Seasonal habitat selection by eland in arid savanna in southern Africa

C. Fabricius *
Chief Directorate Nature and Environmental Conservation, Kimberley, 8300 Republic of South Africa

M.T. Mentis
Botany Department, University of the Witwatersrand, 2050 Wits

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The small scale seasonal habitat selection of eland in a semi-arid savanna was investigated. Linear discriminant functions and suitability index curves were calculated to differentiate between 314 m^2 plots where eland were present and absent. Biological explanations were sought for the results. In winter eland relied on woody evergreen plants, while in summer they selected patches with good grass cover. Eland were independent of shelter and cover in both seasons. The ability of the discriminant functions to predict the presence and absence of eland was validated by classifying independent habitat samples. The functions were found to be reliable.

Die seisoenale habitatseleksie van elande in 'n halfdor savanna is ondersoek. Lineêre diskriminant-funksies en geskiktheidsindeks-krommes is ontwikkel om tussen 314 m^2-persele waar elande teenwoordig en afwesig was te onderskei. Biologiese verklarings vir die resultate is gesoek. In die winter het elande van immergroen houtagtige plante gebruik gemaak, terwyl hulle in die somer gebiede met 'n goeie grasbedekking verkies het. Elande was onafhanklik van skuiling gedurende die winter en somer. Die diskriminant-funksies se vermoeëns om die teenwoordigheid en afwesigheid van elande in onafhanklike steekproewe van die habitat te voorspel is getoets. Die funksies is hiervolgens betroubaar bevind.

* To whom correspondence should be addressed at: Division of Forest Science and Technology, CSIR, Private Bag 6515, George, 6530 Republic of South Africa

Although studies have been done on the food preferences (Nge'the & Box 1976) and habitat selection (Hillman 1988) of eland *Taurotragus oryx*, none of these have attempted to quantify their small scale habitat requirements. We developed functions to predict the presence and absence of eland in 314 m^2 patches in arid savannas, and related these to their food and shelter requirements.

The word 'habitat' is variously used in ecological literature and discussions. It is therefore appropriate to define the term to avoid confusion. Existing definitions can be grouped into two broad categories. First, the popular definitions refer to the locality where an organism is found, i.e. its 'address'. Odum (1971), for example, defines habitat as 'the locality where it (an organism) lives', while Kenneth (1976, in the Dictionary of Biological Terms), defines it as 'the locality or external environment in which a plant or animal lives'. Second, it is defined as the area containing the biological requirements for the survival of an organism (e.g. Harris & Kangas 1988).

A disadvantage of the definitions pertaining to an organism's locality or 'address', is that they can lead to biologically meaningless descriptions of habitat. Some organisms may occupy areas as a result of circumstances beyond their control, e.g. historical factors or artificial relocations. An extreme example is a cage in a zoo, which, according to the popular definition, should be the habitat of the organism found there. To avoid such consequences, it is necessary to define habitat in relation to the survival of an organism or community. For the purpose of this paper the habitat of an organism is defined as 'the area containing the biotic and abiotic environmental components which enable the survival of a population of that organism.'

Johnson (1980) defines four hierarchical orders of habitat selection. The first order selection by a species is the geographical range within which it occurs. The second order selection comprises the home range of a species within its geographical range. Its third order selection is the utilization or avoidance of different habitat components within its home range. The fourth order habitat selection of the animal is defined as the actual food plants the animal selects among the third order habitat components. These selection orders may be even more finely divided.

In the approach described in this paper it was assumed that patches of suitable and unsuitable habitat were interspersed. Patches of Johnson's (1980) third order habitat within first and second order landscape-sized units were distinguished. It was assumed that the size of a habitat patch was determined by the distance at which an animal could recognize the resources in its vicinity.

In order to fully understand the habitat needs of the animals, it was necessary to study their seasonal habitat relations. Hillman (1988) found extensive seasonal movements of eland in East Africa, which suggested seasonal differences in the habitat selection of eland.

Study area

The study was carried out on the farm Rooipoort, 50 km west of Kimberley, northern Cape Province, South Africa. Rooipoort is a privately owned estate of some 430 km^2 which is mostly used for game ranching purposes. It falls within the False Orange River Broken Veld vegetation type, with isolated communities of Kalahari Thornveld invaded by Karoo (Crowe, Schijf & Gubb 1981). The environment is patchy, with small areas of woodland interspersing the predominantly high shrubland.

The mean annual rainfall for the district is 419 mm, based on 90 years' rainfall data. Most of the rain falls in late summer (January to April, Weather Bureau 1986). The rainfall is unpredictable, and the annual amount of rain that can be expected with a 90% probability is approximately 200 mm (Tyson 1986).

Mean monthly minimum and maximum temperatures during the study period ranged from 1,7°C (mean minimum) in July 1987 to 35,6°C (mean maximum) in January 1988. The highest temperature recorded during the study period was 40,4°C in January 1988 while the lowest temperature was –4,8°C in June 1987.

During a game survey by helicopter in March 1987, 547 eland were counted from the air at Rooipoort, which amounted to a density of approximately 1,6/km^2.

Methods

A landscape map of the study area was drawn from aerial photographs and plotless ground surveys. The landscapes consisted mainly of *Acacia mellifera, A. tortilis, A. karroo* and *Tarchonanthus camphoratus* shrubland and woodland, *A. erioloba* woodland, panveld and riverine thicket. The landscape preferences of eland were analysed by a correspondence analysis (Greenacre 1984) of available antelope census data against landscapes. The data consisted of monthly game counts which had been done along a fixed census route for three years prior to this study by the estate managers.

Two census routes ('A' and 'B') about 40 km in length were used for eland surveys. The routes were selected to cover approximately equal amounts of landscapes which were preferred and avoided by eland. Other considerations when selecting the survey areas were whether they were representative of the arid savanna regions of the Cape Province, where the results of the study will be implemented. Accessibility, e.g. the condition of the roads, was also considered. Data from route A were used to quantify the habitat selection of eland, while independent data from route B were used to validate the results of the first analysis.

Censuses were done by day and by night from the back of a four-wheel-drive vehicle. An entire group of animals was used as a unit of observation, regardless of its size. The habitat was sampled only once at a locality where an animal or group of animals was observed to ensure independence of the data.

In order to quantify Johnson's (1980) third order habitat requirements of eland, we had to sample the habitat on a sufficiently small scale to avoid the 'masking' effects of larger scale (first and second order) vegetation units. The most convenient plot shape and size for this purpose was found to be a circular plot with a radius of 10 m.

Habitat surveys were done by a modified version of the Point Centre Quarter (PCQ) method (Mueller-Dombois & Ellenberg 1974). A chain cross was laid out at the point where eland were observed with one of its axes perpendicular to the census route. The chain divided the plot into equally-sized quadrants. Plant species taller than 0,5 m which occurred within a radius of 10 m were scored according to the number of quadrants in which they occurred, scores ranging between zero and four. Plants smaller than 0,5 m in height were difficult to locate and were not recorded (*cf.* Owen-Smith & Cooper 1987).

The structure of the vegetation was quantified by estimating the crown : gap ratio (Edwards 1983) at 1,8 m above ground level between the two plants closest to the centre of the plot which did not share the same quadrant. The distance to the nearest shade tree was paced if it was closer than 30 m or estimated if it was further. A shade tree was defined as a tree or large shrub of which the canopy could be entered by eland (*cf.* Hirst 1975). Grass availability was estimated as the percentage projected canopy cover of grass within the plot.

Additional habitat samples were taken on a monthly basis to obtain data where eland were absent, and to increase the sample size. Plots were placed systematically along both routes at 1-km intervals. The distances and directions of the plots from the road were determined by random digits. The habitat was sampled by the same methods as described above. These plots were searched for any recent (fresher than seven days old) sign of eland. It was estimated that animal tracks and the shiny mucus layer of dung remained visible for approximately seven days, depending on weather conditions. Where no sign could be found, the plot was assigned an 'absent' rating.

Data on plant phenophases were used to draw phenograms for each plant species (Fabricius 1989). The phenograms indicated two major seasons: a period of food shortage (winter, June to August) and a period of food abundance (summer, September to May). Deciduous food plants were ignored when analysing data gathered in winter.

Woody browse plants in the study area were grouped into functional guilds, based on attributes of importance to the food selection of browsers (Owen-Smith 1982). Two-way indicator species analysis or TWINSPAN (Hill 1979) was used to obtain an objective classification of plant species to test the validity of the guilds. A species-by-attributes matrix was used as input to the analysis.

Discriminant function analysis or DFA (Fisher 1936) was used to analyse the data obtained from route A. DFA is a multivariate classification technique which is based on eigen-analysis. It calculates a linear function to separate two or more groups of data as effectively as possible if the affiliation of the members of each group is known. The discriminant function consists of a series of linearly additive weighting coefficients for each input variable. Variables with high discriminating power receive larger weighting coefficients than variables with low discriminating power. The unstandardized discriminant function takes the form

$$Ci = Ci1V1 + Ci2V2 + Ci3V3 + \dots + CijVj + Cio$$

where Ci is the classification score, Cij is a weighting coefficient, V is the raw variable value and Cio is a constant. DFA indicated the important variables which discriminated between the presence and absence of eland. It also produced a function which could be used to classify data not incorporated in the development of the model.

Variables with discriminant function coefficients less than 0,05 and highly correlated variables were removed. New discriminant functions were then calculated with the remaining variables until the best discriminating power with the fewest variables was attained. The end product was a linear model which could be used to classify independent or unknown data. A 'cut-off' value was estimated which separated discriminant function scores which indicated the presence of eland from scores indicative of their absence. The cut-off was determined as the value at which as many as possible of the dependent samples were correctly classified (Snedecor & Cochran 1974). The Statgraphics computer package (Statistical Graphics Corporation) was used to calculate the discriminant functions.

A disadvantage of DFA is the assumption that variables contribute linearly to the discriminant function. This would mean that the greater the magnitude of a variable, the greater its positive or negative contribution would be. This is rarely the case in ecosystems, where there is mostly a Gaussian relation between the magnitude of a variable and its effect on an organism (Johnson 1981). This criticism was particularly relevant to the variables pertaining to vegetation structure, i.e. the crown : gap ratio, percentage canopy cover of grass and proximity of shade.

Response curves were therefore constructed for structural variables to avoid this linear effect. The variables 'shade', 'grass' and 'crown-gap' were categorized according to the frequency distribution of the data. Preference indices (*p*) (Petrides 1975) were calculated for each variable category by dividing the proportional utilization (*pu*) of a category by its proportional availability (*pa*) ($p = pu/pa$). All categories were considered to be available to the study animals.

The preference indices were transformed by scaling them to values between 0 and 1. This was done by dividing the preference indices for a variable by the largest preference index of all categories of that variable. The categories were then plotted against their transformed preference indices to obtain suitability index (SI) curves. The curves were simplified by smoothing to approximate either straight, Gaussian or U-shaped lines. Suitability indices obtained from these curves were used as input to the discriminant function analysis.

The information obtained from route A was validated by applying it to data gathered along route B. Variables were multiplied by their discriminant function coefficients to obtain a discriminant score. Scores above the cut-off values predicted the presence of eland and scores below it, their absence. The percentage of correctly classified independent samples and their 95% confidence limits were calculated to attach a statistical significance to the classification power of the discriminant functions. Because of a shortage of data, the ability of the function to predict the absence of eland in winter could not be validated.

Results

Correspondence analysis of existing census data indicated that eland preferred the landscapes *Tarchonanthus camphoratus – Grewia flava* shrubland and *Acacia erioloba* woodland in summer. In winter, eland appeared to prefer *A. mellifera* woodland and *A. tortilis* woodland.

The only functional plant guild of relevance to this study was 'palatable evergreens'. Members of this guild showed obvious signs of heavy browsing, and had small leaves which were available throughout the year. The other plant species in the study area were abundant enough to be included as single species groups.

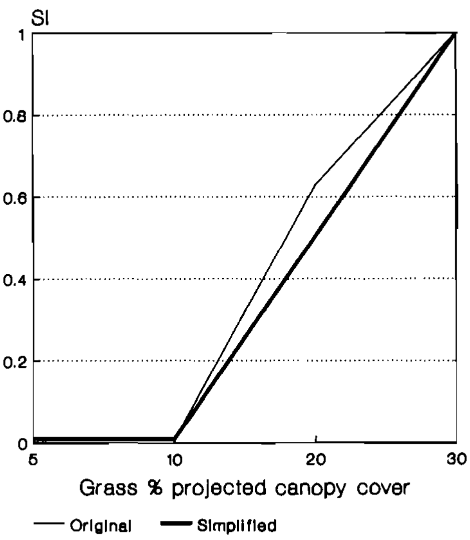

Figure 1 Suitability index curve for percentage canopy cover of grass for eland in summer. SI = suitability index. The simplified curve is a smoothed linear version of the more complex original curve.

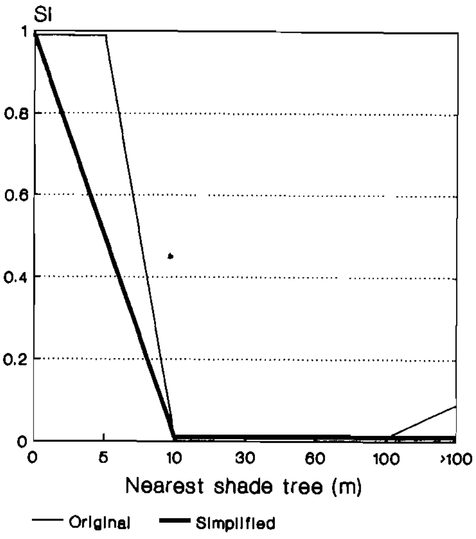

Figure 2 Suitability index curve for proximity of shade for eland in winter.

The SI curves for the variables 'shade' and 'grass' are shown in Figures 1 and 2. The curves were eventually simplified to linearity. The variable 'crown-gap' received a low discriminant function coefficient (0,013) and could be omitted from the analysis without any effect on the classification power of the function.

For eland in summer, the variables with absolute coefficients greater than 0,05 which discriminated between the presence and absence of eland were *Acacia mellifera, A. erioloba, Ziziphus mucronata, Tarchonanthus camphoratus*, 'palatable evergreens', *A. karroo* and 'grass' (percentage projected canopy cover of grass). *A. mellifera* and *Z. mucronata* made a negative contribution to the discriminant function.

The function discriminating between the presence and absence of eland in summer was

$-0{,}58V1 - 0{,}54V2 + 0{,}37V3 + 0{,}13V4 + 0{,}19V5 + 0{,}13V6 + 0{,}41V7$ where

$V1$ = presence of *A. mellifera*
$V2$ =presence of *Z. mucronata*
$V3$ = presence of *A. erioloba*
$V4$ = presence of *A. karroo*
$V5$ = presence of *T. camphoratus*
$V6$ = presence of 'palatable evergreens'
$V7$ = SI for grass density (from Figure 1).

The critical value which separated scores where eland were present from scores where they were absent was – 0,13.

In winter, the variables *A. tortilis*, 'palatable evergreens', *A. erioloba*, *T. camphoratus*, *Rhus ciliata* and 'shade' discriminated between the presence and absence of eland. *A. tortilis* contributed negatively towards the discriminant function.

The function discriminating between the presence and absence of eland in winter was

$-0{,}54V1 + 0{,}23V2 + 0{,}67V3 + 0{,}33V4 + 0{,}5V5 + 0{,}27V6$ where

$V1$ = presence of *A. tortilis*
$V2$ = presence of *A. erioloba*
$V3$ = presence of *T. camphoratus*
$V4$ = presence of 'palatable evergreens'
$V5$ = presence of *R. ciliata*
$V6$ = SI for proximity of shade (from Figure 2)

The critical value which differentiated between the presence and absence of eland was 0,435.

The distribution of 'present' and 'absent' scores on the discriminant functions are shown by means of notched 'box-and-whisker' plots (Tukey 1977) in Figures 3 and 4. The central horizonal line represents the median while the notches coincide with the 95% confidence intervals of the median. Central vertical lines show the range of values.

When validated against independent data obtained from route B, the discriminant functions classified between 57,3 and 65,9% of the independent samples correctly (Table 1). If the functions had classified the data at random, a classification success of 50% would have been expected.

The lower 95% confidence limit of the percentage of correctly classified data was greater than 50% in the case of the function discriminating between the presence and absence of eland in summer. For the function for eland in winter, 50% fell below the 95% confidence interval but above the 90% confidence interval (Table 1).

Discussion

It was assumed that the plant species mostly associated with the animals also represented their preferred food items. This assumption was corroborated for kudu, giraffe and steenbok by Du Toit (1988). Some plant species had similar habitat requirements, however, and were therefore associated with each other. It was therefore possible that a plant which seemed to be preferred was phytosociologically associated with a species which was actually selected. This pitfall was avoided to an extent by considering the correlation coefficients of the variables.

Comparable results were obtained for the second order (landscapes) and third order (10 m radius patches) habitats preferred by eland in summer. *A. erioloba* and *T. camphoratus* were identified as important habitat components at both orders. The avoidance of *Z. mucronata* was also indicated by both analyses. Grass could not be identified as an important habitat component for eland's second order habitat

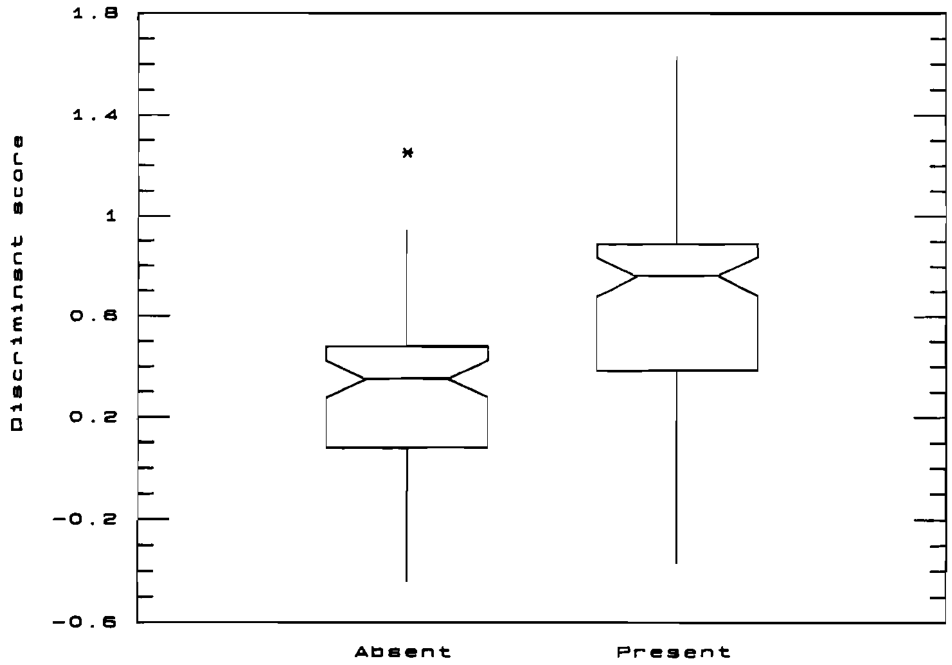

Figure 3 Notched box-and-whisker plot depicting the distribution of 'present' and 'absent' scores on the discriminant function for eland in winter. Central horizontal lines represent medians and notches indicating 95% confidence intervals of the median. Central upper and lower vertical lines represent limits of the range above the interquartile values.

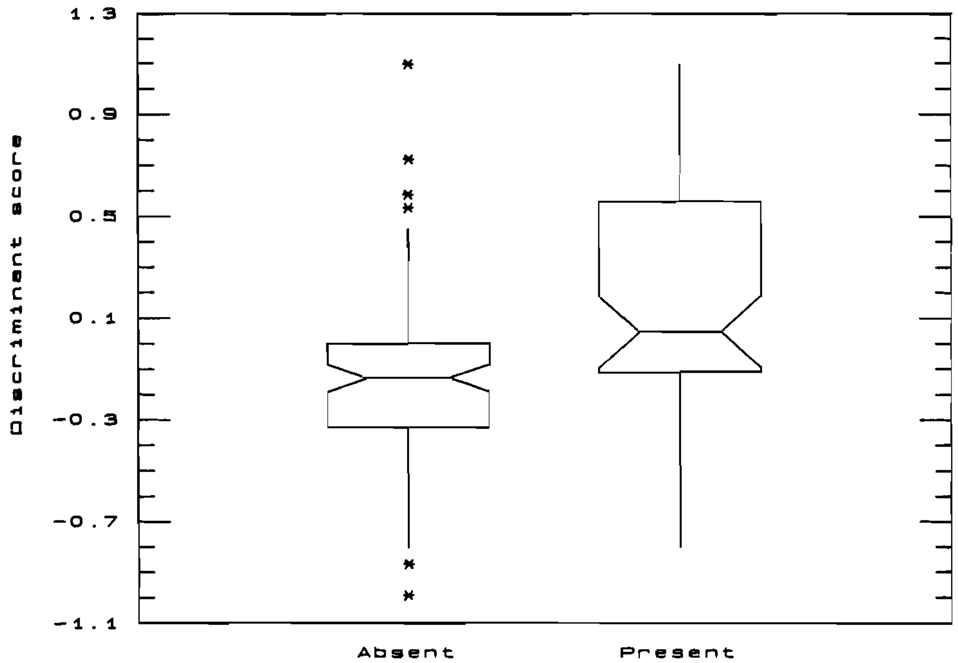

Figure 4 Notched box-and-whisker plot showing the distribution of 'present' and 'absent' scores on the discriminant function for eland in summer.

Table 1 Validation of the discriminant functions by independent data

Season		Correctly classified	Wrongly classified	% Success	95% Confidence limits
Summer	Present (n = 41)	27	14	65,9	
	Absent (n = 67)	40	27	59,7	
	Combined (n = 108)			62,0	9,6
Winter	Present (n = 75)	43	32		
	Absent**	**	**		
	Combined (n = 75)			57,3	11,9

** Not tested.

selection but was indicated as a third order habitat element by discriminant function analysis. At the landscape scale, grass was 'masked' by the dominant woody vegetation.

The second and third order habitat preferences of eland in winter were not comparable. In this instance, a habitat component which was shown to be avoided by eland at the patch scale (*A. tortilis*), appeared to be preferred at the landscape scale. In winter the 'masking' effect of the coarse-scaled landscapes was more pronounced than in summer.

The discriminant functions showed that in summer eland preferred patches where *A. erioloba*, *A. karroo*, *T. camphoratus*, 'palatable evergreens' and good grass cover were present. They avoided patches where *Z. mucronata* and *A. mellifera* occurred, as shown by the large negative contributions of those species to the discriminant function. In winter, eland preferred areas where *A. erioloba*, *T. camphoratus*, 'palatable evergreens' and *Rhus ciliata* were found and where shade was nearby. They avoided patches where *A. tortilis* was present. Eland did not seem to prefer any cover or shelter in summer, since the coefficients for proximity of shade and crown : gap ratio were small (below 0,05). In winter, eland preferred areas which were in close proximity to shade or shelter.

Eland vary their diet according to the availability and protein content of grass or browse. Hofmann & Stewart (1972) classified eland as 'mixed feeders preferring browse'. The high discriminant function coefficient for grass cover in summer was in accordance with studies elsewhere, where large proportions of the wet season diet of eland consisted of grass (Nge'the & Box 1976; Kelso 1987; Buys 1987). Buys (1987) and Kelso (1987) recorded *T. camphoratus* as one of eland's favourite food plants.

A striking feature of both discriminant functions is the large negative contribution of species with hooked thorns (*Z. mucronata*, *A. mellifera* and *A. tortilis*). The null hypothesis that eland were present in equal proportions in patches where hook-thorned species were present compared to patches where these species were absent was tested by a 2×2 table. The hypothesis was rejected ($p << 0{,}001$). The avoidance by eland of species with hooked thorns has two possible explanations. First, the thorns could have deterred eland from feeding on the above-mentioned species. Second, thorny plants generally occur on high nutrient soils (Owen-Smith & Cooper 1987). Such soils are heavily utilized by grazers which denude them of grass cover, rendering the habitat unsuitable for eland.

The validation of the discriminant functions by independent data might appear to be a waste of data, since such data could have been better used to generate more reliable statistics. Like many other multivariate techniques, one of the disadvantages of DFA is that it is 'forced to' generate statistical relations between variables, whether such biological relations exist or not. The resulting function therefore almost always classifies more than 50% of the dependent data correctly (Prof. W. Zucchini, Dept. of Mathematical Statistics, University of Cape Town, Rondebosch, South Africa, pers. comm.). Rextad, Miller, Flather, Anderson, Hupp & Anderson (1988) analysed a data set consisting of functionally unrelated variables by DFA. The analysis produced seemingly significant results and suggested strong relations between variables. They concluded that statistical and biological significance were not necessarily related. The risk of committing type I errors in multivariate statistics is therefore high. It was thus necessary to validate the biological significance of the discriminant functions developed in this study. One of the ways to achieve this was to evaluate the ability of the functions to classify data which were not used for the derivation of the functions.

The techniques of data collection could have influenced the performance of the functions. It was, for example, possible that eland could have left dung or tracks in a plot without actually feeding there. In such instance the plot would have been falsely assigned a 'present' rating and a misclassification would have been recorded if the presence of eland was predicted there. On the other hand, lack of sign need not necessarily have meant that the animals were absent, but merely that they were not present at the time of the survey. Many of the misclassified samples in Table 1 could have resulted from such errors.

The next step should be to compare the functions to the food preferences of eland in Orange River Broken Veld. The models should also be exercised and adapted for other vegetation types and bioclimatic regions.

Conclusions

The discriminant functions developed in this study could differentiate between the seasonal presence and absence of eland in the study area. The variables of importance to the habitat selection of eland could be identified and plausible biological explanations could be found for the results. The ability of the functions to classify independent data better than would be expected of randomly developed functions was fair but not excellent. The validation of the functions did, however, indicate that biological significance could be attached to the results.

The discriminant functions can be used for the assessment of habitat suitability for eland in the Orange River Broken Veld. Further research is, however, needed towards the refinement of the functions to enable their application over a wider geographical range.

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