

SPATIAL DYNAMICS OF ELEPHANT IMPACTS ON TREES  
IN CHOBE NATIONAL PARK, BOTSWANA

By

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To my parents, who have encouraged my love of wildlife and enabled me to be where I am today, and to my Lord, who made all the animals I love

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Abstract of Thesis Presented to the Graduate School  
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SPATIAL DYNAMICS OF ELEPHANT IMPACTS ON TREES  
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By

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The African elephant (*Loxodonta africana*) regulates shifts between different savanna states, primarily through herbivory of woody vegetation. As a water-dependent herbivore, these impacts on trees are constrained by water availability, potentially leading to a gradient of degradation known as the piosphere effect. Transects evaluating vegetation status with increasing distance from the Chobe River were conducted in Chobe National Park, Botswana, to test whether predictions of the piosphere effect can be applied at multiple scales. Trends varied depending on the type of utilization, with debarking by elephants decreasing with distance from the Chobe River and branch herbivory showing a bimodal distribution. Results suggest that piosphere predictions may be applicable over greater distances, with important implications for monitoring species changes far from water points. Managers should consider this as they evaluate landscape stability and discuss provisioning of waterpoints in semi-arid habitats.



## CHAPTER 1 INTRODUCTION

Herbivory affects the structure and dynamics of African savannas (Skarpe, 1992; van Langevelde *et al.*, 2003). Understanding the impacts large mammals have on savannas is critical for management of these systems. The African elephant (*Loxodonta africana* (Blumenbach)) has long been seen as one of the principle drivers regulating shifts between different savanna states (Laws, 1970; Dublin, Sinclair, & McGlade, 1990; Augustine & McNaughton, 2004). Often described as a keystone species and ecosystem engineer (Jones, Lawton, & Shachak, 1994), elephants can have a profound influence on woody vegetation, browsing trees and shrubs, and can impede woodland formation (Pellew, 1983; Holdo, 2007).

At larger spatial scales, herbivore distribution is determined primarily by abiotic factors, such as distance to water, with smaller-scale processes such as herbivory operating within this framework (Bailey *et al.*, 1996). Concentration of large herbivores near waterpoints may lead to development of a gradient of degradation that increases with proximity to water, termed the ‘piosphere’ (Lange, 1969). This phenomenon is well documented in Kruger National Park (Thrash *et al.*, 1991; Thrash, 1998; Brits, van Rooyen, & van Rooyen, 2002) and in other arid and semi-arid systems across Africa (e.g., Child, Parris, & Riché, 1971).

As a water-dependent species (Redfern *et al.*, 2003), elephant distribution is regulated by water availability (Chamaillé-Jammes, Valeix, & Fritz, 2007). This constraint, along with the tremendous impacts allowed by their body size, creates great potential for elephants to contribute to the piosphere effect. Indeed, increased utilization of vegetation around water sources by elephants has been seen in Etosha National Park, Namibia (de Beer *et al.*, 2006) and forest reserves in Tanzania (Afolayan, 1975). Increased understanding of the spatial heterogeneity of elephant impacts on vegetation is needed (Valeix *et al.*, 2007).

Chobe National Park (Chobe), Botswana provides an excellent case to test piosphere effect theory as it relates to elephants. Botswana is home to the largest known elephant population on the continent with over 150,000 individuals (Blanc *et al.*, 2007). Mosugelo *et al.* (2002) found wooded areas along the Chobe riverfront have decreased over time. Congruent with piosphere effect predictions, their study found decreasing elephant browsing with increasing distance from the river. Previous studies have been conducted within 10 km inland from the river (Mosugelo *et al.*, 2002; Nellemann, Moe, & Rutina, 2002), but did not evaluate the rest of the park, which extends over 50 km further to the south.

This study expands evaluation of spatial dynamics of elephant impacts on vegetation from the riverfront to the south-eastern border of the park. Vegetation transects evaluated tree utilization by elephants and fire at multiple scales to see whether a traditional piosphere effect is maintained or if elephant utilization of trees is bimodal as elephants drink and browse near the river and then walk inland to browse again. My results are discussed within the framework of elephant management and the influences browse patterns might have on the vegetation and wildlife of Chobe and other semi-arid protected areas.

## CHAPTER 2 MATERIAL AND METHODS

### Study Area

This study was conducted in Chobe National Park in the northeastern corner of Botswana from May to July 2008 (Figure 2-1). Rainfall averages 600-700 mm per year and occurs primarily between November and March (Child, 1968). Average temperatures range between 15.2°C - 30.2°C (Child, 1968). The Chobe River borders the northern part of the park, forming the boundary between Botswana and the Caprivi Strip in Namibia. Ephemeral pans across the park fill during the wet season and slowly disappear as the dry season progresses, providing additional water sources. Several artificial borehole waterpoints have also been established by the Botswana Department of Wildlife and National Parks near the south of the study area.

Vegetation along the riverfront is primarily scrub dominated by *Croton megalobotrys* (Müll.Arg.), *Capparis tomentosa* (Lam.), and *Combretum mossambicense* (Engl.; Herremans, 1995). About 1-2 km from the river the vegetation changes to a shrub-woodland mixture dominated by *Baikiaea plurijuga* (Harms) and including *Burkea africana* (Hook.), *Croton gratus* (Burch.), *Combretum elaeagnoides* (Klotzsch), *Baphia massaiensis* (Taub.), and *Terminalia sericea* (Burch ex DC.; Mosugelo *et al.*, 2002; for a more detailed description of vegetation see Simpson, 1975). Farther inland, the vegetation type changes to a mixed Kalahari savanna woodland with dominant species including *Colophospermum mopane* (J.Kirk ex Benth.), *Combretum apiculatum* (Sond.), *Burkea africana*, and *Combretum hereroense* (Schinz).

Child (1968) reported 38 mammal species jackal-sized or larger in Chobe including elephants, buffalo (*Syncerus caffer* (Sparrman)), giraffe (*Giraffa camelopardalis* (L.)), zebra (*Equus burchelli* (Gray)), warthog (*Phacochoerus aethiopicus* (Pallas)), hippopotamus (*Hippopotamus amphibious* (L.)), kudu (*Tragelaphus strepsiceros* (Pallas)), sable (*Hippotragus*

*niger* (Harris)), and impala (*Aepyceros melampus* (Lichtenstein)). Major carnivores include lion (*Panthera leo* (L.)), leopard (*Panthera pardus* (L.)), spotted hyena (*Crocuta crocuta* (Erleben)) and African wild dog (*Lycaon pictus* (Temminck)).

### **Elephant Impacts on Vegetation**

Thirty-four transects investigating vegetation status with increasing distance from the Chobe River were conducted in Chobe National Park. Transects were located running roughly south following a one-lane dirt track from the Chobe River to the southeastern border of the park (Figure 2-1). The initial transect location was randomly determined and subsequent transects were conducted systematically every 2.5 km. Distance between transects was determined using a GPS receiver (Garmin Rino 120, Garmin Ltd., Olathe, KS, USA). Two additional transects were conducted farther east along the riverfront to increase sample size within the thin riparian strip bordering the river. All transects were established at least 50 m from tracks to minimize any track-based effects on vegetation or browsing (Mosugelo *et al.*, 2002). A line 100 m long was marked off parallel to the track to define the start point. Heading away from the track, transects were continued until 50 trees were recorded or, in areas of very low tree density, a one hectare (10,000 m<sup>2</sup>) area was surveyed. Any plant greater than 3 m tall was classified as a tree (Walker, 1976). Each tree was identified to species level and spatially georeferenced using GPS. Characteristics including height, DBH (diameter at breast height), number of stems, and percent green vegetation in the crown were recorded, as well as whether the tree was alive or not and the presence of ground and aerial coppicing.

Elephant utilization of trees occurred in two primary forms, debarking and damage to branches/trunks. Ringbarking occurs when bark is completely removed from a strip spanning the tree's circumference and results in death as the tree can no longer transport sugars. Debarking herbivory was evaluated using six categories: 0 = no bark removal, 1 = 1-20% of circumference

debarked, 2 = 21-40% debarked, 3 = 41-60% debarked, 4 = 61-80% debarked, and 5 = 81-100% debarked. Branch herbivory was assessed using five categories: 0 = no utilization, 1 = minor utilization (a few minor branches broken), 2 = moderate utilization (many minor branches broken), 3 = high utilization (main branches broken), and 4 = main stem utilization (main meristem broken off). Fire damage was also evaluated using four categories: 0 = no damage, 1 = light damage, 2 = moderate damage, and 3 = heavy damage.

Distance of transects to water was determined using GIS software (ArcView 9.3, ESRI, Redlands, CA, USA). Water body locations for the Chobe region were obtained from the Botswana Department of Surveys and Mapping in Gaborone and verified against remotely sensed images.

### **Relative Dung Density**

A dung count was also conducted at each site beginning at the start point for the vegetation transect and extending 100 m perpendicular to the track. Mammalian dung within 5 m on either side of the line was enumerated (for animals that defecate many pellets, one cluster was counted as a single dropping). Dung was identified to species using a guidebook (Stuart & Stuart, 2000) and help from local guides. Dung counts were conducted to give an estimate of relative animal use of transect sites (Young, Palmer, & Gadd, 2005). While issues have been raised about the use of dung counts to measure mammal densities (e.g., Fuller, 1991), Barnes (2001) showed that they are as effective as other methods of estimation for elephants as well as for other vertebrate species.

### **Analysis**

Data were analyzed using SAS software (Version 9.2, SAS Institute Inc., Cary, NC, USA). Linear regression was performed upon utilization categories and potential predictor variables including distance from the Chobe River, distance from all water, tree height, tree density,

percent green vegetation in crown, and relative abundance of elephant and total dung. Stepwise multiple regression was used to select the best model for changes in utilization based on all potential predictors.

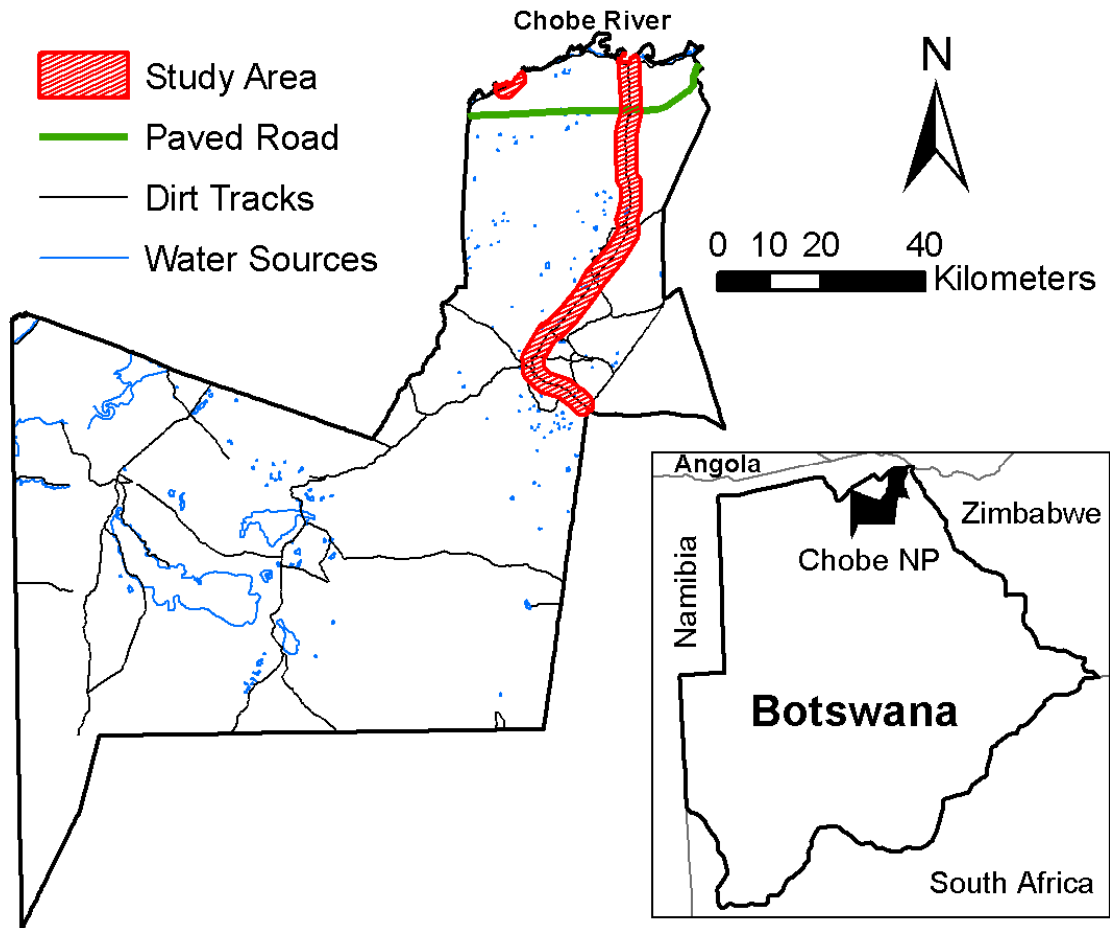


Figure 2-1. Map of Chobe National Park, Botswana including study area.

## CHAPTER 3 RESULTS

A total of 1600 trees were evaluated. Twenty-five species were identified. Ten species had more than 50 individuals recorded. *Combretum apiculatum* was the most prevalent ( $n = 437$ ), followed by *Baikiaea plurijuga* ( $n = 166$ ), *Terminalia sericea* ( $n = 153$ ), *Colophospermum mopane* ( $n = 148$ ), *Combretum elaeagnoides* ( $n = 130$ ), *Burkea africana* ( $n = 118$ ), *Combretum mossambicense* ( $n = 89$ ), *Croton megalobotrys* ( $n = 72$ ), *Combretum hereroense* ( $n = 61$ ), and *Terminalia brachystemma* (Welw. Ex Hiern,  $n = 53$ ; for descriptive statistics of these species see Table 3-1). Between 32 and 50 individual trees were sampled per transect and species density ranged from two to ten species per transect. Total utilization of trees by elephants was not correlated to distance from the Chobe River ( $p = 0.388$ ). Mean tree density increased linearly with distance from the Chobe River ( $R^2 = 0.2333$ ,  $p < 0.005$ ,  $n = 34$ , Figure 3-1A), but showed no relation to distance from water ( $p = 0.39$ , Figure 3-1B). Mean tree diameter at breast height (DBH) exhibited a cubic relationship with distance from the Chobe River ( $R^2 = 0.7878$ ,  $p < 0.0001$ ,  $n = 34$ , Figure 3-1B), and increased linearly with distance from all water ( $R^2 = 0.3821$ ,  $p < 0.0001$ ,  $n = 34$ , Figure 3-2B). For a summary of relationships between predictor variables and distance to the river and to all water, see Figure 3-1 and Figure 3-2, respectively.

Debarking by elephants decreased with distance from the Chobe River ( $R^2 = 0.6217$ ,  $p < 0.0001$ ,  $n = 34$ , Figure 3-3A). When considered in relation to all water, debarking patterns exhibited a quadratic distribution with peaks both near to and far from water ( $R^2 = 0.2986$ ,  $p < 0.01$ ,  $n = 34$ , Figure 3-4A). Debarking density was also positively related to mean tree DBH ( $R^2 = 0.2117$ ,  $p < 0.01$ ,  $n = 34$ ). Using stepwise multiple regression, distance to river provided the best predictor of debarking ( $R^2 = 0.6217$ ,  $p < 0.0001$ ,  $n = 34$ ), with a negative relationship.



The best predictors of debarking (in descending order) were distance to river, total dung density, and mean tree DBH ( $R^2 = 0.7203$ ,  $p < 0.0001$ ,  $n = 34$ ). Dung density and DBH were positively correlated with debarking while tree density was negatively correlated. A similar coefficient of determination is obtained by a model using just distance to river and total dung density ( $R^2 = 0.6838$ ,  $p < 0.0001$ ,  $n = 34$ ).

Branch herbivory peaked closest to the river and again at the farthest point from the river, best fitting a cubic regression ( $R^2 = 0.4923$ ,  $p = 0.0001$ ,  $n = 34$ , Figure 3-3B). When the heavily utilized riverfront areas were excluded from analysis, transects greater than 4 km from the river showed a linear increase in mean branch herbivory with increasing distance from the river ( $R^2 = 0.4919$ ,  $p < 0.0001$ ,  $n = 30$ , Figure 3-3C). Finer scale analyses considering all water found that branch herbivory decreased linearly with distance from water ( $R^2 = 0.1834$ ,  $p < 0.05$ ,  $n = 34$ , Figure 3-4B). Branch herbivory is also negatively related to tree height ( $R^2 = 0.2071$ ,  $p < 0.01$ ,  $n = 34$ ). Overall, branch utilization is best predicted by elephant dung density ( $R^2 = 0.3048$ ,  $p < 0.001$ ,  $n = 34$ ), exhibiting a positive relationship. The best model is predicted by elephant dung density, mean tree height, and distance from river, in descending order ( $R^2 = 0.5622$ ,  $p < 0.0001$ ,  $n = 34$ ). Tree height exhibited a negative relationship with branch herbivory and the other predictors a positive relationship. For the reduced sample of transects greater than 4 km from the river, branch utilization is best predicted by distance from the river ( $R^2 = 0.4919$ ,  $p < 0.0001$ ,  $n = 34$ ) and the overall best model contained distance from the river and total dung density ( $R^2 = 0.6127$ ,  $p < 0.0001$ ,  $n = 30$ ).

Fire damage residual diagnostics showed deviation from normality assumptions. A square-root transformation was used to correct this for analysis. Fire damage exhibited a quadratic distribution, lowest near the river and southern border of the park, and highest about 40 km from

the river ( $R^2 = 0.3438$ ,  $p < 0.01$ ,  $n = 34$ , Figure 3-3D). In general, fire damage increased with distance from water ( $R^2 = 0.1453$ ,  $p < 0.05$ ,  $n = 34$ , Figure 3-4C). Fire damage was best predicted by elephant dung density, exhibiting a negative relationship ( $R^2 = 0.1949$ ,  $p < 0.01$ ,  $n = 34$ ). The best model contained, in descending order, elephant dung density, mean percent green vegetation in crown, tree density, and distance to water ( $R^2 = 0.5205$ ,  $p < 0.001$ ,  $n = 34$ ). There was a positive relationship to distance from water and a negative relationship with the other three predictor variables.

Table 3-1. Descriptive statistics for the most common tree species (n ≥ 50)

Species	n	Mean DBH (cm)	Mean height (m)	Mean percent green vegetation in canopy	Mean debarking	Mean branch herbivory	Mean fire damage	Mean distance from river (km)	Mean distance from all water (km)
<i>Burkea africana</i>	118	23.43	7.19	57.92	1.09	1.99	1.55	19.87	2.81
<i>Colophospermum mopane</i>	148	13.79	4.00	69.83	0.54	3.80	0.41	49.61	1.57
<i>Combretum mossambicense</i>	89	8.89	3.98	11.73	0.84	3.42	0.17	22.76	0.48
<i>Combretum apiculatum</i>	437	11.79	4.63	43.12	0.35	2.90	0.57	37.62	1.87
<i>Combretum elaeagnoides</i>	130	9.18	3.99	47.62	0.20	3.38	0.40	46.26	1.82
<i>Combretum hereroense</i>	61	22.11	5.50	65.80	0.36	2.31	0.56	38.53	2.02
<i>Croton megalobotrys</i>	72	14.69	4.86	49.88	1.32	3.15	0.11	0.44	0.28
<i>Terminalia brachystemma</i>	53	12.99	4.05	61.32	0.57	3.23	1.09	33.59	1.95
<i>Baikiaea plurijuga</i>	166	29.13	7.55	82.52	0.58	1.65	0.84	15.04	3.33
<i>Terminalia sericea</i>	153	9.94	3.97	26.75	0.28	3.05	1.82	39.19	2.02

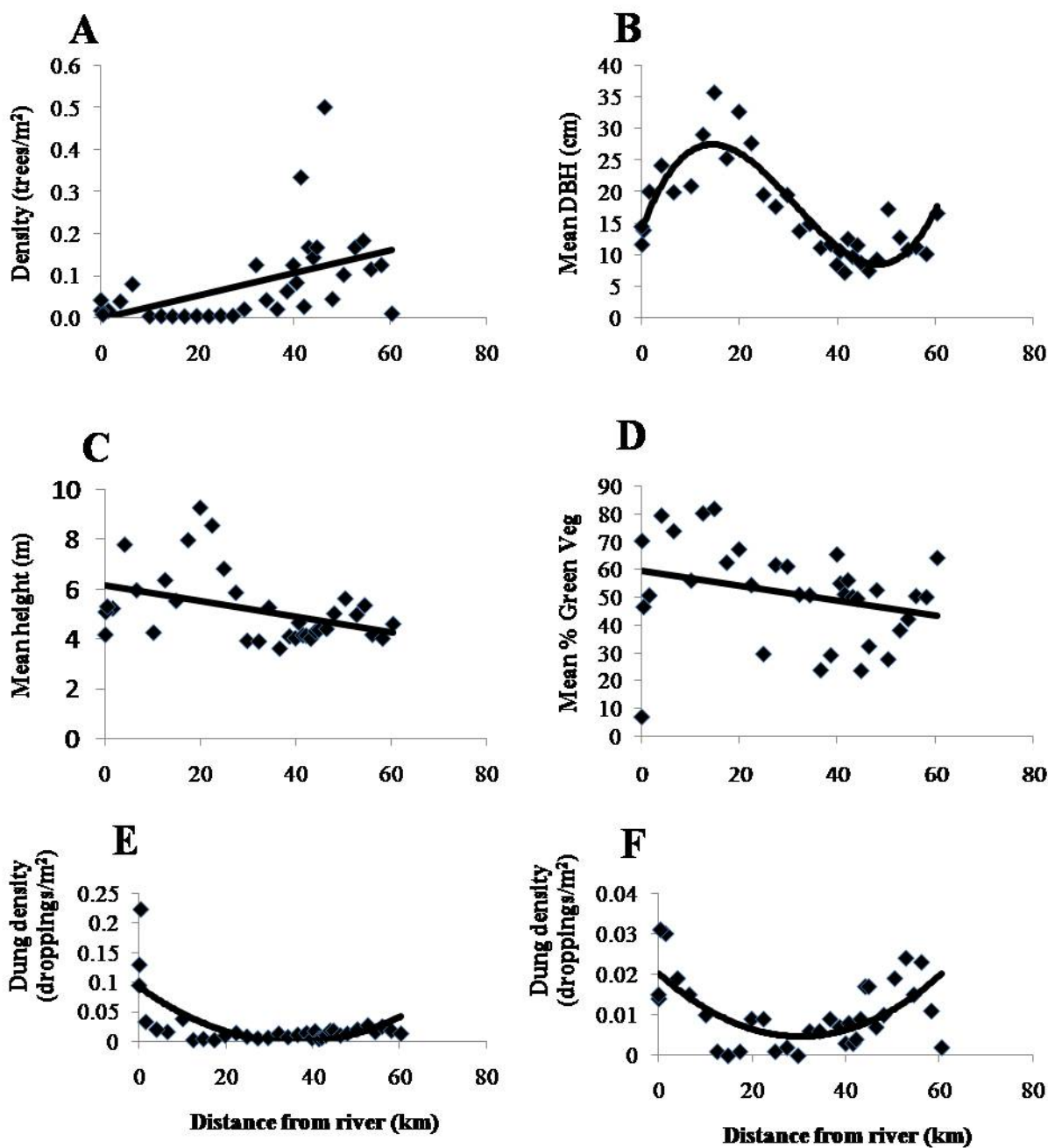


Figure 3-1. Predictor variables by distance from the Chobe River. A) tree density ( $R^2 = 0.2333$ ,  $p < 0.005$ ,  $n = 34$ ), B) mean diameter at breast height (DBH;  $R^2 = 0.7878$ ,  $p < 0.0001$ ,  $n = 34$ ), C) mean tree height ( $R^2 = 0.1704$ ,  $p < 0.05$ ,  $n = 34$ ), D) mean percent green vegetation in crown of tree ( $R^2 = 0.0863$ ,  $p = 0.09$ ,  $n = 34$ ), E) total dung density ( $R^2 = 0.4792$ ,  $p < 0.0001$ ,  $n = 34$ ), and F) elephant dung density ( $R^2 = 0.3918$ ,  $p < 0.0005$ ,  $n = 34$ ).

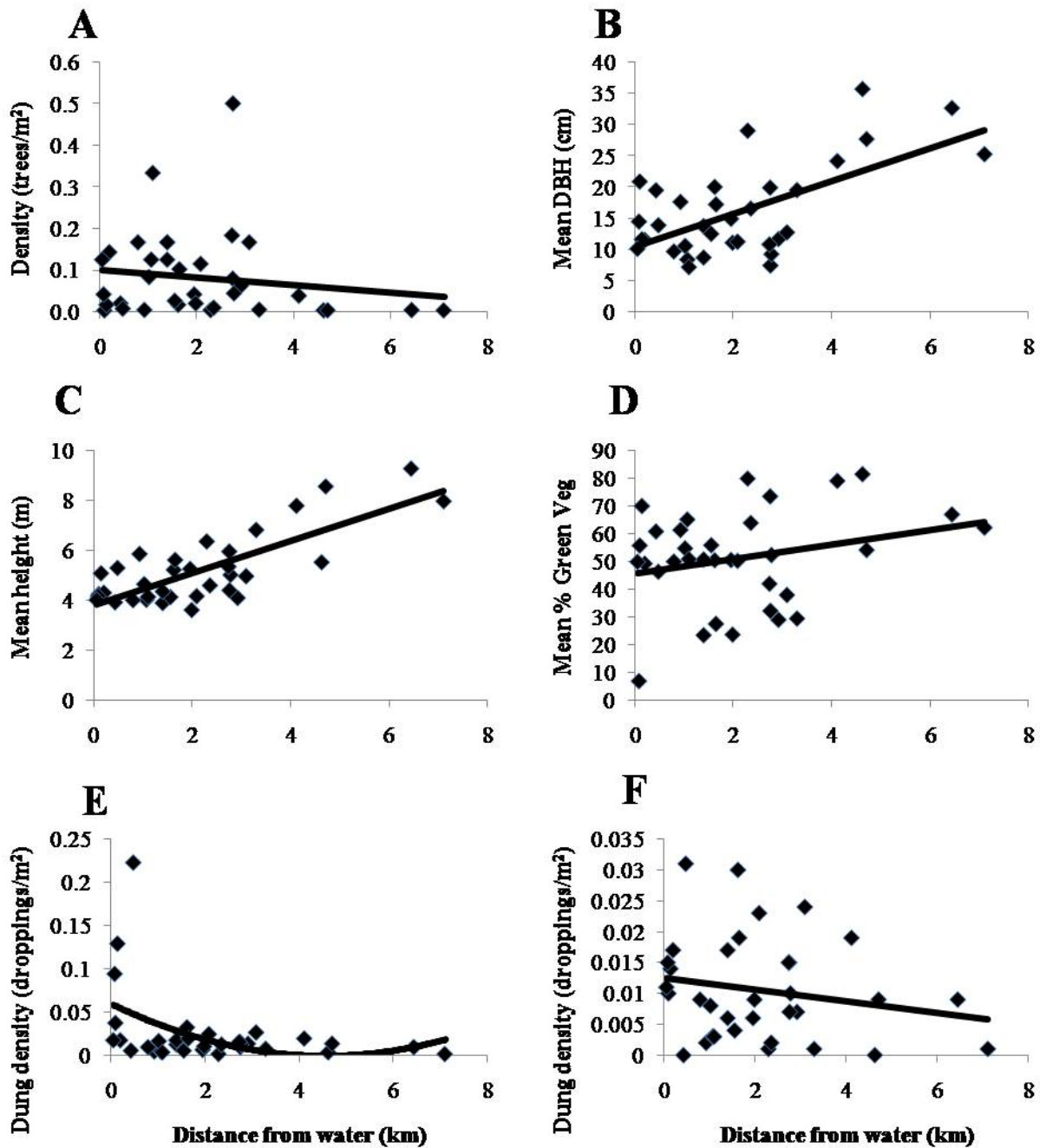


Figure 3-2. Predictor variables by distance from all water. A) tree density ( $R^2 = 0.0235$ ,  $p = 0.39$ ,  $n = 34$ ), B) mean diameter at breast height (DBH;  $R^2 = 0.3821$ ,  $p < 0.0001$ ,  $n = 34$ ), C) mean tree height ( $R^2 = 0.6009$ ,  $p < .0001$ ,  $n = 34$ ), D) mean percent green vegetation in crown of tree ( $R^2 = 0.06$ ,  $p = 0.14$ ,  $n = 34$ ), E) total dung density ( $R^2 = 0.1904$ ,  $p < 0.05$ ,  $n = 34$ ), and F) elephant dung density ( $R^2 = 0.0382$ ,  $p = 0.27$ ,  $n = 34$ ).

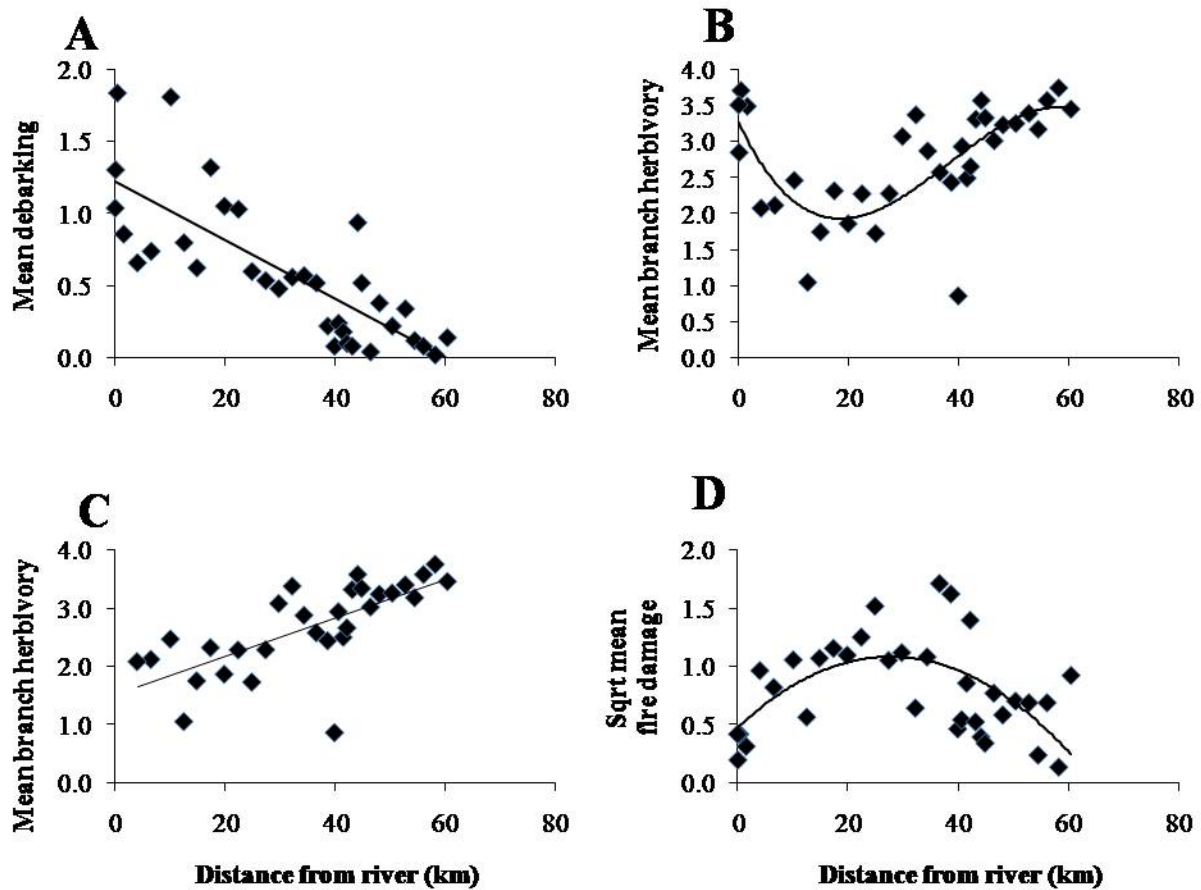


Figure 3-3. Mean utilization at different distances from the Chobe River. A) debarking ( $R^2 = 0.6217$ ,  $p < 0.0001$ ,  $n = 34$ ), B) branch herbivory ( $R^2 = 0.4923$ ,  $p = 0.0001$ ,  $n = 34$ ), C) reduced branch herbivory, greater than 4 km from river ( $R^2 = 0.4919$ ,  $p < 0.0001$ ,  $n = 30$ ), and D) fire damage ( $R^2 = 0.3438$ ,  $p = 0.0015$ ,  $n = 34$ ).

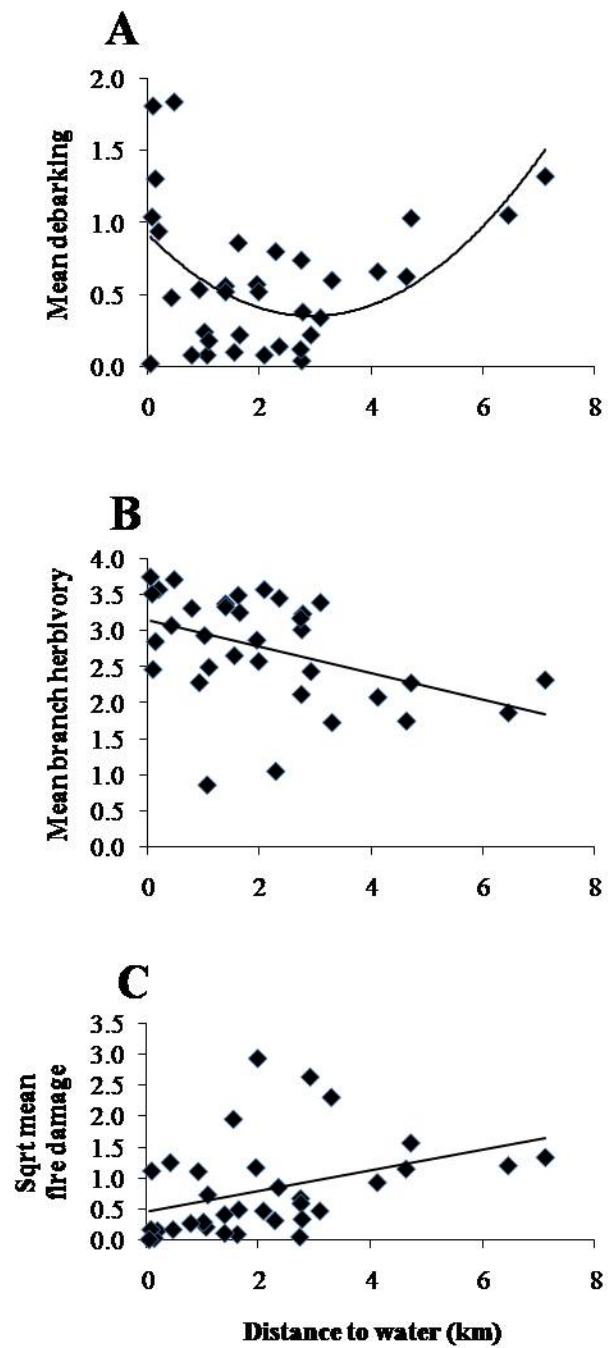


Figure 3-4. Mean utilization at distances from all water in Chobe National Park, Botswana. A) debarking ( $R^2 = 0.2986$ ,  $p = 0.0041$ ,  $n = 34$ ), B) branch herbivory ( $R^2 = 0.1834$ ,  $p = 0.0115$ ,  $n = 34$ ), and C) fire damage ( $R^2 = 0.1453$ ,  $p = 0.0261$ ,  $n = 34$ ).

## CHAPTER 4 DISCUSSION

Patterns of herbivory have important ramifications for overall landscape stability and resilience, especially for keystone species such as elephants. Effective management plans rely on an understanding of the major ecological processes that create these patterns. In this study, I consider the effects of water on tree utilization in Chobe National Park, Botswana to test whether predictions of the piosphere effect can be applied on a larger scale.

### **Large-Scale Trends**

Distribution of elephant impact varied depending on the type of utilization and on the scale considered. At a broad scale, debarking decreased with distance from the Chobe River (Figure 3-3A), aligning with piosphere predictions. Branch herbivory also initially decreased with distance, confirming findings from previous studies (e.g., Mosugelo *et al.*, 2002), as well as piosphere effect predictions (Figure 3-3B). It is interesting to note, however, that after this initial decrease, mean branch utilization increased again. In fact, if the highly utilized sections around the riverfront are removed from analysis, branch herbivory beyond about 4 km correlates strongly to a linear increase with distance from the river (Figure 3-3C). This is in contrast with the piosphere effect, though a recent study in Kruger National Park found a similar pattern of increasing tree utilization by elephants with distance from water (Shannon *et al.*, 2008), albeit at smaller spatial scales (up to 4 km from water). They suggested these trends might be explained by tree density, terrain ruggedness, or soil depth. Tree density in Chobe also increased linearly with distance from the Chobe River (Figure 3-1A), but was not correlated with branch herbivory suggesting some other factor is responsible for the apparent deviation from piosphere predictions.



These large-scale trends in elephant utilization may be related to broader climatic conditions and seasonality, rather than variation in tree characteristics. During the wet season, temporary water pans across the park fill and animals disperse away from the river (see Skarpe *et al.*, 2004 for an example of this in buffalo). During this time, there is an abundance of vegetation on trees leading elephants that have moved farther away from the river while dispersing to browse mostly on branches, leading to the increasing pattern of branch herbivory with distance from the Chobe River that was observed. In the dry season, animals move back to the permanent water of the Chobe River. The reduction in available forage at this time of year pushes a shift towards increased debarking to provide water and sugars, leading to increased debarking with proximity to the river. There is also browsing on what vegetation is available near the river, causing the elevated branch herbivory levels within four kilometers of the riverfront. Unfortunately, this hypothesis cannot be tested with the current dataset as data were recorded at only a single time period, necessitating further study on this issue.

Fire damage exhibits trends opposite those seen by elephant herbivory, with low fire damage at either end of the distance spectrum (Figure 3-3D). The negative relationship between fire damage and elephant dung density suggests that elephant impacts may reduce chances of fire. This result contrasts with studies that have found that elephant utilization of trees, particularly debarking, may increase tree susceptibility to fire (Beuchner & Dawkins, 1961; Holdo, 2007; Moncrieff, Kruger, & Midgley, 2008). Higher elephant impact, however, could also remove potential fuel load, reducing fire intensity in the event of a burn. Additionally, fire is actively suppressed in Chobe National Park and the patterns observed may simply reflect anthropogenic activity, and not be indicative of natural herbivore-fire interactions.

### Small-Scale Trends

At a smaller scale, debarking initially follows piosphere effect predictions, decreasing with distance from water up to about 3 km (Figure 3-4A). Beyond this, however, it increases again, contrasting with expected piosphere theory, but aligning with my proposed bimodal distribution. One explanation for this trend is the increase in mean diameter at breast height (DBH) of trees with distance from water. Debarking increased with DBH in Chobe, as has been seen in other areas (e.g., Afolayan, 1975). It is possible that around 3 km from water a threshold is reached where tree size is large enough that debarking is profitable for the elephants and so prevalence increases. More research is needed to elucidate these fine-scale trends.

Branch herbivory trends also differed across scales. Although large-scale branch utilization contrasts with piosphere predictions, small-scale patterns considering distance from all water fit well within a piosphere effect framework (Figure 3-4B). This trend seems further confirmed by patterns of tree size and distance from water. Both mean tree height and DBH increase with distance from water (Figure 3-2B,C). A study in semi-arid grazing lands in Australia found that distance to water did not influence plant characteristics (Foran *et al.*, 1982). That this was not found in my study site suggests elephants may be preferentially browsing species near water, creating a traditional piosphere effect. The reduction of elephant branch herbivory with increasing tree height, presumably because branches become less accessible on higher trees, may also contribute to the overall reduction in branch utilization with distance from water.

Fire damage increased with distance from water (Figure 3-4C). Areas farther from waterpoints tend to be drier and burn more than those close to water (Larsen, 1997; Wallenius *et al.*, 2004). In light of this, small-scale fire patterns are likely to be an effect of habitat characteristics rather than influence of megaherbivores.

## Management Implications

Previous studies have typically considered piosphere effects at distances of up to about 10 km from water (Child *et al.*, 1971; Thrash *et al.*, 1991; Thrash, 1998; Thrash & Derry, 1999; Brits *et al.*, 2002). My large-scale findings for both debarking and branch herbivory suggest that these utilization trends may continue far beyond that which has been previously suggested. This has important implications for the stability of landscapes in semi-arid systems. Instead of just influencing a “sacrifice area” and utilization zone several kilometers around a waterpoint (Brits *et al.*, 2002), elephants may be affecting trees across the landscape. This may result in unexpected shifts in land cover and species composition if these more distant areas are not monitored.

One trend observed during the course of this study suggests these shifts may already be happening. Chobe National Park was famous for its *Acacia* woodlands up until the 1960s (Child, 1968; Simpson, 1975; Skarpe *et al.*, 2004). In my study, however, only three individuals of a single species were recorded out of 1600 total trees. This phenomenon has been observed by other studies in the area as well (e.g., Lewin, 1986; Skarpe *et al.*, 2004; Wolf, 2008. Master’s Thesis University of Florida. Gainesville, Florida, USA.). It is generally accepted that elephants have played a role in this decline, perhaps in conjunction with other species, such as impala, which prevented woodland regeneration and growth of seedlings (Lewin, 1986; Rutina, 2004. Impalas in an elephant-impacted woodland: browser-driven dynamics of the Chobe riparian zone, northern Botswana. PhD Thesis Agricultural University of Norway. Ås, Norway.). Skarpe *et al.* (2004) suggest that in light of these influences, species such as *Acacia* may require local refuges to persist. The findings from my study indicate inland areas farther from the river may not provide these refuges and that further evaluation is needed to better understand the mechanisms behind species reductions and what steps could be taken to prevent future losses.

It is possible that the expanded piosphere effect seen in this study reflects the large size of the Chobe River and the influence it has on wildlife movements and dynamics. In places with smaller rivers or more abundant alternative water sources, different utilization patterns may occur. Further research should test whether an extended piosphere effect is seen for elephants in other semi-arid systems and whether this is applicable both to artificial waterpoints as well as large natural sources such as rivers.

Multiple regression models evaluating predictors of elephant utilization suggest more efficient strategies for monitoring through vegetation surveys. Researchers and managers must balance minimizing time and cost while maximizing information yield. All three types of tree utilization were predicted by dung density as well as distance to the river or water. While predictions could be improved by adding measurements of the trees themselves, dung counts may provide a quick and coarse method to estimate levels of elephant impact for an area. For the manager or researcher surveying wide areas with limited resources, spatially located dung counts combined with geographic information systems software containing water locations may be the most efficient broad survey method, to be followed up with more detailed tree evaluations in areas of concern.

The characteristics of the study location constrained tree evaluation to areas accessible from tracks. While only small dirt tracks were utilized and all transects were located at least 50 m from tracks to avoid potential negative effects, there is still a chance that the presence of these structures influenced my results. Unfortunately, the nature of the park and the high density of elephants necessitated proximity to an area accessible to a vehicle. Future work will use satellite remote sensing to investigate how vegetation trends vary over wider areas of the park to test further application of my findings, as well as the potential effect of tracks.

This study has examined the utility and application of the piosphere effect at multiple scales in southern Africa. While the piosphere effect generally seems to be upheld near waterpoints, over a larger scale this is more questionable and seems to relate to the type of herbivory that is occurring. It is possible that in some contexts piosphere effects may extend much farther than previously suggested. Further study into the dynamics of the piosphere effect on woody vegetation is needed to understand these complex trends and see how far they may extend, as well as considering what other factors are influencing patterns of vegetation utilization by elephants.

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## BIOGRAPHICAL SKETCH

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