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Links between terrain characteristics and forage patterns of elephants (*Loxodonta africana*) in northern Botswana

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ABSTRACT. Spatial vegetation utilization of elephants was investigated within mixed woodland savanna along the Chobe River in northern Botswana in the dry season of 1998. Using multiple linear regression, accumulated stem breakage by elephants was predicted by a terrain index, distance to water, stand density, number of trees > 4 m tall, tree height, density of *Combretum apiculatum*, *C. elaeagnoides*, *C. mossambicense* and the density of other (accumulated) tree species. Within mixed woodland at 2–7 km distance from the river fine-grained terrain ruggedness was the most important factor contributing to 55% of observed differences in use by elephants, while distance to water and the density of *C. apiculatum* contributed an additional 20% and 4%, respectively to the multiple linear regression model. Stem breakage was, on average, almost twice as high in rugged terrain compared with flat terrain at similar distance to water within the same vegetation type. Rugged terrain had 2–3-fold higher proportion of plots with very high *Combretum* shrub densities. These results suggest that the terrain index may be useful in management, predicting the areas most sensitive to vegetation change in a woodland system with increasing elephant densities.

KEY WORDS: Botswana, browsing, *Combretum*, elephants, savanna, terrain use

INTRODUCTION

The high densities of African elephant (*Loxodonta africana* (Blumenbach)) seen in many conservation areas today are known to have profound effects on vegetation (Ben-Shahar 1993, van de Vijver *et al.* 1999) and on biodiversity in general (Cumming *et al.* 1997). The substantial impact results from the large daily food requirement of elephants, with an average elephant consuming (on

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a wet weight basis) around 100 kg, while adult bulls require 300 kg food daily (Laws 1970). Elephants are also known to utilize a wide range of species when available (Owen-Smith 1998), relying heavily on graminoids in the wet season and almost exclusively on woody browse during the dry season (Barnes 1982, Croze 1974, Field & Ross 1976, Wyk & Fairall 1969). While elephants invariably need large quantities of forage daily, most descriptions of elephant spatial foraging patterns have been limited to the substantial vegetation impacts observed in terms of broken trees within close vicinity to river fronts and other water sources during the dry season (Eltringham 1980, Field & Ross 1976, Jachmann & Croes 1991), or to assessments of the diversity in diet composition within and between seasons (Barnes 1982, Mueller-Dombois 1972, Wing & Buss 1970). Although elephants can move up to 100 km over the course of a few days (Thouless 1995, 1996), generally utilizing extensive areas of mixed woodland (Armbruster & Lande 1993, Lindeque & Lindeque 1991), very little is known about which factors, beyond availability of water, affect habitat use by elephants within these vegetation types at more regional scales (Ben-Shahar 1993, 1996). Several studies have, however, pointed to a considerable patchiness in use by elephants (Anderson & Walker 1974, Ben-Shahar 1993). Apart from the water aspect this spatial pattern of elephant damage has been difficult to explain (Anderson & Walker 1974), and elephant impact on the vegetation has been described as random (Ben-Shahar 1993).

Availability and production of forage may, within general vegetation types, vary with soil type, water and nutrient availability (Ben-Shahar 1996, Guy 1989, Lewis 1991). It is well known from African savannas that large herbivores move down the catena during the dry season because of the increased moisture retention in the depressions during dry periods (Bell 1971). Soil nutrients like Ca, Mg, Na, N and C have been shown to accumulate in the slopes of the catena (Ben-Shahar 1990). With water and nutrients accumulating in valley slopes and smaller depressions, undulating and relatively rugged terrain could potentially serve as nutrient hot spots attracting herbivores. Preference for relatively rugged terrain has indeed been shown for a number of temperate and arctic species (Bergerud & Page 1987, Nellemann 1997, Nellemann & Cameron 1996, 1998; Nellemann & Reynolds 1997). As used here, the term rugged does not necessarily imply very steep terrain. Rather it is an index of landscape undulations and could therefore be used also in very flat areas. In fact, the terrain ruggedness index (Nellemann & Fry 1995, Nellemann & Thomsen 1994) has been successfully used to explain animal distribution on an extremely flat arctic coastal plain (Nellemann & Cameron 1996). The goal of this study was to test the prediction that terrain ruggedness may explain part of the spatial patterns seen in elephant vegetation utilization outside of riparian areas.

STUDY AREA

The study was conducted within the Chobe National Park in northern Botswana (approx. 17°80′S 25°00′E). The study area included a 50-km-wide and

10-km-long section along the Chobe River. The terrain varies from relatively flat in the central parts of the study area to generally more rugged conditions in the east and west. Elevations range between 930 and 1040 m asl. An annual average rainfall of about 600 mm occurs during the summer between October and March. Mean monthly temperatures range from a maximum of 34 °C in October to a minimum of 6 °C in June (Bhalotra 1987). The vegetation graduates from a riparian forest along the Chobe River into shrubland in the adjacent uplands (Mosugelo *et al.* 2001). Further inland woodland vegetation is more common with the main species *Baikiaea plurijuga* Harms gradually becoming more dominant with distance from the river. Other common species in the woodlands are *Combretum elaeagnoides* Klotzsch, *C. apiculatum* Sonder, *C. mossambicense* (Klotzsch) Engl. and *Baphia massaiensis* Taub. More-or-less pure patches of *Combretum* shrubland are found within the woodlands. Common large herbivores in the area are elephant, buffalo (*Syncerus caffer* (Sparrman)), greater kudu (*Tragelaphus strepsiceros* (Pallas)) and impala (*Aepyceros melampus* (Lichtenstein)). Elephants, with their large body size and high population density, averaging 7.6 animals km^{-2} in Chobe National Park (Gibson *et al.* 1998), are by far the most important browsers in this system. The elephant population in northern Botswana has been increasing at an annual rate of about 6% since the early 1980s (Gibson *et al.* 1998).

METHODS

Within mixed woodland, we randomly selected 30 sites, each 20 m × 50 m (Nellemann 1997). Randomization was performed using a randomization table on a 1-km^{-2} grid system divided into 100 × 100 cells. Elephant browsing in the area has been shown to be dependent on distance to the Chobe River. Mosugelo *et al.* (2001) found that elephant impact was high (80–100%) within 2 km from the river while at distances greater than 7 km it rapidly declined below 10%. Thus only sites within the 2–7 km section from the river were selected, avoiding the most extreme values. Additionally, no sites closer than 50 m to roads and firebreaks were used to avoid potential confounding effects of these trails on vegetation composition. Within each site, three plots, each 5 × 5 m were randomly selected; again using a randomization table starting from the south-western corner of the site.

Within each plot, both broken and intact stems of *Combretum apiculatum*, *C. elaeagnoides*, *C. mossambicense*, and other woody species (combined) were counted, and the percentage of broken stems was recorded to estimate elephant browsing. Elephant browsing can be separated from that of other ungulates by the large break diameter and by remaining twigs with a shredded appearance (Dierenfeld *et al.* 1995). We focused on *Combretum apiculatum* and *Combretum elaeagnoides* as indicators of elephant impact because these species are common throughout the study area and they are both utilized by elephants in proportion to availability (Stokke 1999). Twigs browsed by elephants after the last rainy season are characteristically yellow in appearance while older breakage is greyish (Ben-Shahar 1993). We included both new (yellow appearance) and old (grey appearance) elephant damage in our estimates.

Number of trees > 4 m tall was counted to evaluate if relatively mature trees dominated the site. The density of stands or basal area (m^2 ha^{-1}) was measured using a relascope (Staaland *et al.* 1998). The height of the tallest tree on the site was measured using a Suunto tree height meter (Staaland *et al.* 1998). All trees < 4 m were also counted within each plot. Position of each site was determined using a NAV 6000 GPS. Distance to river was measured from 1:50 000 topographic maps, with contour intervals of 10 m.

Indices of terrain ruggedness were derived from topographic maps (Nellemann & Fry 1995, Nellemann & Thomsen 1994). In brief, four transects, each 1 km long, were centred across each site in N–S, E–W, NW–SE and NE–SW direction. On each transect, the number of fluctuations in the terrain (TNF) (ups and downs) and total number of contours traversed (TNC) were recorded. The transect with the highest index-value according to the following index of terrain ruggedness (TRI) was used:

$$\mathrm{TRI} = ((\mathrm{TNF})(\mathrm{TNC}))\ (\mathrm{TNF} + \mathrm{TNC})^{-1}$$

Differences in stand characteristics between flat (TRI < 1.0) and rugged (TRI > 1.0) terrain were assessed statistically using Mann–Whitney tests. TRI values vary within the study area in the range of 0.0 to 3.0, with 0 as being completely flat and 3.0 the most rugged. Rugged terrain in the study area is characterized by small gently undulating valleys with few minor steep bluffs.

We used stepwise multiple linear regression with TRI, distance to water, stand density, number of trees > 4 m, tree height, the density of *Combretum apiculatum*, *C. elaeagnoides*, *C. mossambicense* and the density of other (accumulated) tree species as predictors of elephant browsing impact (% broken stems of *C. apiculatum* and *C. elaeagnoides*). Forward selection was used, accepting additional variables in the model if the associated P-value was below 5% (Weisberg 1985). Statistical analysis was performed in Sigmastat (Kuo *et al.* 1992).

RESULTS

In the zone 2–7 km from the Chobe River only terrain ruggedness, distance to water and the density of *Combretum apiculatum* contributed significantly to explain the spatial variation of elephant browsing (Figure 1). The terrain ruggedness index explained 55% of the variation in elephant browsing impact ($R^2 = 0.55$, $P < 0.0001$), while distance to Chobe River explained an additional 20% to the model ($R^2 = 0.20$, $P < 0.0001$). Also, the density of *Combretum apiculatum* contributed significantly to the model ($R^2 = 0.04$, $P = 0.04$), although this variable only added 4%. Stand density, no. of trees > 4 m, tree height, the

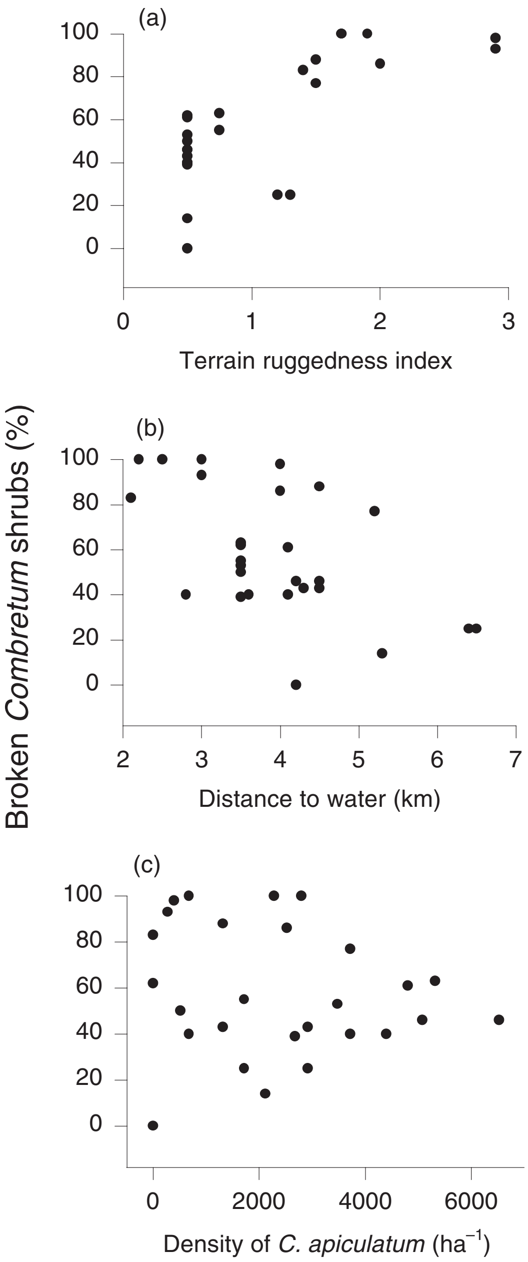

Figure 1. (a) The relationship between terrain ruggedness index (TRI) and percentage *Combretum apiculatum* and *C. elaeagnoides* stems broken by elephants (EBI). (b) The relationship between distance to water (DW) and EBI. (c) The relationship between *C. apiculatum* density (CAD) and EBI. All data were collected in mixed woodland savanna at 2–7 km distance from water in Chobe National Park, Botswana. In a multiple linear regression model were TRI, distance to water, stand density, no. of trees > 4 m, tree height, density of *Combretum apiculatum*, *C. elaeagnoides*, *C. mossambicense* and the density of other (cumulated) tree species were used as predictors of elephant browsing impact, only the three predictors shown above contributed significantly ($P < 0.05$). Regression model: EBI = 70.5 + 28.2TRI −12.9DW + 1.4 CAD ($F = 29.1$; df = 3, 23; $P < 0.0001$; $R^2 = 0.79$. Delta $R^2 = 0.55$, 0.20 and 0.04 for TRI, DW and CAD, respectively).

density of *C. elaeagnoides* and *C. mossambicense* and the density of other species did not significantly contribute to the model (P > 0.05).

There were no significant differences in basal area, no. of trees > 4 m, broken trees and tree height or distance to river between rugged (TRI ≥ 1.0) and flatter (TRI < 1.0) terrain (Table 1). Both *C. apiculatum* and *C. elaeagnoides* were more intensively browsed in rugged terrain than in flat terrain, while the browsing pressure on *C. mossambicense* did not differ between flat and rugged terrain (Table 1). No significant differences in densities of *C. apiculatum* and *C. mossambicense* were found between rugged and flat terrain (P > 0.05, Table 1). The density of *C. elaeagnoides* was higher on rugged compared with flat terrain (P = 0.03, Table 1). A frequency diagram combining *C. apiculatum* and *C. elaeagnoides* showed that the occurrence of plots with high density of these species were generally higher on rugged compared with flat terrain (Figure 2).

DISCUSSION

Beyond 2 km from the river front, terrain ruggedness was clearly the most significant factor affecting degree of use by the elephants. Elephant browsing on *C. apiculatum* and *C. elaeagnoides* was on average nearly 2-fold higher in rugged terrain compared with flat areas, at similar distance to water. Similar preferences for undulating and relatively rugged terrain in an otherwise flat landscape, have been recorded for both intermediate browsers and bulkfeeders in the Arctic (Bergerud & Page 1987, Nellemann 1997, 1998; Nellemann & Cameron 1996, 1998; Nellemann & Reynolds 1997). The high patchiness in elephant browsing within the Chobe mixed-woodland corresponds with other studies on elephant browsing in African woodlands (Anderson & Walker 1974, Ben-Shahar 1993).

Ben-Shahar (1990) has shown that in a South African woodland savanna, soil

Table 1. Stand characteristics and degree of browsing by African elephants (*Loxodonta africana*) on relatively flat terrain (TRI mean ± SD: 0.5 ± 0.1, n = 16) and on more rugged terrain (TRI mean ± SD: 1.8 ± 0.6, n = 11) in the zone 2–7 km from available water in Chobe River, Botswana, 1998.

Stand characteristics (mean ± SD)	Flat terrain (TRI < 1.0)	Rugged terrain (TRI ≥ 1.0)	t-test (P)
Basal area (m^2 ha^{-1})	5.4 ± 2.9	6.2 ± 3.2	0.46
No. of trees > 4 m (no. ha^{-1})	365 ± 448	244 ± 309	0.44
Broken trees (%)	9.9 ± 26	4.6 ± 15	0.55
Tree height	12.3 ± 2.4	12.3 ± 2.5	0.97
Distance to water (km)	3.9 ± 0.6	4.0 ± 1.6	0.93
Browsing			
Combretum apiculatum (no. ha^{-1})	2830 ± 2040	1695 ± 1247	0.11
Broken stems (%)	45 ± 12	82 ± 30	<0.001
Combretum elaeagnoides (no. ha^{-1})	608 ± 1317	3106 ± 4076	0.03
Broken stems (%)	45 ± 12	88 ± 10	<0.001
Combretum mossambicense (no. ha^{-1})	815 ± 1820	1753 ± 2028	0.22
Broken stems (%)	4.6 ± 10	24 ± 36	0.28
Other (no. ha^{-1})	2448 ± 2414	847 ± 1161	0.05
Broken stems (%)	30 ± 32	11 ± 17	0.08

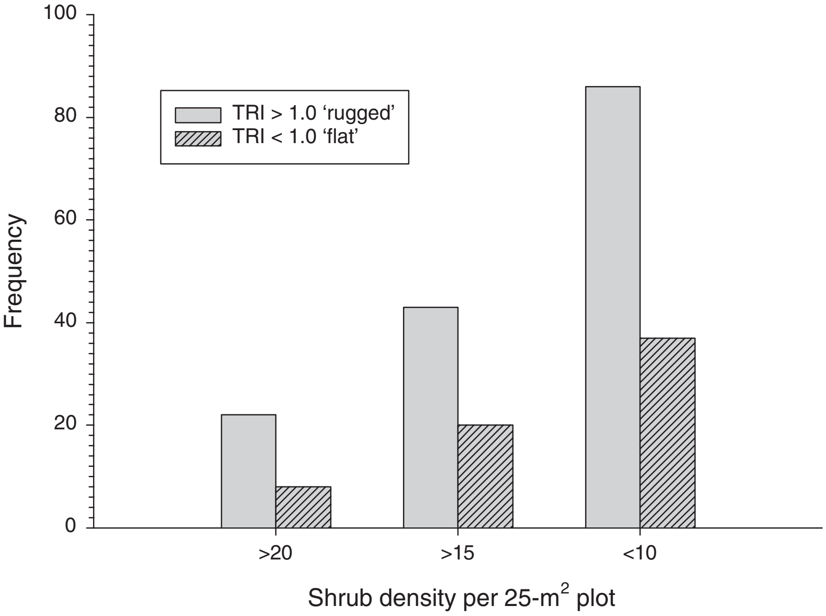

Figure 2. The occurrence (frequency) of plots with a high density of *Combretum apiculatum* and *C. elaeagnoides* shrubs in rugged (TRI > 1.0) and flatter terrain (TRI < 1.0) within the mixed woodland savanna vegetation type, Chobe, Botswana.

nutrients accumulate in the slopes of the catena while the crests are highly leached. The Kalahari sands in Chobe produce a dystrophic savanna landscape. Accumulation of nutrients in slopes may therefore serve as nutrient hot-spots for plants and for herbivores. Also, improved soil water availability to plants will further improve the quality of these browsing areas. Bell (1970, 1971) described how African mammals moved up and down the catena between wet and dry seasons. In northern Chobe where elephants congregate along the riverfront in the dry season one would, based on the catena effect, expect a heavier browsing pressure in the lower areas and valley bottoms. Our study showed that the TRI index is effective in predicting areas of high elephant browsing impact. The sensitivity of the TRI index also goes beyond high- and low-level elevations. In addition the TRI index accounts for the number of undulations within a given area (Nellemann & Fry 1995). Thus a relatively flat valley floor will have a low TRI index, while a slope containing many undulations will have a high TRI index and probably a higher density of nutrient hot-spots.

Rugged terrain generally contained a higher proportion of patches with high density of *Combretum* plants. Whereas some earlier studies have indicated that the *Combretum* species are preferred forage of elephants (Anderson & Walker 1974, Guy 1976, Ruggiero 1992), a recent study from Chobe has shown that *C. apiculatum* and *C. elaeagnoides* are selected in proportion to availability in this area, while *C. mossambicense* is utilized less than expected (Stokke 1999). A study of the vegetation change over the last 36 y in Chobe indicates that the increase in *Combretum* shrubs in this area is primarily a result of elephant utilization (Mosugelo *et al.* 2001). In 1962, the area within 2–7 km was entirely dominated ($> 70\%$) by *Baikiaea* woodland, while today the area has changed into mixed woodland and shrubland (Mosugelo *et al.* 2001). The fact that the densities of shrubs are particularly high in the more rugged terrain, and that these changes probably have been triggered by intensive elephant browsing, suggest that the TRI index may be used by managers to predict areas susceptible to vegetation change when elephant populations are increasing.

Possibly plant production is higher in rugged terrain as a function of higher nutrient and water availability in lower slopes, pans and other low-lying terrain, crucial factors affecting the natural patchiness of vegetation (Guy 1989, Lewis 1991). Rugged terrain also offers a greater diversity of potential forage species and vegetation types within short horizontal distances, which, in turn, may be important for a balanced nutrient intake of larger mammals (Nellemann 1997).

Summarizing, we hypothesize that relatively rugged or undulating terrain within a dystrophic woodland savanna offers superior foraging conditions through the establishment of nutrient hot-spots leading to greater patchiness and diversity in forage. We have shown that the TRI index may be useful in predicting areas of high elephant use and therefore of potential value to management. The analysis of terrain ruggedness using simple indices may add to a better understanding of habitat selection within a seemingly uniform landscape.

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