ± 50.1	138.6 ± 97.4	–	8.0 ± 4.3
F value		(7,82) 1.173 NS	(7,64) 0.891 NS	(7,64) 1.342 NS	(7,82) 0.658 NS	(7,136) 3.133**
(h) Warthog						
1991	long dry	73.6 ± 18.6	22.9 ± 7.0	229.7 ± 59.9	11.1 ± 4	36.0 ± 8.1
	long rains	66.3 ± 17.9	5.5 ± 3.2	90.7 ± 18.6	2.3 ± 1.5	32.5 ± 11.2
	short dry	57.9 ± 20.3	13.0 ± 4.3	212.2 ± 67.7	11.5 ± 8.9	49.8 ± 16.4

Table 1 (*Continued*)

Year	Season	Grassland	Woodland	Shoreline grassland	Bushed grassland	Wooded grassland
	short rains	83.9 ± 38.4	6.5 ± 3.9	179.9 ± 54.9	0.7 ± 0.7	22.8 ± 8.8
1992	long dry	74.7 ± 20.2	21.4 ± 4.4	354.1 ± 84.0	18.1 ± 7.6	25.3 ± 4.5
	long rains	70.9 ± 27.9	13.0 ± 3.3	113.9 ± 26.1	0.5 ± 0.3	26.4 ± 7.7
	short dry	33.1 ± 22.8	4.3 ± 3.2	101.6 ± 40.8	5.0 ± 3.4	15.7 ± 5.6
	short rains	47.1 ± 27.0	13.7 ± 5.9	46.1 ± 15.6	–	34.6 ± 15.5
F value		(7,82) 0.24 NS	(7,64) 1.616 NS	(7,64) 2.048 NS	(7,82) 1.174 NS	(7,136) 0.962 NS
(i) Zebra						
1991	long dry	–	–	–	–	14.6 ± 6.4
	long rains	7.9 ± 4.3	–	2.8 ± 1.9	–	32.0 ± 30.1
	short dry	5.7 ± 5.7	–	–	–	9.1 ± 5.2
	short rains	7.6 ± 7.6	–	–	–	8.3 ± 4.6
1992	long dry	6.1 ± 4.2	–	1.4 ± 1	0.6 ± 0.6	12.6 ± 4.6
	long rains	0.6 ± 0.6	–	–	–	34.3 ± 19.4
	short dry	–	–	–	–	–
	short rains	–	–	2.4 ± 2.4	–	24.0 ± 21.9
F value		(7,82) 0.659 NS	(7,64) –	(7,64) 1.105 NS	(7,82) 0.353 NS	(7,136) 0.599 NS

Degrees of freedom in parenthesis; NS, non significant result; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

Discussion

The community under study is totally enclosed, preventing movements across the park boundaries. Any fluctuations observed in the density of a species in any habitat type are, therefore, indicative of temporal changes in level of use. Such patterns are greatly influenced by the quality and quantity of various resources.

A study of eight ungulate species found the common waterbuck (*Kobus e. ellipsiprymnus* Ogilby) to prefer the widest range of habitat types (Melton, 1987). This was inconsistent with results from most previous studies (Lamprey, 1963; Hanks *et al*., 1969; Spinage, 1970). In fact, Hirst (1975) found the waterbuck to be the most stenoecious of five grazer species in his study.

This study indicates distinct preferences for the five major habitat types by waterbuck which were found in unchanging densities over the entire habitat spectrum, except the wooded grassland whose importance varied with seasons. The waterbuck also displayed some degree of ecological segregation from other species. Their presence at high density in any habitat type or area led to the competitive exclusion of most other grazers. In the Umfolozi Game Reserve, asymmetric competition for resources was suggested as the ultimate cause of population decline in the common waterbuck (Melton, 1987).

This study provides evidence for separation among the park's grazers. The Thomson's gazelle and warthog were found in close association throughout their range. Being small-

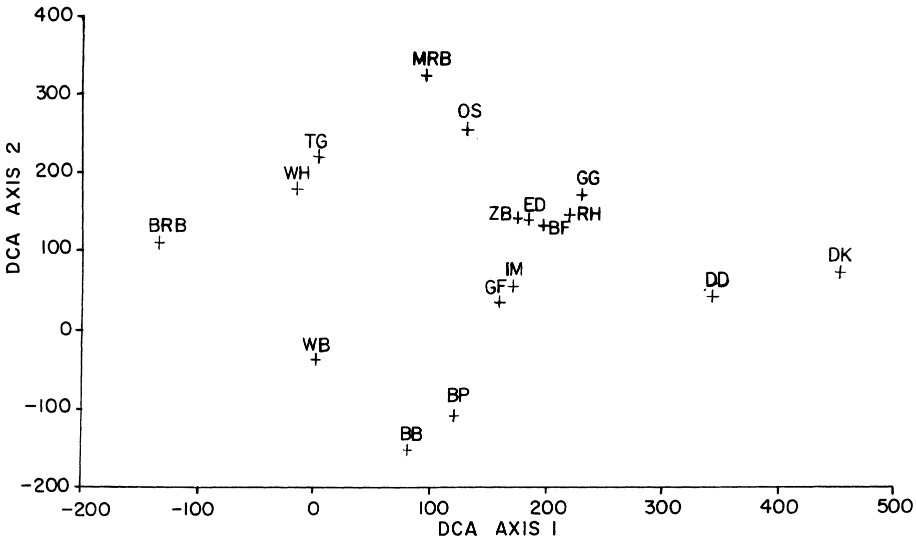

Figure 1. A scattergram resulting from DCA on the relative abundance of 17 large herbivore species encountered in the five habitat types during the eight seasons of the study.
Key to species codes: BB, bushbuck (*Tragelaphus scriptus* Pallas); BF, buffalo; BRB, Bohor reedbuck (*Redunca redunca* Pallas); DD, Kirk's dikdik (*Rhyncotragus kirkii* Gunther); DK, duiker; ED, eland; GF, Rothschild's giraffe; GG, Grant's gazelle; IM, impala; MRB, mountain reedbuck (*Redunca fulvorufula* Afzelius); OS, Masai ostrich (*Struthio camelus Masaicus* Neumann); RH, black rhinoceros; TG, Thomson's gazelle; WB, defassa waterbuck; WH, warthog; BP, bush pig (*Potamochoerus porcus* L.); ZB, zebra.

bodied grazers, they are likely to benefit from the presence of bulk feeders like the zebra. In addition, warthogs dig up rhizomes, bulbs, tubers and corms from below the soil surface with increasing intensity during the dry seasons. This broadens the warthog's niche and introduces some ecological segregation between the two species. It is a widespread behavioural adaptation that becomes particularly important to the survival of warthogs during drought (Mason, 1990).

The buffalo and eland are large bodied and range over large areas in order to meet their dietary requirements. In this study, the two species exhibited little habitat selectivity. The zebra preferentially avoided the woodland but utilized areas with tall and relatively low quality grass, suitable for its non-ruminant bulk feeding habits.

The black rhinoceros and Rothschild's giraffe were the only exclusive browser species encountered in Lake Nakuru. Although the extent of any competition between them could not be adequately assessed, the part still probably has sufficient woody cover to support their current population levels. The species browse at different heights, producing considerable ecological separation. The interaction between the two species needs to be closely watched in the future, as they cannot continue to increase without more intense competition ensuing.

Food varies in quality and quantity between seasons and habitats. In this study, the variation forced some species to utilize habitats of relatively low value during the dry season. There is general agreement that large herbivore populations are regulated by food

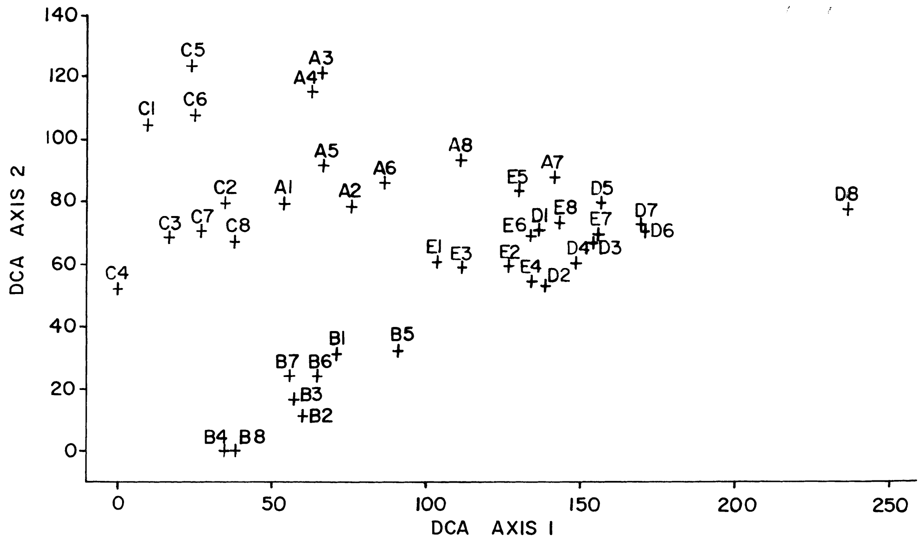

Figure 2. A scattergram resulting from DCA on the relative abundance of 17 large herbivore species in a season by habitats matrix, covering all seasons included in this study.
Key to habitat by season combinations:

A1 = grassland, 1991 long dry; A2 = grassland, 1991 long rains; A3 = grassland, 1991 short dry; A4 = grassland, 1991 short rains; A5 = grassland, 1992 long dry; A6 = grassland, 1992 long rains; A7 = grassland, 1992 short dry; A8 = grassland, 1992 short rains.

B1 = woodland, 1991 long dry; B2 = woodland, 1991 long rains; B3 = woodland, 1991 short dry; B4 = woodland, 1991 short rains; B5 = woodland, 1992 long dry; B6 = woodland, 1992 long rains; B7 = woodland, 1992 short dry; B8 = woodland, 1992 short rains.

C1 = shoreline grassland, 1991 long dry; C2 = shoreline grassland, 1991 long rains; C3 = shoreline grassland, 1991 short dry; C4 = shoreline grassland, 1991 short rains; C5 = shoreline grassland, 1992 long dry; C6 = shoreline grassland, 1992 long rains; C7 = shoreline grassland, 1992 short dry; C8 = shoreline grassland, 1992 short rains.

D1 = bushed grassland, 1991 long dry; D2 = bushed grassland, 1991 long rains; D3 = bushed grassland, 1991 short dry; D4 = bushed grassland, 1991 short rains; D5 = bushed grassland, 1992 long dry; D6 = bushed grassland, 1992 long rains; D7 = bushed grassland, 1992 short dry; D8 = bushed grassland, 1992 short rains.

E1 = wooded grassland, 1991 long dry; E2 = wooded grassland, 1991 long rains; E3 = wooded grassland, 1991 short dry; E4 = wooded grassland, 1991 short rains; E5 = wooded grassland, 1992 long dry; E6 = wooded grassland, 1992 long rains; E7 = wooded grassland, 1992 short dry; E8 = wooded grassland, 1992 short rains.

supply, but not without considerable debate (Phillipson, 1973; Sinclair, 1974, 1975; Western, 1991).

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