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FEATURES OF HABITAT SELECTION BY LARGER HERBIVOROUS MAMMALS AND THE OSTRICH IN THE SOUTHERN KALAHARI CONSERVATION AREAS

P. T. VAN DER WALT* and P. F. RETIEF

Department of Research and Information
National Parks Board of Trustees
Private Bag X402
Skukuza
1350

E. A. N. LE RICHE and M. G. L. MILLS**

Kalahari Gemsbok National Park
Private Bag X5890
Gemsbokpark
8815

G. DE GRAAFF

Department of Research and Information
National Parks Board of Trustees
P.O. Box 787
Pretoria
0001

*New address: *Directorate of Nature Conservation and Recreation Resorts*
Private Bag 13306
Windhoek
9000

**New address: *Department of Research and Information*
National Parks Board of Trustees
Private Bag X402
Skukuza
1350

Abstract – A Chi-squares contingency table was used to extensively analise animal/habitat interactions in the southern Kalahari conservation areas between 1978 and 1982. The effect of changing environmental conditions on the distribution of five large mammalian species (eland *Taurotragus oryx*, gemsbok *Oryx gazella*, blue wildebeest *Connochaetes taurinus*, red hartebeest *Alcelaphus buselaphus*, springbok *Antidorcas marsupialis*) and the ostrich *Struthio camelus* is indicated by definite seasonal preferences. A general habitat-use pattern, whereby each habitat type was utilised at some stage during the year by one or more species, as well as a response by the different species to other environmental attributes was found revealing an ecological balance which will be maintained only if the present physical size of the conservation areas in question is maintained indefinitely.

Introduction

A sound, long-term management policy for any conservation area is based primarily on an understanding of the seasonal usage by animals of the available habitat diversity. This practice indicates the relative suitability of the habitat and its role in determining population trends of the associated fauna.

The southern Kalahari conservation area which is formed jointly by the Kalahari Gemsbok National Park in the Republic of South Africa and the Gemsbok National Park in the Republic of Botswana, represents such a conservation area and is probably one of the largest near natural units on the continent of Africa (approximately 3 620 000 ha in extent). Certain regions of this conservation area have been described in greater detail by Leistner (1967), Weare & Yalala (1971), Bothma & De Graaff (1973), Parris (1976) and Mills (1977).

In this semi-desert area where the average annual rainfall of 233 mm falls mainly in a short spell from January to March (Table 1), a study was made of certain salient factors which could influence the seasonal preferences of five antelope species, as well as the ostrich, for the major habitats.

Methods

The species included in this investigation were eland *Taurotragus oryx*, gemsbok *Oryx gazella*, blue wildebeest *Connochaetes taurinus*, red hartebeest *Alcelaphus buselaphus*, springbok *Antidorcas marsupialis* and the ostrich *Struthio camelus*.

In order to obtain a more comprehensive understanding on a large scale of animal/habitat interactions in this vast conservation area, animal occurrence was related to a set of environmental attributes. The data were obtained from ten aerial surveys conducted between 1978 and 1982. Every aerial survey was conducted in the same manner. The total area was divided into a grid system with a repeatable flight pattern superimposed. Details pertaining to height, air speed, strip width and aircraft are dealt with elsewhere (Van der Walt *in prep.*). The entire surface of the Kalahari Gemsbok National Park was dealt with this strip-flying, while only a section of the Gemsbok National Park was covered due to the vastness of the area.

Table 1

Monthly rainfall figures (in mm) for Nossob Camp in the Kalahari Gemsbok National Park, 1978 – 1982. Medium Term (1967 – 1983) monthly averages shown in brackets

Year \ Month	J (54,0)	F (54,6)	M (44,4)	A (25,4)	M (11,4)	J (1,2)	J (0,6)	A (2,6)	S (3,2)	O (16,2)	N (16,2)	D (20,3)	Total (250,1)
1978	9,2	41,2	41,6	8,6	1,6	0	0	0	0,1	0,2	0	4,0	106,5
1979	39,0	52,8	0,1	27,1	16,0	0,3	2,0	3,3	0	16,0	34,7	32,9	224,2
1980	17,3	40,0	39,1	8,3	0	0	0	6,0	7,9	1,4	7,0	24,3	151,3
1981	0,8	54,2	57,0	0	0	2,2	0	24,7	1,2	8,1	41,4	23,5	213,1
1982	12,9	20,3	4,0	25,2	7,2	0	8,0	0	7,3	31,2	6,5	62,4	185,0

The vegetal cover (as seen from the air) in each grid square was classified on a physiognomic basis into six habitats to be described in the following section (Table 2). In addition, due to the ease with which they are recognisable from the air, the availability of water (from either natural sources or windmills) were also recorded on the grid squares. As seasonal attributes, the following were also determined for each grid square according to the following characteristics:

Table 2

The general occurrence (%) of major habitat types in the Kalahari Gemsbok National Park and the Gemsbok National Park

	Savanna	River	High Dunes	Low Dunes	Plains
KGNP	7,7	2,4	31,8	51,7	6,4
GNP	62,0	1,6	24,0	11,4	1,0

a) Veld condition.
   1. Grasses mostly dry and dark brown in colour.
   2. A definite tint of greenness among old growth due to new growth.
   3. A general green image.

b) Height of grasses.
   1. Long grass.
   2. Short grass.

c) Recent burning history.
   1. Burnt this summer.
   2. Burnt last summer.
   3. No sign of burning.

For each habitat factor, a contingency table was constructed, to contrast the relative frequencies of each herbivore in each habitat category. These tables were constructed according to the method described by Strahler (1978). Each table was tested by using a chi-squared test for significance at the 0,05% level (Siegel 1956).

If the herbivore frequencies showed significant differences in their habitat category occurrences, the frequencies were converted to Haberman residuals (Haberman 1973; Strahler 1978). These residuals indicate significant presence or absence values in a standardised fashion. Generally, residual values of two or more show above-expected frequencies, while values lower than –2 show below-expected frequencies. For the purpose of this discussion, these will be referred to as "preference" or "avoidance" by the herbivore for the respective habitat category, although such inference can only be made on biological grounds. Note that the "preference" or "avoidance" values are relative terms, and relate to the comparison between that herbivore and all the others in habitat selection.

Savanna

A prominent tree stratum occurs, averaging some 5 metres in height. A number of species dominate, including *Acacia erioloba, A. reficiens, Terminalia sericea* and *Boscia albitrunca*. The abundant palatable pod and leaf production of this tree stratum ensures an adequate fodder bank for browsing antelope species. During the colder season, fodder availability drops considerably (Van der Walt *pers. obs.*). A tall shrub layer, dominated by the palatable *Grewia flava* attains its peak importance in this habitat type. The presence of trees and large shrubs, averaging not more than 200 individuals/ha (Van der Walt *pers. obs.*) leads to a scattered grass/dwarf shrub layer and an extensive development of an annual layer dominated by stoloniferous plants. The animals use the abundant fruit and underground storage organs extensively and lends a unique quality to the effective utilisation of food in this part of the Kalahari system.

Riverbeds

Only the two well-developed river valleys in the area, the Nossob and Auob, are included in this habitat. Brackish places which are apparently related to fossilised river courses such as the Polentswa are dealt with together with pans (see below). Associated with the rivers are major features such as well-developed calcareous flats and slopes covered with *Stipagrostis obtusa*, with the river course dominated in places by *Panicum coloratum* and tall (averaging 8 m) *Acacia erioloba* and *A. haematoxylon* trees, together with the presence of artificial watering points.

High dunes

This habitat is restricted and confined to the immediate proximity of the two river courses and consists of high sand dunes in excess of 7 metres in height. The tree and tall shrub strata are of lesser importance than is the case in the savanna and riverbed habitats while the grass/dwarf shrub layer, as well as the geophyte component are well represented.

Low dunes

This is an extensive habitat with prominent dune formation in the more southern areas. The tree stratum is absent while the tall shrub and grass/dwarf shrub strata are dominant. *Boscia albitrunca* and *Acacia haematoxylon* occur here as tall shrubs and attain their highest density. Their role in the browsing scene as evergreens is of great significance. Because of the dominance of perennial grasses, annuals are of lesser importance.

Plains

In between the low dune areas are relatively small patches of plains, areas with a slightly undulating topography. The plant composition differs only in degree from that of the previous habitat, the most conspicuous difference being the absence of *B. albitrunca.*

Pans and brackish areas

These saline areas with their associated dominant dwarf shrub cover are, together with the rivers, focal areas for the large herbivores (Parris 1976; Mills & Retief 1984a). They are a source of minerals to animals at all times and a source of water in the rainy season.

A most interesting pattern of ecological diversity exists within the relatively simple topographic complex. This pattern is brought about mainly by the influence of the three basic ecological seasons (Mills & Retief 1984b), namely hot and wet (January – April), hot and dry (October – December) and cold and dry (May – September), on the palatable components found in the four vegetational strata.

Results and discussion

This method reveals a definite seasonal preference by all animals for some of the environmental attributes dealt with. The most significant preferences are given in Tables 3–6.

Table 3

Haberman (1973) residuals indicating habitat preferences of some animals in the southern Kalahari conservation areas during the dry season

Habitat / Animal	I Savanna	II River	III High Dunes	IV Low Dunes	V Plains
Springbok	6,2	10,1	3,2	−8,1	−3,2
Gemsbok	−3,0	−2,1	0,3	1,9	1,3
Wildebeest	−1,0	−1,1	−0,8	2,2	−1,1
Hartebeest	2,7	−1,4	1,9	−2,6	−2,1
Eland	−6,1	−1,9	0,8	3,5	2,4
Ostrich	3,4	0,5	−3,4	−0,2	0,8

Springbok

Springbok generally favour the riverine areas. The apparent attraction for springbok to water (Tables 5 and 6) is almost certainly an artifact caused by their attraction to the rivers where artificial watering points are at their densest. Mills & Retief (1984b) have shown that artificial water is unimportant to springbok. There is an added marked preference for savannas during the dry season, accompanied by a slight preference for unburnt areas in the savanna and high dune habitats (see Tables 3 and 4). As the drought, which is a regular occurrence, progresses, so the search for brackish areas, such as pans, is intensified. Wet season conditions along the rivers seem to suit the requirements of this abundant Kalahari antelope.

Table 4

Haberman (1973) residuals indicating habitat preferences of some animals in the southern Kalahari conservation areas during the wet season

Habitat / Animal	I Savanna	II River	III High Dunes	IV Low Dunes	V Plains
Springbok	1,5	11,9	−1,5	−3,1	−1,3
Gemsbok	−5,5	−3,0	0,4	4,9	3,3
Wildebeest	9,1	3,8	−3,0	−6,7	−2,1
Hartebeest	7,1	−1,7	1,2	−7,3	−2,0
Eland	5,6	−1,0	−1,5	−3,5	−1,2
Ostrich	−6,8	−1,1	1,3	6,1	−0,1

Gemsbok

Well-adapted to desert conditions, this animal displays a versatile usage of all habitat types (Tables 3 and 4). A more distinct preference for the waterless long grass and the low dune areas is, however, prevalent in the wet season, with a marked avoidance of the savanna. Of all the habitat factors dealt with in this study, grass type and height seem to be of great significance to the gemsbok. When contrasted with the other herbivore species, gemsbok appear to utilize areas devoid of water in both the wet and dry seasons.

Gemsbok show no definite tendency to migrate to areas with new growth following rain and/or veld burning, or to areas with a high frequency of pans. This may be due to the animal's generalised feeding habits whereby use is made (both as a grazer and a browser (Leistner 1967)) of all localised fodder reserves. Preference is given in high rainfall periods to new growth, grass or annuals (Van der Walt *pers. obs.*), while during the dry season there is a tendency to select short grass areas with a high incidence of bulbous plants (Van der Walt *pers. obs.*). Heavy use is then made of subterranean storage organs, particularly in times of long droughts. These bulbs or corms are dug up by hoof to a depth of approximately one metre.

Blue wildebeest

Burned areas and a tendency to keep in the proximity of water (in the riverbeds and the adjoining savanna areas) are two highly preferred factors during the dry season for this species known for its migratory tendencies over large areas (Le Riche *pers. obs.*). This behaviour is not shown during the wet season (Tables 5 and 6).

The high preference in the wet season for areas with fresh green foliage (Table 6) emphasises the dependence of this animal on regular rainfall for its survival. During the wet season short grass areas are moderately preferred. Pans or brackish spots do not seem to be preferred areas for the wildebeest.

Table 5

Significant preferences (Haberman (1973) residuals) showed by animals in the southern Kalahari during the dry period for environmental attributes as determined by BDA (Strahler 1978)

	Veld Condition			Grass Height		Veld Burning			Water		Brackish Preference		
	1	2	3	1	2	1	2	3	Available	Not Available	None	Brackish Spot	Pan
Springbok							−2	+2	+7	−7			
Gemsbok				−4	+4		−4	+4	−5	+5		+2	
Wildebeest	−4	+4				+5	+9	−10	+11	−11	+3	−3	
Hartebeest	−5	+5		+4	−4		+7	−6	−2	+2	−3	+3	
Eland				+3	−3			+2			+3	−2	
Ostrich	+4	−4					−5	+5	−3	+3			

Table 6

Significant preferences (Haberman (1973) residuals) showed by animals in the southern Kalahari during the wet period for environmental attributes as determined by BDA (Strahler 1978)

	Veld Condition			Grass Height		Veld Burning			Water		Brackish Preference		
	1	2	3	1	2	1	2	3	Available	Not Avaiable	None	Brackish Spot	Pan
Springbok	+3								+7	−6			
Gemsbok	+3	−3		+4	−4				−5	+4			
Wildebeest	−4	−4	+7	−3	+3						+2	−3	
Hartebeest	−4		+2	−4	+4				+3	−3	−4	+3	+3
Eland	−2			−2	+2								
Ostrich			−2										

Red hartebeest

Habitat type seems to be very important for this animal's survival. In the wet season they prefer burnt short grass areas with much green growth in the savanna and avoid the tall grass low dune areas. In the dry season the same tendency is less conspicuous. Brackish areas and pans are frequented throughout the year. Riverine areas are visited sporadically and in fact show negative values for rivers in both seasons (Tables 3 and 4).

Eland

A very marked seasonal difference in habitat use is shown. During the wet season eland greatly prefer short grass savanna areas (Table 4) while during the dry season they are found more in the tall grass, low dune and plain areas (Table 3). A very definite avoidance of savannas is shown during the dry season (Table 3). Pans, brackish and burnt areas are also of no definite attraction (Tables 5 and 6).

Ostrich

The ostrich, despite a distinct preference for low dune areas during the wet season, displays an almost general usage of all habitat types. It prefers the savanna during the dry season. The ostrich appears to be not very dependent on regular rainfall, as no preference is shown for either green growth or water. Burnt areas with any amount of regrowth are also of no definite attraction. A slight influence is, however, shown by most of the environmental attributes on this bird which indicates and opportunistic utilisation pattern.

Conclusions

The methods used to gain insight into animal/habitat relationships of this unique area indicated some very definite seasonal preferences.

With the exception of springbok and ostrich the animals tend to utilise a smaller range of habitats in the wet than in the dry season. This indicates the need for each animal to be opportunistic in times of stress in order to survive, a tendency which increases during a prolonged drought.

Despite the relatively intensive artificial programme of water provision in the KGNP, only blue wildebeest showed a definite preference for this commodity, and mainly during the dry season.

A higher preference rating than that shown by red hartebeest and gemsbok for brackish areas was expected because these animals are often seen in the areas. The year-round tendency of hartebeest only to frequent these mineral rich areas, the seasonal preference thereof by the gemsbok, and the definite avoidance thereof by all the other animals, indicate a lesser ecological significance of these areas than is generally recognized. However, because of the low incidence of pans in the survey area the use of pans *per se* was not investigated in this study.

The advantageous ecological balance so characteristic of the Kalahari is shown by the response of the animals to the other environmental attributes. No preference for incidentally burnt areas during the wet season is shown by any species, stressing

the availability of ample fodder resources. During the dry season a definite response is, however, shown by all animals. The more specialised grazers (wildebeest and hartebeest) exhibit the most significant preference, that is in favour of burnt areas, while the mixed feeders (the others) show a significant preference for unburnt areas.

The alternate seasonal preference shown by gemsbok, wildebeest and eland for attributes such as veld condition and grass height, is further evidence of the prevailing ecological balance in the system.

The relatively slight influence of man up to now *inter alia*, by starting fires and providing water, did not affect the natural occurring utilization pattern significantly. This situation will continue only if the present size of the conservation area is maintained.

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REFERENCES

BOTHMA, J. DU P. and G. DE GRAAFF. 1983. A habitat map of the Kalahari Gemsbok National Park. *Koedoe* 16: 181-190.

HABERMAN, S. J. 1973. The analysis of residuals in cross-classified tables. *Biometrics* 28: 205-220.

LEISTNER, O. A. 1967. The plant ecology of the southern Kalahari. *Mem. bot. Surv. S. Afr.* 38: 1-172.

MILLS, M. G. L. 1977. *Diet and foraging behaviour of the brown hyaena* Hyaena brunnea, *Thunberg 1820, in the southern Kalahari.* M.Sc. thesis, University of Pretoria, Pretoria.

MILLS, M. G. L. and P. F. RETIEF. 1984a. The response of ungulates to rainfall along the riverbeds of the southern Kalahari 1972-1982. *Koedoe* 27 (Supplement): 129-141.

MILLS, M. G. L. and P. F. RETIEF. 1984b. The effect of windmill closure on the movement patterns of ungulates along the Auob riverbed. *Koedoe* 27 (Supplement): 107-118.

PARRIS, R. 1976. *A study of the major components of the Kalahari pan ecosystem.* M.Sc. thesis, University of Pretoria, Pretoria.

SIEGEL, S. 1956. *Nonparametic statistics for the behavioural sciences.* Tokyo: McGraw Hill.

STRAHLER, A. H. 1978. Binary Discriminant Analysis: A new method investigating species-environment relationships. *Ecology* 59(1): 108-116.

WEARE, P.R. and A. M. YALALA. 1971. Provisional vegetation map of Botswana. *Botsw. Notes and Records* 3: 131-147.