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Large vegetated termitaria and fire impacts on reptilian community assemblage in a miombo woodland system heavily impacted by elephants

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Abstract

Habitat change is the principal cause of wildlife population declines worldwide. Elephant densities have altered the vegetation structure in many southern African reserves which, combined with the affect of fire and anthropogenic disturbances, have enormous consequences for biodiversity and faunal community structure. *Macrotermes* mounds serve as nutrient hotspots in miombo woodlands and support higher species richness and abundance of small mammals, cavity-nesting birds and vegetation compared to the surrounding woodland matrix. This study tested whether termitaria serve as refugia for reptiles in Chizarira National Park, Zimbabwe where elephants and fire have impacted the landscape. The study compared nine paired mound and matrix plots in burned miombo to nine paired plots in unburned areas of the woodland. A total of 116 reptiles representing 13 species were captured mainly by pitfall traps and time/area constrained searches. Species richness and abundance tended to be higher on mounds than in the matrix, but this difference was not significant. Burned sites had significantly higher number of species and burned mounds supported a greater abundance of reptiles among habitat types. Two species (*Ichnotropis* sp. and *Mabuya striata wahlbergii*) showed significant habitat preferences for mound habitats while *Nucras holubi* exhibited habitat preference for burned matrix plots. This study concludes that although mounds increase habitat heterogeneity and contribute to overall species diversity, the greater difference of reptilian assemblage in the modified miombo of Chizarira was found between burned and unburned plots.

Chapter 1: Introduction

The miombo is the most expansive dry deciduous forest in the world covering 2.7 million km² and ranging from Tanzania in the north east, to Angola and DR Congo to the west and Zimbabwe in the south (Campbell, Frost and Byron 1996). It is single storied woodland with a canopy of 15-20 m dominated by *Brachystegia*, *Julbernardia* and *Isoberlina* trees (Lawton 1978). The miombo is a region of considerable plant endemism and has been identified as a biodiversity hotspot in need of a conservation strategy (Mittermeier et al. 2003). Miombo is used extensively by people for food, fuel, timber, medicinal, cultural, and spiritual purposes (Campbell et al. 1996). Miombo woodlands also have profound impacts on soil, hydrology and climate (Gambiza et al. 2000). Most studies of animal diversity in miombo woodlands have focused on larger mammals (e.g. Lichtenstein's hartebeest and sable antelope) and avifauna (Rodgers, Salehe and Howard 1996). Fewer studies have been conducted on the herpetofauna and invertebrates, however, perhaps because the harsh dry season is thought to be responsible for low insect and herpetofaunal diversity (Rodgers et al. 1996). In the late 1990s, a new reptilian species was discovered approximately every 44 days in southern Africa, emphasizing the gaps in knowledge that persist in this region (Branch 1998). Currently, amphibians and reptiles have the dubious distinction of having the highest threat status of terrestrial vertebrates worldwide (IUCN 2006). In view of the global decline of biodiversity, more research is needed to understand the impact of habitat transformation on the pattern of diversity in the miombo (Frost 1996). This study examined how large vegetated termitaria, elephant impacts and fire influenced the diversity and abundance of reptiles in a miombo woodland study site in the Chizarira National Park in Zimbabwe.

Role of termitaria in miombo woodlands

Large vegetated termite mounds formed by *Macrotermes* species (Isoptera) are prominent features in *Brachystegia* and *Julbernardia*-dominated miombo woodland as well as *Acacia*, mixed riverine, and *Colophospermum mopane* woodland (Loveridge and Moe 2004). Mounds can reach heights of up to nine meters with diameters of 20-30 m, and are found in densities of 2-7 per hectare (Fleming and Loveridge 2003). The presence of these mounds creates habitat heterogeneity, and has also been found to increase species richness of plants (Humphrey 2008), cavity-nesting birds (Joseph 2008) and small mammals (Fleming and Loveridge 2003). Termites are considered ecological engineers because they can alter the availability of resources to other species and change the physical states of the abiotic and biotic elements of the ecosystem (Jones, Lawton and Shachak 1994). Termitaria serve as 'nutrient hotspots' as they have higher pH, moisture, organic material and concentrations of calcium, potassium, magnesium and phosphorus in mound soils and vegetation when compared to surrounding landscapes (Holdo and McDowell 2004). Mounds play host to a different suite of tree species as the surrounding woodland areas and have higher species richness of tall trees (Humphrey 2008). Due to their high nutrient levels, large vegetated *Macrotermes* mounds attract large herbivores and exhibit higher rates of browsing (Holdo 2003, Loveridge and Moe 2004). Changes in edaphic conditions caused by termites can influence the foraging behavior of large ungulates and elephants which will in turn impact vegetation structure (Holdo and McDowell 2004).

Fire and elephant ecology

Release of hunting pressure and a decrease in available habitat within the last century have concentrated elephant populations which now pose a threat to biodiversity within some southern

and east African wildlife reserves (Chafota and Owen-Smith 2009, Cumming et al. 1997).

Woody cover was negatively correlated with elephant density in the Sengwa Wildlife Research Area south of Chizarira National Park (Mapaure and Campbell 2002). When elephant densities exceed 0.5 km^{-2} savannah woodlands are likely to be converted to grass or shrub-land (Cumming et al. 1997). Recent growth rates for elephant populations in many southern and eastern African reserves have reached 5% and current numbers are higher than historic figures (Cumming et al. 1997). The current population in the Sebungwe region of Zimbabwe is more or less constant at 14,000-16,000 elephants as a result of a recent increase in anthropogenic mortality (Dunham 2008). Cumming et al. (1997) illustrate how high densities of elephants can threaten miombo biodiversity as impacted miombo woodlands exhibit lower bird and ant richness when compared to areas where canopies remain intact.

Fire is another important factor in forest-grassland succession in savanna ecosystems (Trollope 1982, Guy 1989, Frost 1996, Mapaure 2001). Fire has been a component of miombo woodlands for the past 60,000 years (Zolho 2005). Today the most common source of fire in the miombo system is anthropogenic as people use fire to prepare land for cultivation and livestock, make charcoal, create firebreaks around homesteads, hunt for bushmeat, and to smoke out beehives (Sileshi and Mafongoya 2006, Kikula 1986). In tropical regions the most common fire type is low intensity high frequency grass fires (Braithewaite 1987). Research conducted in *Baikaea* woodlands (Gambiza et al. 2000) explains how fire regimes vary by interval, severity and season and are influenced by moisture content, particle size, particle density, fuel load and ambient conditions at the time of burn. Highly seasonal rainfall and nutrient-poor soils influence plant production and quality in miombo systems, which in turn affect the rate of herbivory and intensity of fires and ultimately direct vegetation structure and soil nutrient cycling (Frost 1996).

This feedback loop determines the moisture and soil regimes of the woodland (Frost 1996). Grass and ground litter are the primary fuel source to savanna fires (Gambiza et al. 2000). Grass fires usually occur during the dry season resulting from fuel build up during the wet season (Higgins, Bond and Trollope 2000). The response of woody vegetation to fire will vary among species and size classes (Gambiza et al. 2000). Fire has the potential to damage regenerating trees thus preventing maturity (Chidumayo, Gambiza and Grundy 1996). The combined effect of fire and herbivory can maintain trees as small, multistemmed shrubs for decades (Gambiza et al. 2000). An inverse relationship exists between tree canopy and grass density due to competition for sunlight (Gambiza et al. 2000). Consequently, grasses do well where large trees that shade out grasses have been removed, and these grasses contribute to a fuel build up that creates conditions for destructive fires which further inhibit recruitment of younger trees. Examples exist throughout southern and eastern Africa of woodlands being converted to grassland dominated ecosystems due to the combination of herbivory and fire (Mapaure and Campbell 2002). A common management practice in miombo woodlands is to burn early in the dry season to prevent more intense and damaging fires later in the season (Chidumayo 1988). Fire exclusion practices carry the risk of decreasing the number of understory species in the coppice, however, as observed in miombo woodlands in the Copperbelt, Zambia (Chidumayo 1988). This practice also allows ground fuels to accumulate and leaves the woodland vulnerable to more destructive, higher intensity fires later on (Chidumayo 1988). A study of changes in miombo woodland cover in Sengwa Wildlife Research Area, Zimbabwe found a negative trend, but no correlation between fire and woody species; suggesting that elephants and other herbivores act with fire to suppress woody vegetation (Mapaure and Campbell 2002). A recent study using remote sensing to assess the impacts of herbivory and fire on canopy height and foliage distribution within the

vertical canopy profile of Kruger National Park determined that herbivory has a greater influence on vegetation structure and heterogeneity than fire (Levick et al. 2009). At the fine scale areas where herbivores were excluded had five times the canopy coverage of trees taller than nine meters and 66 times greater canopy coverage of trees in the three to six meter size class than areas lacking herbivores (Levick et al. 2009). Fire suppressed growth of smaller vegetation (trees < three meters height) in areas with herbivores and without (Levick et al. 2009).

Reptiles as bioindicators

Reptile assemblages exhibit a diverse use of trophic, temporal and spatial niches (Pianka 1973). This variation in activity patterns allows for many species to coexist by reducing competition (Pianka 2000). Herpetofauna are an important prey base to many predators and often recognized as bioindicators for ecosystem health (Vallan 2000, Lawler et al. 2003). Their adaptive traits of permeable membranes and thermoregulation leave them vulnerable to changing environmental conditions (Vallan 2000). In particular, reptiles are frequently used as indicators to the impact disturbances have on biodiversity because they occupy relatively small home ranges and are sensitive to changes in habitat structure (Valentine and Schwarzkopf 2008).

Impact of fire on reptiles

Models aimed at predicting reptilian community assemblage following a fire have thus far had only weak predictive power (Driscoll and Henderson 2008, Lindenmayer et al. 2008). Long-term empirical studies have established faunal changes associated with plant succession following a disturbance (Valentine and Schwarzkopf 2009). Observations in deforested valleys in Puerto Rico illustrate that arboreal reptilian species richness was correlated with an increase in woody vegetation, and demonstrated how reptile assemblage composition changed with habitat

(Rios-Lopez and Aide 2007). This pattern does not hold in tropical savannas, however, where high fire frequency impedes plant succession (Braithwaite 1987). Wild fires in tropical regions are most often patchy, low intensity burns that occur at high frequency making fire regime a more determining factor to reptilian assemblage (Braithwaite 1987). In Chizarira, the pattern of reptilian assemblage may differ due to the predominance of hot, late dry season burns. Fire regime will have different effects on different reptilian species, because of differing life history traits of seasonal activity, timing of reproduction and dietary requirements (Braithwaite 1987). The obvious direct affect of fire on herpetofauna is mortality (Russell, Van Lear and Guynn 1999). Due to their sedentary nature and limited dispersal ability reptiles are at higher risk from fire than mammal and bird taxa (Braithwaite 1987, Russell et al. 1999). Adaptive behavior towards fire includes seeking refuge in burrows or under surfaces or fleeing by the larger and more mobile species (Russell et al. 1999). Fire will affect reptiles indirectly by detrimentally altering the resource availability within a patch following a burn (Valentine and Schwarzkopf 2009). Burrowing reptile species are most likely the first to recolonize recently burned areas (Lindenmayer et al. 2008). Species that are closely associated to leaf litter are most vulnerable to indirect impacts of fire (Russell et al. 1999, Lindenmayer et al. 2008, Valentine and Schwarzkopf 2009). The patchy distribution typical of fires in tropical savannas support a mosaic of plant species composition, successional stages and habitat structure on the landscape thus outweighing the negative affects of fire in a patch by increasing reptile diversity on a broad scale (Russell et al. 1999).

Species behavior including locomotion, digestion, gestation and growth in reptiles is related to optimal body temperature (Braithwaite 1987). Structural differences among patches are critical predictors of reptilian assembly due to variation in shelter and micro-climatic conditions

(Braithwaite 1987). Species that prefer early or late successional vegetation stages face extinction with fire exclusion practices of human dominated landscapes (Driscoll and Henderson 2008). Dense vegetation build up in areas with no fire tolerance policies ultimately results in high intensity ‘incineration’ fires that threaten reptile populations with high mortality (Driscoll and Henderson 2008). In Australian *Eucalyptus* forests, approximately two thirds of reptilian species exhibit some response to fire and are at risk to local extinction in small reserves with inappropriate fire regimes (Driscoll and Henderson 2008). Wild fires and other large natural disturbances have the potential to become more intense, frequent and widespread as a result of climate change (Lindenmayer et al. 2008). In the miombo woodlands of Zimbabwe, fire and herbivory are incessant disturbances to the ecosystem and likely determinants of reptilian composition. Further disturbance in areas where there is already considerable environmental stress has the potential to reach a species threshold of resilience leaving them vulnerable to extirpation (Valentine and Schwarzkopf 2008).

Impact of canopy structure and termitaria on reptiles

Large scale disturbance of vegetation structure and habitat fragmentation have been found to impact negatively on the make up and population structure of herpetofauna (Brown 2001, Vallan 2000). The close association of reptile abundance with vegetation structure suggests that modifications to miombo woodland structure by elephants and microhabitats created by termites may result in changes to amphibian and reptile species richness and abundance. A study in the Cerrado of Brazil found positive correlations between reptile species richness and termite mounds (Colli, Constantino and Costa 2006). Disturbance to closed-canopy forests alter the habitat structure and light levels that reach the forest floor; these disturbances have resulted in changes in faunal communities, however there is limited knowledge of the effect changes in

forest structure have on reptile and amphibian populations (Greenberg 2001). In forest ecosystems, other aspects of herpetofaunal habitat associated with changes in canopies include the percent cover, length and diameter of coarse woody debris on the forest floor which serves as an important structural feature for herpetofauna by providing habitat for nesting, mating, feeding and thermoregulation (Greenberg 2001).

Fleming and Loveridge (2003) conducted the first study of small vertebrates on large vegetated termite mounds. They found greater abundance and diversity of small mammals on mounds, but no significant difference was observed with reptiles and amphibians (Fleming and Loveridge 2003). Seasonal variation emerged as the main determinant of the herpetofaunal diversity and abundance. The authors acknowledged that previous studies suggest that reptiles do utilize mounds to a greater degree than established in their research and that their data were insufficient to draw firm conclusions, and so recommended further trapping (Fleming and Loveridge 2003). Their study was carried out in the miombo woodlands of Zimbabwe (Carolina Wilderness and Lake Chivero near Harare) in a system with limited browsing pressure and no elephant population. Conservation of African herpetofauna against the prevalent threats of habitat fragmentation, loss and deterioration is hampered by a lack of research throughout the continent (Gardner, Barlow and Peres 2007).

Study objective

The focus of this research is to determine if termitaria function as refugia for reptiles by examining the spatial distribution of the reptile community in a miombo system where the vegetation structure has been heavily impacted by fire and megaherbivores.

Chapter 2: Methods

Study Area

This study was conducted during the months of October and November 2009 in the Zimbabwean province of Matabeleland North at Chizarira National Park (17°42'S, 27°55'E) (Figure 1).

Twenty-five km² of the park burned from the 22nd to 24th of September 2009. Chizarira covers 1910 km² of the southern escarpment of the Zambezi valley sloping south to the Busi/Sengwa valleys from altitudes of 760m to 1445m (Thomson 1974). The area experiences three separate seasonal conditions characterized as: cool and dry from May to July, hot and dry from August to October and hot and wet from November to April (Guy 1989). The annual average temperature is 23.2°C peaking in November at 29.5°C and falling to 16.9°C in July (Hutchinson et al. 1995).

The terrain is undulating and supports relatively poor soils typical of miombo woodlands (Campbell et al. 1996) which are composed of luvisols bedrock (Thomson 1974). Aside from topographical features, termitaria formed by *Macrotermes falciger* (Malaisse 1978) and the large trees they support are prominent visual components of the landscape and are most often surrounded by smaller trees that show clear signs of heavy herbivory. Herbivores found at Chizarira include African elephant, bushbuck, waterbuck, warthog, sable, plains zebra, greater kudu, eland and impala (Dunham et al. 2006).

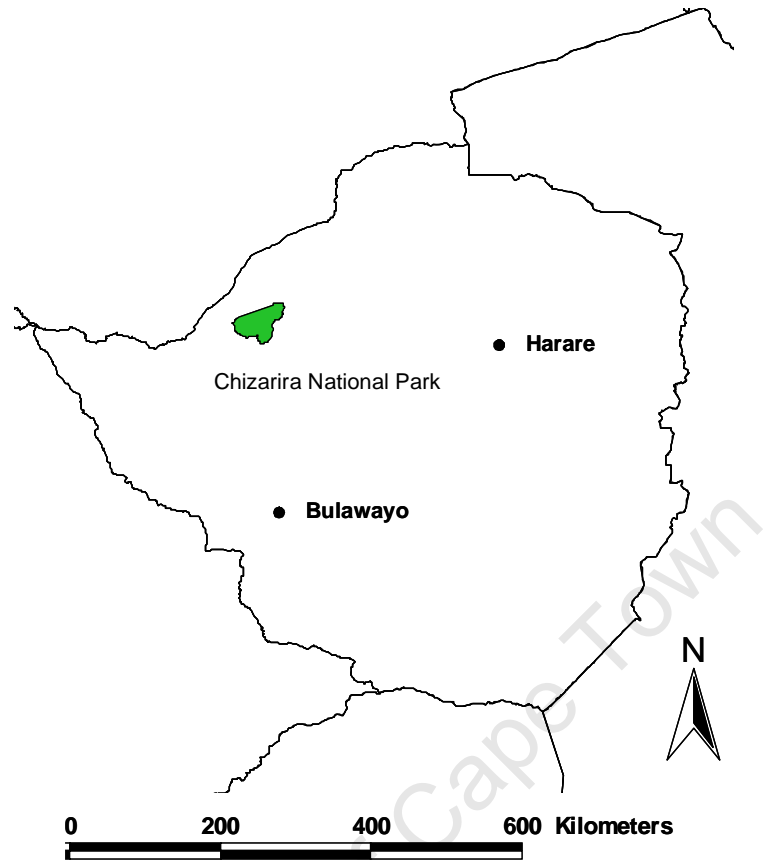


Figure 1. Chizarira National Park, Zimbabwe. 17°42'S, 27°55'E (Map composed in ArcView)

Study Design

To maximize catch-effort and thoroughly sample the habitat for all potential reptilian taxa this study used a variety of trapping methods. I used time/area-constrained searches, coverboards and drift fences equipped with pit-fall traps and funnel traps (Greenberg, Neary and Harris 1994, Webb 1999, Ryan et al. 2002, Doan 2003). A total of 18 vegetated mounds (nine in burned areas nine in unburned) greater than 1.5 m in height were randomly selected along with 18 corresponding 'matrix' sites in the surrounding woodland. All mounds used were found within the same catenal position. The paired matrix site was placed so that the centre of the matrix plot was at the greatest distance from its paired mound and all other surrounding termitaria. Distances from mound to matrix plots range from 26 m to 50 m. Each plot contained a drift fence made of

black plastic (40 cm width by 40 m length) with 20 cm lying flat to the ground and covered with soil for stability and 20 cm stapled to poles perpendicular to the ground. Fences were constructed in a semicircle around the most densely vegetated side of the mound, within a meter of the mound, or where possible on the mound base, with two open pitfall traps (20 liter white buckets: 30 cm diameter x 36 cm depth) sunk into the ground and centered under the fence at either end. This set up was designed to encompass the influence of the termitaria on the local environment including hard-pack soils and vegetation and to catch reptiles moving towards or dispersing from the mound habitat. A small piece of shade cloth or leaf litter was added to each pitfall trap to provide cover from the sun. Double-ended shade cloth funnel traps (750 mm in length with 50 mm openings) were centered on the mound side of the fence. Matrix fences were fashioned in semi-circles mimicking the form of the mound fence with the same orientation. A cover board (1x1 m cupboard backing) was placed in the center of each mound and matrix plot. This study considered one trap as all the equipment set on one plot including: one coverboard, one funnel trap, two pitfall traps and drift fence (Figure 2). Traps were checked twice daily (morning 08:00 to 10:00 and afternoon 14:00 to 16:00), coinciding with two minute time/area constrained searches at each plot. Times were chosen to capture peak reptile activity (Raxworthy and Attuquayefio 2000) and minimize chance of mortality. Termitaria served as the entire plot area for time/area constrained searches in the mound plots. Plot areas in the matrix in which to perform time/area constrained searches were established based on an equation with the assumption that mounds are conical in shape and marking an equivalent circular area in the matrix centering the diameter on the coverboard.

$$\text{Surface Area of Mound} = (\pi * \text{Radius}) * [\sqrt{(\text{Radius}^2 + \text{Height}^2)}] + (\pi * \text{Radius}^2)$$

$$\text{Diameter of Matrix Search Area} = 2 * \sqrt{(\text{Mound Surface Area} / \pi)}$$

Specimens were photographed, identified, marked on the belly with a non-toxic marker to record recapture data, weighed and measured (snout to vent length and vent to tail length), then released. Reptile nomenclature follows Branch (1998). Habitat features were recorded for each plot by taking two line-intercept transects and recording bare ground, coarse woody debris and multi-stemmed tree stalks and averaging out the percent cover. Canopy cover was measured four times around each plot and once in the center by looking skywards through a 3 cm diameter cylinder and estimating the proportion of cover than averaging out the five estimates. To ensure each mound fit the height requirement of >1.5 meters, mound height was estimated by standing back from the mound and comparing the height to a two meter measuring stick planted upright at the mound base, this same technique was used to estimate tree height. A measuring tape was used to record basal circumference at breast height for trees with >6 cm basal diameter.

Vegetation was identified to species with the aid of a Zimbabwean botanist (Appendix 2 and 3).

Traps were left open for ten days at a time. The first group of plots (consisting of four mound and four matrix burned sites and four mound and four matrix unburned) were set from the 19th to the 28th of October. The second group of plots (consisting of five mound and five matrix burned sites and five mound and five matrix unburned) was set from the 29th of October until the 7th of November. In all data from 36 (18 paired) plots were compiled and analyzed.

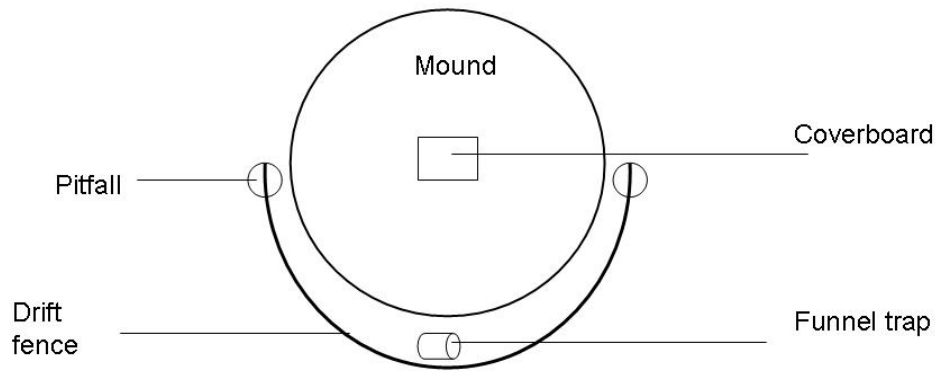


Figure 2. Diagram of trap components.

Data Analysis

Data for 18 paired mound and matrix plots were analyzed using PC-ORD 5.10 (McCune and Mefford 2006) and Statistica version 8.0 (Statsoft Inc. 2007). Variables from all data sets failed to fit normal distribution curves, typically species data sets fit Poisson distributions, and nonparametric methods were used.

I examined patterns of reptile abundance, species richness and habitat features between the four habitat types. Habitat variables included percentage canopy cover, bare ground, coarse woody debris and multi-stem trees. Kruskal-Wallis tests and Spearman Rank Order Correlations were applied to examine abundance and richness relationships among habitat features and habitat types, using Statistica v. 8.0 (Statsoft Inc. 2007).

A pairwise Multi-Response Permutation Procedure (MRPP) detected differences in reptilian community assemblages among habitat types for 30 sites (6 sites had no capture success) using a Sørensen (Bray-Curtis) distance measure and a natural weighting (Mielke 1984). This type of

distance measure is advised for abundance data with zero dominated data sets (McCune & Grace 2002). The A statistic ranges from 0-1 and explains effect size (McCune and Mefford 2006). When A equals 0, groups are no different than a chance result; when A equals 1, sample units within groups are identical (McCune and Mefford 2006). Community assemblages were represented with a dendrogram from a two way cluster analysis. Individual species abundances and occurrences among habitat types were examined using Indicator Species Analysis (McCune and Mefford 2006) with a Monte Carlo Test of significance, using 5000 permutations (Dufrêne and Legendre 1997). A species that is represented in only one habitat type is considered a 'perfect indicator'. I calculated Shannon's Diversity Indices for all 36 sites, using PC-ORD 5.10 (McCune and Mefford 2006). Non-metric Multidimensional Scaling ordinations (Kruskal 1964, Mather 1976) were used to represent differences in replicate sites in terms of reptile species assemblage composition and habitat features for all sites where reptiles were caught. This was achieved with Sørensen (Bray-Curtis) distance measure of 250 runs and 500 iterations and random starting configurations with a maximum of six axes. Dimensionality was assessed by choosing the solution with the minimum number of axes and lowest stress.

Chapter 3: Results

Capture effort totaled 24 hours of time-area constrained searches and 8,640 trap hours and yielded 116 reptiles representing 13 species (Table 1). Numbers of reptile species observed among habitat types were as follows: eight species observed in burned mound plots, nine species in unburned mound, six species in burned matrix and five in the unburned matrix. *Ichnotropis* sp. was the most abundant species caught representing 53% of all captures. Combining burned and unburned areas, termitaria supported 12 of 13 species, compared to only 8 species in matrix sites.

Pit fall traps were the most effective trapping method, accounting for 66 % of all individuals caught, followed by time-area constrained searches (30%), funnel traps (3%) and coverboards (1%). The sample-based species accumulation curve did not reach the asymptote but started to level off (Appendix 1) indicating that the majority of species in this habitat were sampled. The first order jackknife estimate of PC-ORD 5.10 suggests that with more catch effort, the sampling methods of this study could yield 18 species of reptile.

Table 1. Number of reptiles found on burned and unburned matrix and termitaria plots.

Taxon	Number of individuals				Total
	Burned Plots		Unburned Plots		
	mound	matrix	mound	matrix	
<i>Ichnotropis</i> sp. Rough-scaled Lizard	47	13		1	61
<i>Nucras holubi</i> Holub's Sandveld Lizard	2	10	1	2	15
<i>Leptotyphlops longicaudus</i> Long-tailed Thread Snake	2	2	2	4	10
<i>Mabuya varia</i> Variable Skink	4	2	2		8
<i>Lygodactylus capensis</i> Cape Dwarf Gecko	1		3	2	6
<i>Gerrhosaurus nigrolineatus</i> Black-lined Plated Lizard	2	2			4
<i>Mabuya striata wahlbergii</i> Striped Skink	1		3		4
<i>Panaspis</i> sp. Spotted-neck Snake-eyed Skink			1	2	3
<i>Agama armata</i> Peter's Ground Agama		1			1
<i>Amblyodepsis polyepsis</i> Purple-glossed Snake			1		1
<i>Geochelone pardalis</i> Leopard Tortoise			1		1
<i>Hemidactylus mabouia</i> Moreau's Tropical House Gecko	1				1
<i>Leptotyphlops</i> sp. Unidentified Thread Snake	1				1
Total	61	30	14	11	116

Reptilian abundance and richness patterns among habitat types

There was no significant difference in species richness between mound vs. matrix sites (Kruskal-Wallis test: $H=2.38$, $p=0.122$, $N=36$). Both mound and matrix sites that had been burnt had significantly higher species richness than unburned sites (Figure. 3). Reptiles were significantly more abundant on burned mounds (Kruskal-Wallis test: $H=10.81$, $p=0.0128$, $N=36$) (Figure 4).

Diversity

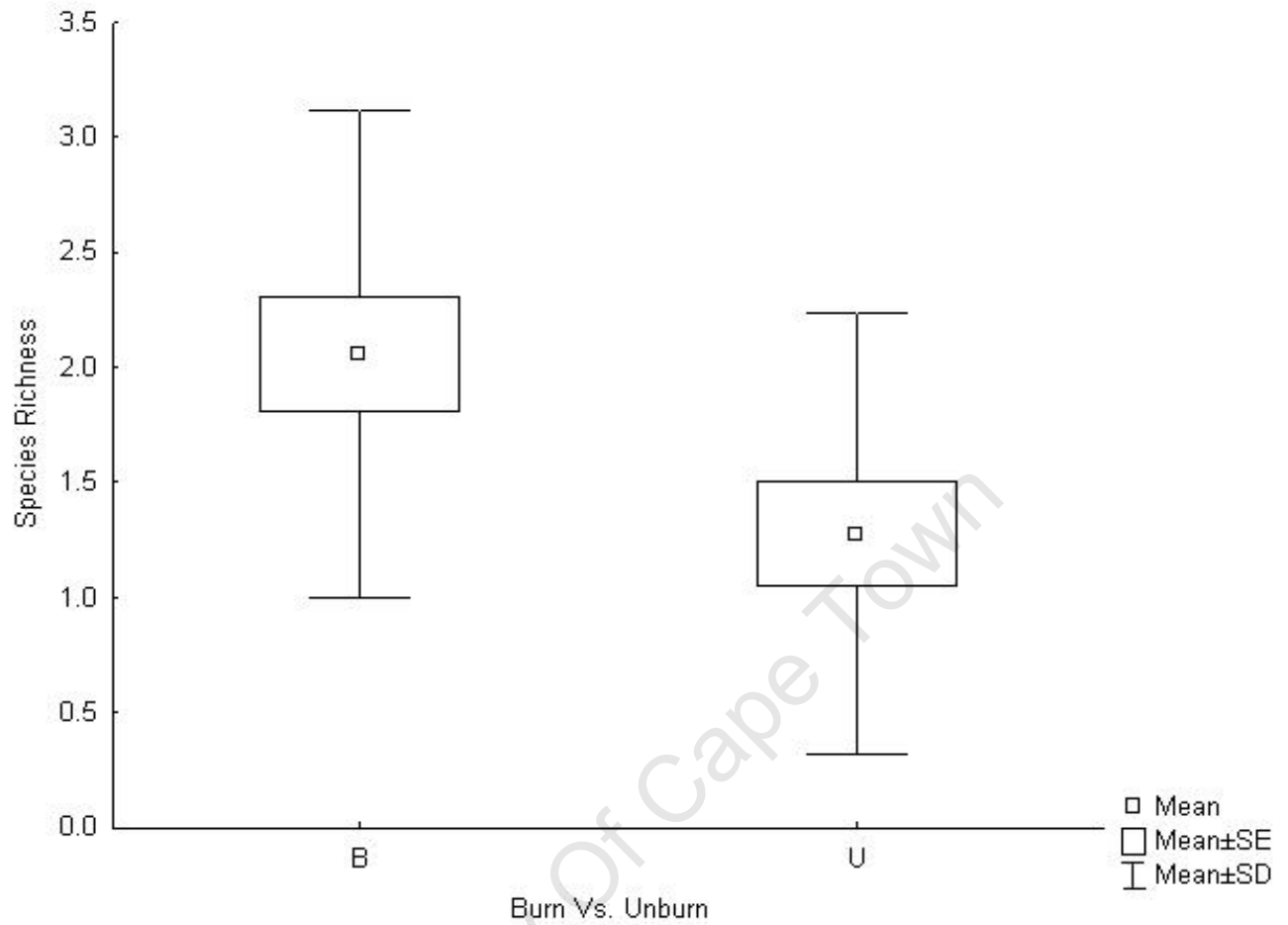


Figure 3. Box and whisker graphs showing species richness (average number of species per sample site) in burned sample sites was higher than unburned sample sites (Kruskal-Wallis test: $H=4.99$, $p=0.025$, $df=1$, $N=36$).

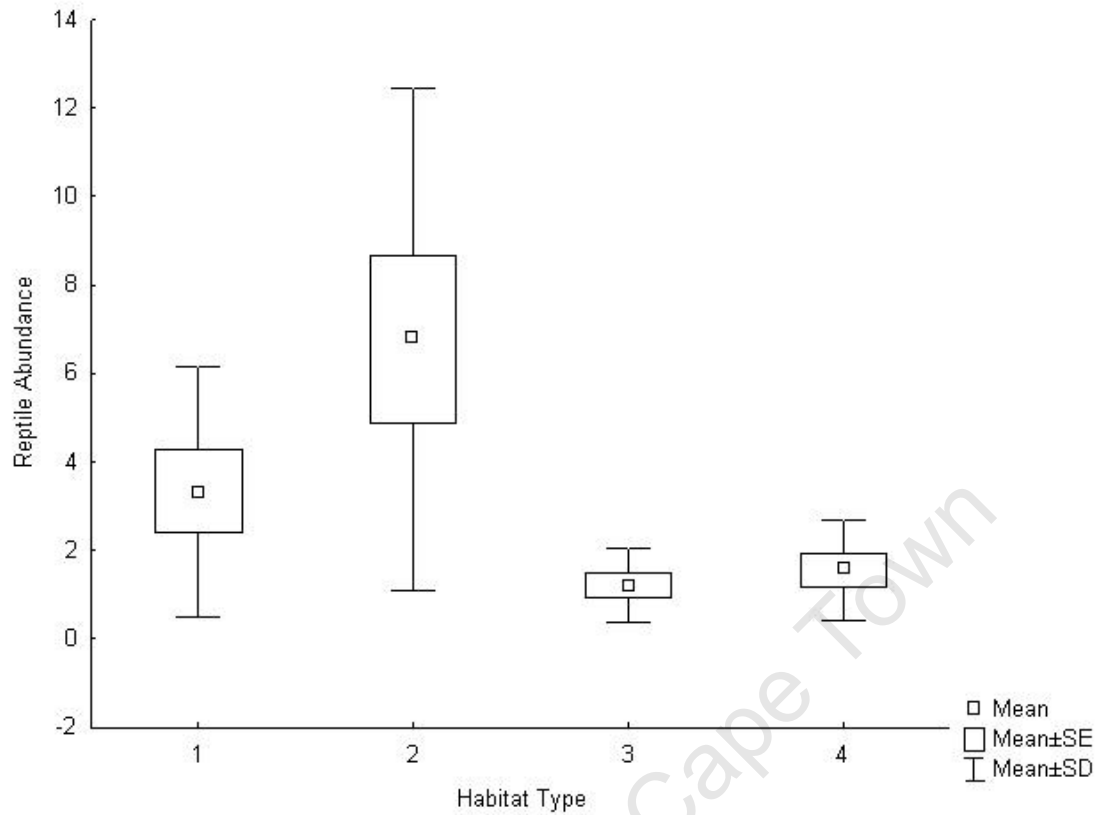


Figure 4. Box and whisker plot showing reptile abundance (average number of individuals caught per sample site) and habitat types where codes are; 1= burned matrix, 2=burned mound, 3=unburned matrix and 4= unburned mound (Kruskal-Wallis test: $H=10.81$, $p=0.0128$, $df=3$, $N=36$).

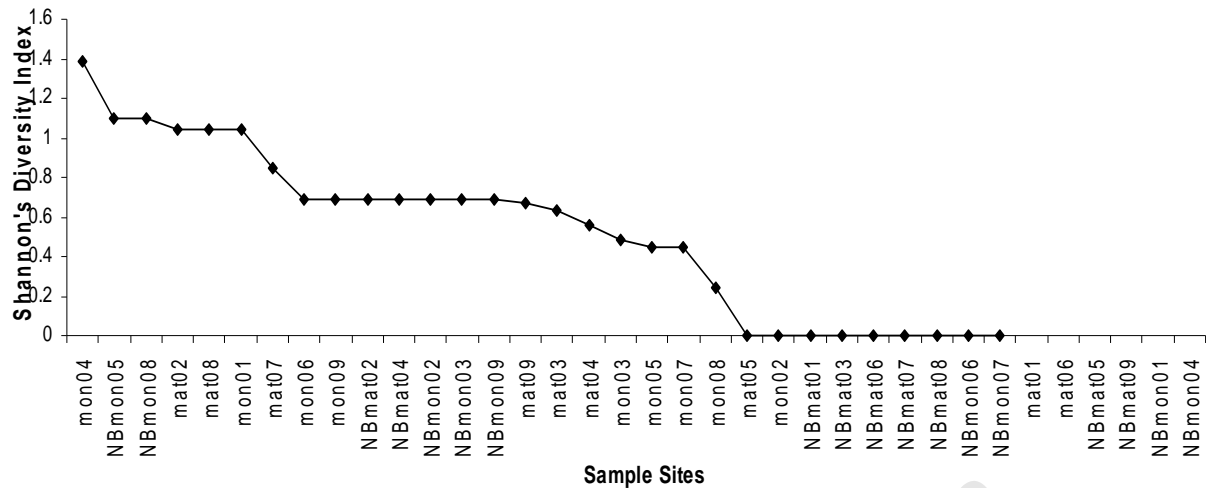


Figure 5. Shannon's Diversity Index calculated for 36 sample sites showing a pattern of low diversity ($H < 0.2$) in the majority of unburned sites.

Abundance and richness patterns among habitat characteristics

There was a positive correlation between reptile abundance and bare ground ($p < 0.05$, $R = 0.458$, $n = 36$) and reptile species richness and bare ground ($R = 0.388$, $p < 0.05$, $n = 36$). No correlation was found between species richness and abundance for percent multi-stem trees or coarse woody debris.

Composition and Structure of Reptilian assemblages

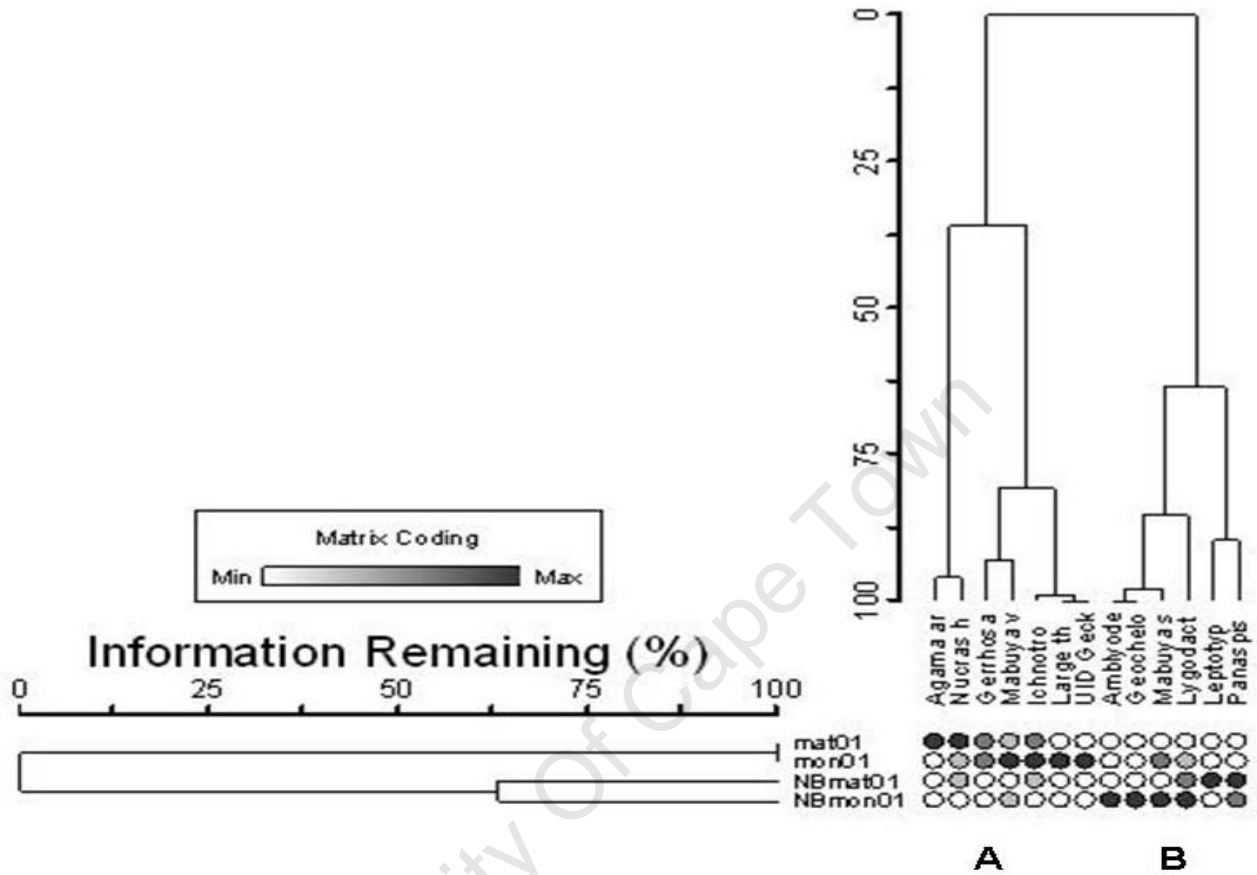


Figure 6. Two way cluster dendrogram conducted with PC-ORD 5.10. Darker shading represents greater importance of habitat to species. Group A species show a preference for burned habitats while Group B species are more commonly found in unburned miombo.

A pairwise comparison of reptile community assemblages among habitat types for 30 sites with capture success detected significant differences between burned matrix and unburned mound groups ($p=0.005$, $A=0.162$) as well as burned mound and unburned matrix/mound ($p=0.018$, $A=0.097$; $p=0.01$, $A=0.116$, respectively).

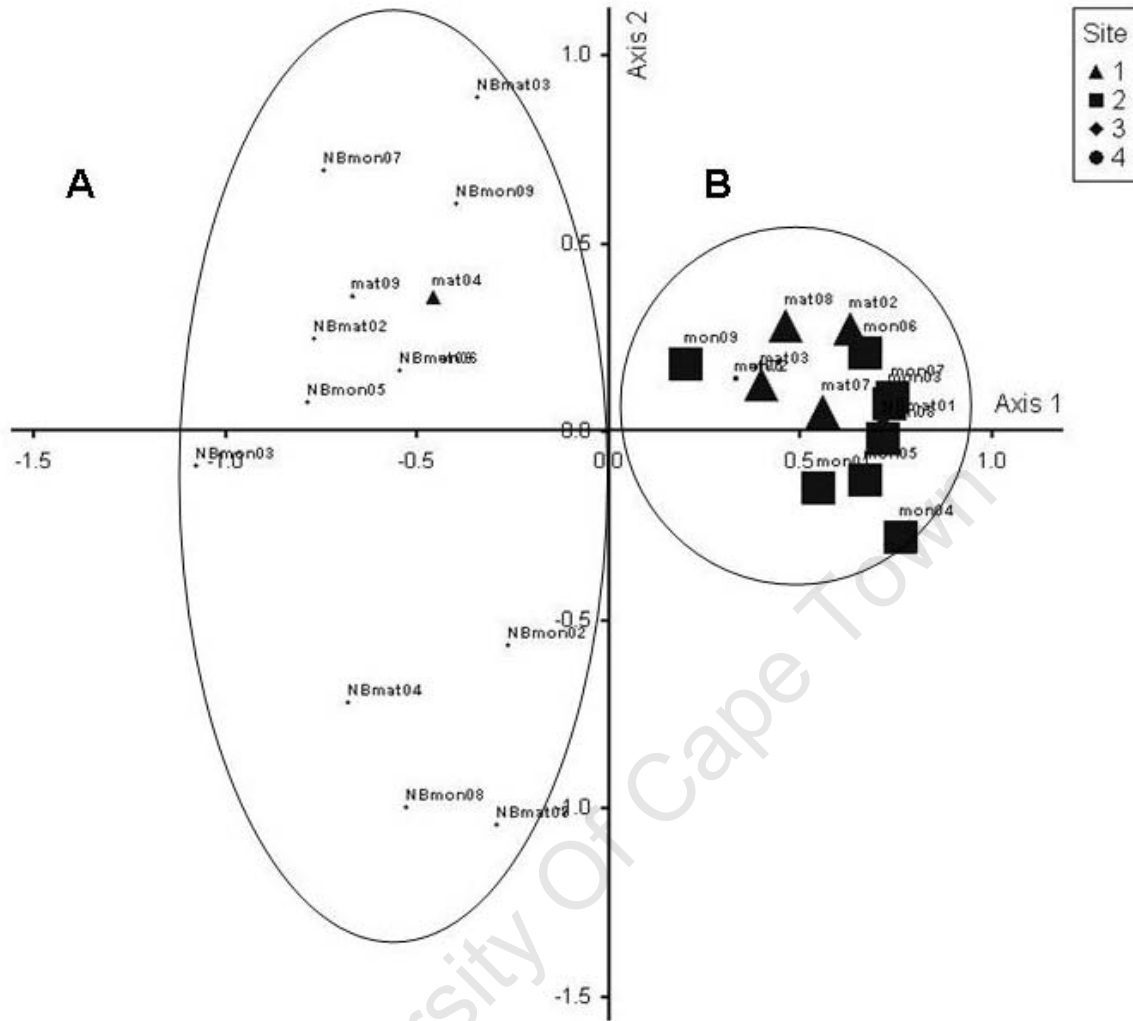


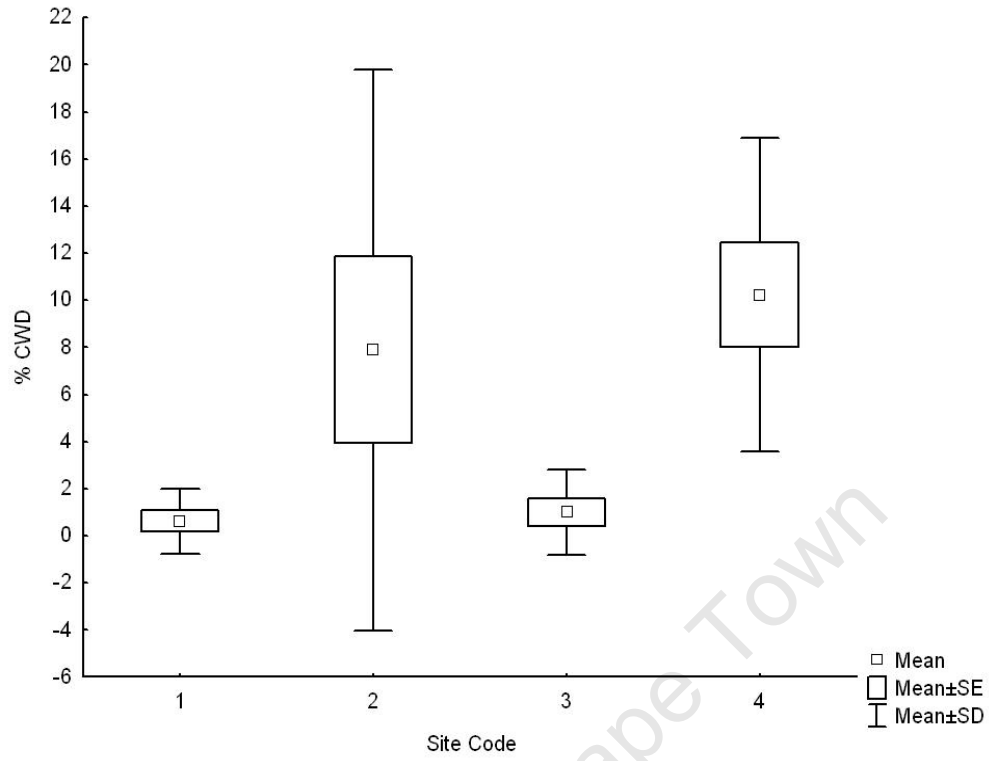
Figure 7. Non-metric Multidimensional Scaling plot showing habitat preference of *Ichnotropis* for unburned sites (PC-ORD 5.1). Group A is primarily composed of unburned sample sites. Tight clustering of Group B shows that *Ichnotropis* has a strong preference for predominantly mound habitats that have recently burned (size of symbol indicates degree of importance). Site symbols are; ▲ = burned matrix, ■ = burned mound, ◆ = unburned matrix and ● = unburned mound. A two dimensional solution was used in NMS. Axes 1 and 2 Monte Carlo test result for mean stress is 53.7 ($p=0.004$) for axis 1 and 27.8 ($p=0.032$) for axis 2.

Table 2. 'Indicator Species Analysis' (PC-ORD 5.10) showed that *Nucras holubi*, *Ichnotropis sp.* and *Mabuya striata wahlbergii* exhibit significant habitat preferences (marked in bold typeface). Site codes are: 1= burned matrix, 2=burned mound, 3=unburned matrix and 4= unburned mound. Indicator value is from randomized groups. * equals the proportion of randomized trials with indicator value equal to or exceeding the observed indicator value. $p = (1 + \text{number of runs} \geq \text{observed}) / (1 + \text{number of randomized runs})$.

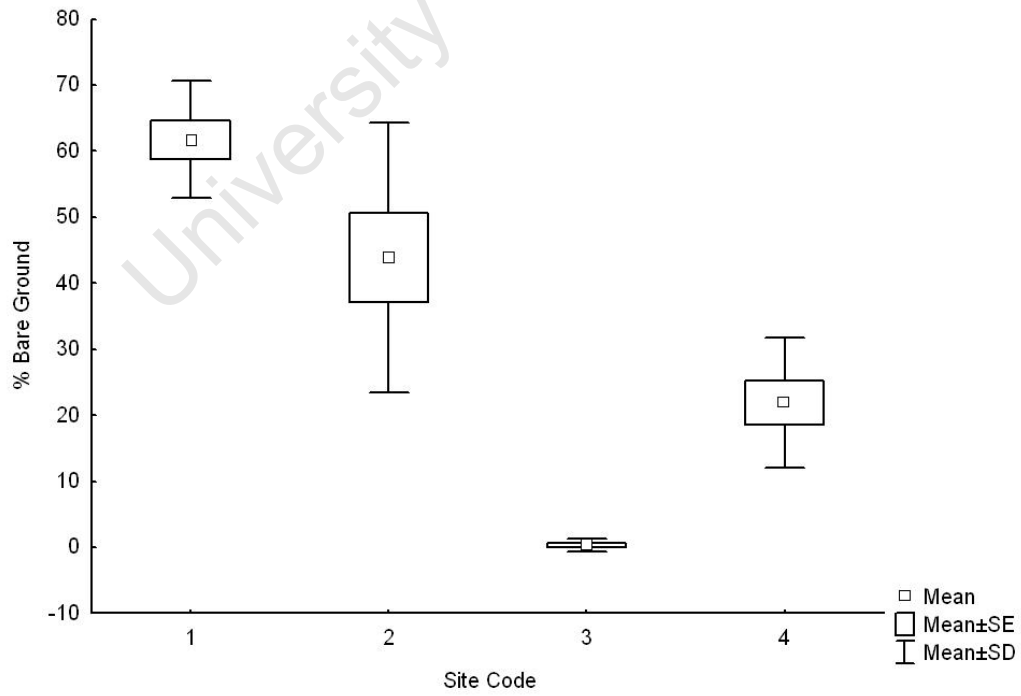
Taxon	Site Code	Observed Indicator Value	Mean	S. Dev	p*
<i>Agama armata</i>	1	14.3	13.3	1.48	0.6922
<i>Amblyodepsis polyepsis</i>	4	14.3	13.4	1.46	0.7066
<i>Gerrhosaurus nigrolineatus</i>	1	16.1	15.1	7.86	0.2442
<i>Nucras holubi</i>	1	49.1	20.8	8.24	0.009
<i>Ichnotropis sp.</i>	2	64.3	26.9	9.24	0.0026
<i>Hemidactylus mabouia</i>	2	11.1	13.3	1.46	1
<i>Geochelone pardalis</i>	4	14.3	13.3	1.47	0.7012
<i>Leptotyphlops longicaudus</i>	3	17.9	20.3	7.64	0.5988
<i>Lygodactylus capensis</i>	4	22.3	16.8	7.93	0.2752
<i>Mabuya striata wahlbergii</i>	4	34	15	7.83	0.0394
<i>Mabuya varia</i>	2	14.6	17.6	8.27	0.6024
<i>Panaspis sp.</i>	3	19	13.4	8.72	0.4002
<i>Leptotyphlops sp.</i>	2	11.1	13.3	1.46	1

Habitat characterization

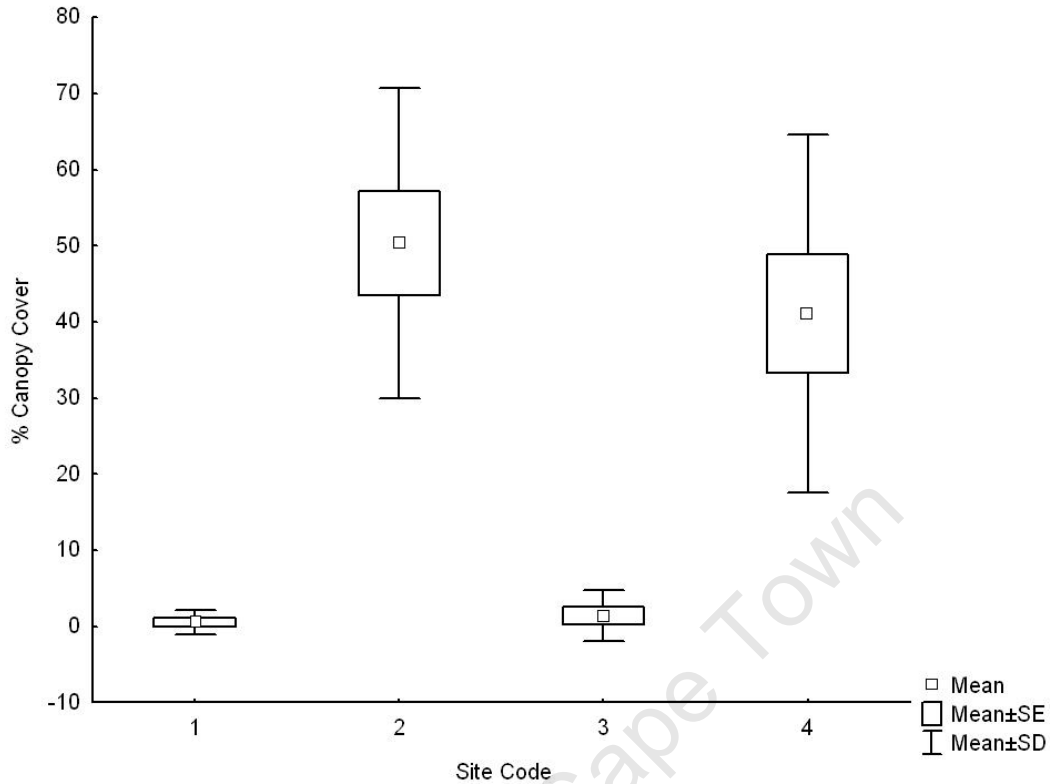
Habitat variables for coarse woody debris (CWD), bare ground, and canopy cover varied significantly among sites (Figure 8). The impact of herbivores on the landscape is apparent from the low canopy cover found on matrix sites and the corresponding lack of coarse woody debris. The recent fire resulted in high percentages of bare ground (40-65%) at these burned sites (Figure 8 and Figure 9). Unburned sites are also distinguished from the burned sites from the distribution and abundance of multi-stemmed trees (Figure 10).



A



B



C

Figure 8. Differences in habitat features amongst habitat types. A) Matrix sites had a low percentage of coarse woody debris found in sites 1 and 3 (Kruskal-Wallis test: $H = 13.97$, $p = 0.0029$, $n = 36$). Graph B shows a significantly lower percentage of bare ground (Kruskal-Wallis test: $H = 28.20$, $p = 0.000$, $n = 36$) in the unburned matrix sites. A lack of big trees represented by the low levels of canopy cover shown in Graph C (Kruskal-Wallis test: $H = 28.60$, $p = 0.000$, $df = 3$, $n = 36$), corresponds to the low percentages of CWD. Habitat type codes are; 1= burned matrix, 2=burned mound, 3=unburned matrix and 4= unburned mound.

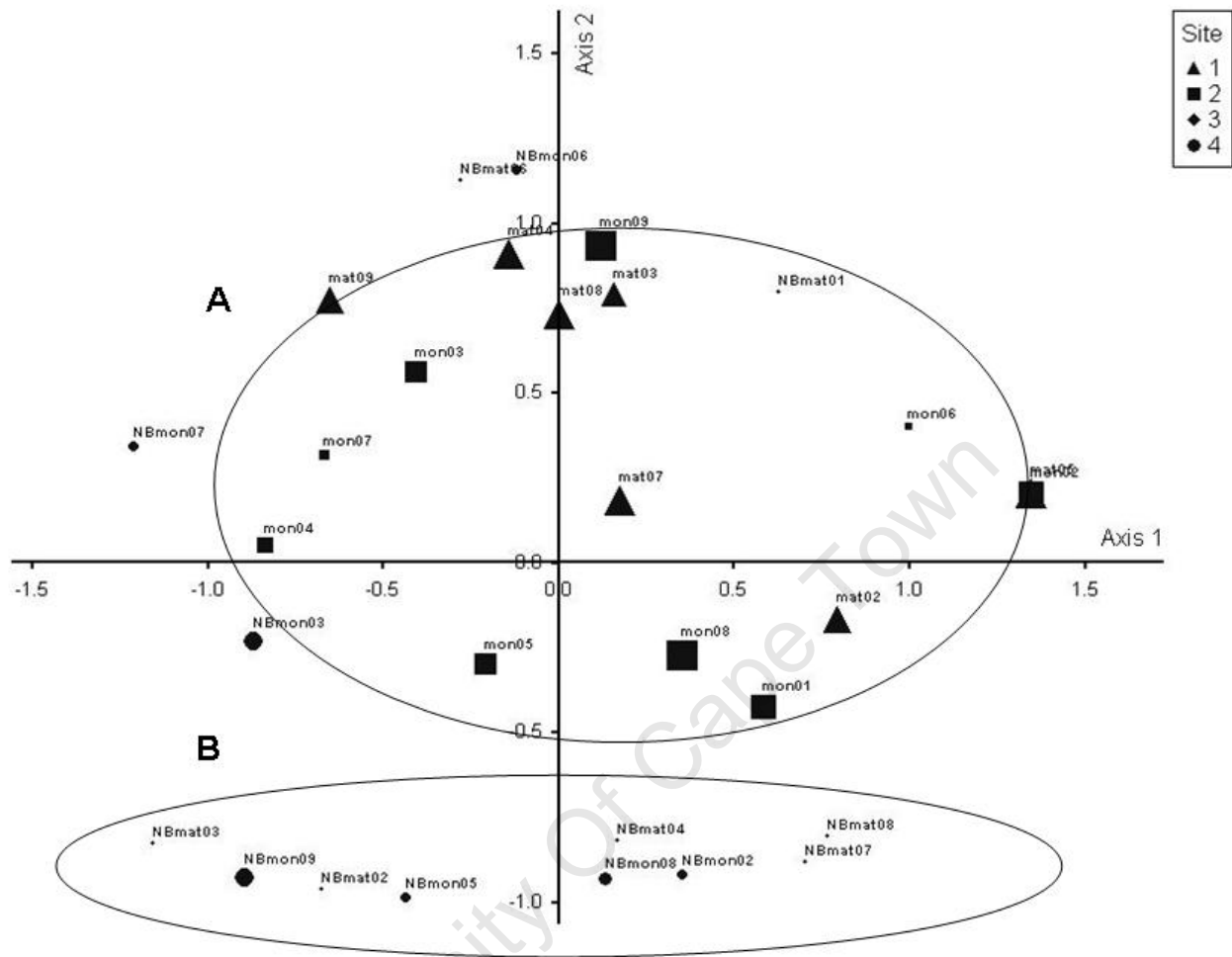


Figure 9. Non-metric Multidimensional Scaling plot showing percentage of bare ground among sites (PC-ORD 5.1). Group A is primarily composed of burn sample sites. Group B is composed entirely of unburned sites indicating that vegetation cover is higher in these plots (Size of symbol indicates degree of importance). Site symbols are; ▲= burned matrix, ■=burned mound, ◆=unburned matrix and ●= unburned mound. A two dimensional solution was used in NMS. Axes 1 and 2 Monte Carlo test result for mean stress is 53.73 ($p=0.0040$) for axis 1 and 27.79 ($p=0.0319$) for axis 2.

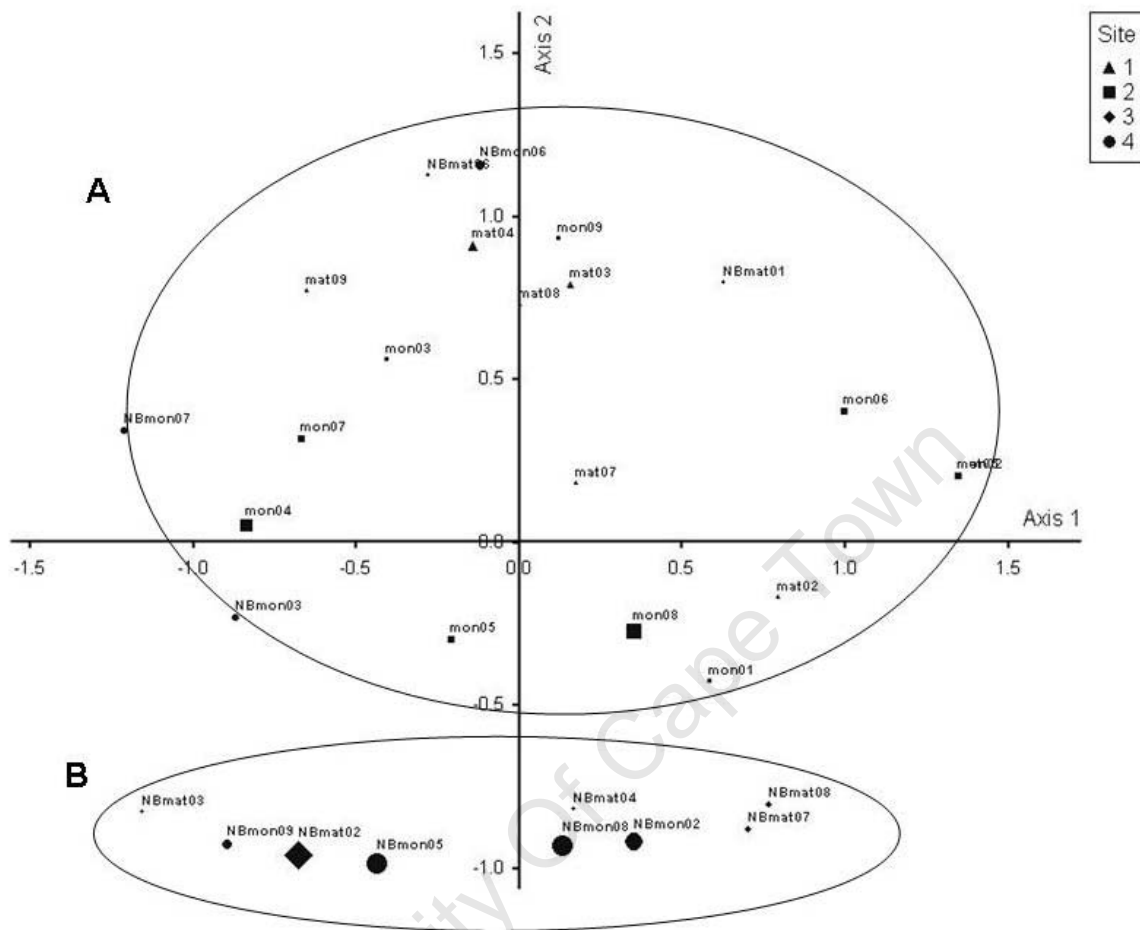


Figure 10. Non-metric Multidimensional Scaling plot showing the distribution of trees <6 m. (PC-ORD 5.1). Group A is primarily composed of burn sample sites. Group B are all unburned sites indicating that small trees are more common in these plots (Size of symbol indicates degree of importance). Site symbols are; ▲=burned matrix, ■=burned mound, ◆=unburned matrix and ● = unburned mound. A two dimensional solution was used in NMS. Axes 1 and 2 Monte Carlo test result for mean stress is 53.73 ($p=0.0040$) for axis 1 and 27.79 ($p=0.0319$) for axis 2.

Chapter 4: Discussion

Patterns of reptile richness, abundance and community assemblage

Significant differences in species richness, abundance and reptilian assemblage between burned and unburned plots suggests that fire has an influence on reptiles in Chizarira. A greater number of species and nearly twice as many specimens were captured on mounds, however, results do not provide significant supporting evidence for the hypothesis that termitaria serve as refugia for reptile diversity in elephant and fire impacted miombo. The pattern of reptile distribution in this study is supported by evidence gathered by Fleming and Loveridge (2003) and shows similar but less prevalent diversity patterns of plants (Humphrey 2008), cavity-using birds (Joseph 2008) and small mammals (Fleming and Loveridge 2003) on *Macrotermes* mounds. This study is limited by low sample numbers yet raises concern for the use of reptiles as bioindicators in savanna environments because of the diverse life histories and habitat requirements among species. The pattern of community structure, abundance among treatments (Figure 6 and Figure 3 and 4 respectively) and habitat preference by 'indicator' species (Table 2) suggest that fire and termitaria increase landscape heterogeneity and contribute to greater species diversity on a local scale.

Although the major delineation of reptile species richness, abundance and community assemblages were found between burned and unburned areas, three of the thirteen species in this study had significant preferences for specific habitat types, though the evidence for one species, *Mabuya striata wahlbergii*, is drawn from four individuals. Figure 6 indicates a pattern of distinct species assemblages between all four habitat types which can only be confirmed with further sampling.

Comparison of findings with previous studies

The influence of fire on the structure and composition of reptile communities is evident in the literature (Braithwaite 1987, Russell et al. 1999, Lindenmayer et al. 2008, Valentine and Schwarzkopf 2009), and supported in this study by differences in richness, abundance, diversity (Figure 5) and community assemblage. However, the fire in this study was recent to the sampling time (~ 4 weeks) and data regarding the preexisting reptile community and reptile mortality due to fire is lacking. Without this data it is not possible to draw accurate conclusions to the exact influence fire has on the reptile population, i.e. if the reptiles found in the burned plots selected these sites due to habitat preference, were pre-existing residents or if the area was rapidly recolonized.

A fire that precluded trapping in a study conducted by Legge et al. (2008) was five weeks prior to trapping, yet the authors deem it reasonable to assume that differences in abundance and diversity are caused by the direct or indirect effects of fire because of carefully matched habitats in the burned/unburned paired plots. The study design at Chizarira took similar consideration for habitat matching.

Higher abundance and diversity patterns of reptiles found in burned areas in bottomland-hardwood forests of the southeast U.S.A. were attributed to decreased ground cover and therefore greater opportunities for thermoregulation (Moseley, Castleberry and Schweitzer 2003). Other studies of the short-term influence fire has on reptiles portrayed an opposite response with an overall decline of fauna with fire (Braithwaite 1987, Woinarski et al. 1999, Legge et al. 2008). These studies acknowledge the diverse foraging habits and space use of reptilian taxa and admit to heterogeneous species-specific responses due to diverse life history

traits (Legge et al. 2008). Evidence of higher abundances in the burned areas in this study is seriously affected by the dominance of *Ichnotropis* sp. which is an annual species (Branch 1998). Making the assumption that fire is a driver behind the pattern observed at Chizarira, an examination of the habitat preferences and foraging behavior of the species represented in this study may yield insights to explain their distribution.

Species distribution-life traits and niche guild

Results show that termite mounds, fire and herbivory have modified the miombo at Chizarira and that for reptiles, this represents four distinct habitat types that influence the pattern of species assemblages in the study area. Unburned mound sites had the highest feature diversity yet had similar percentages of coarse woody debris and canopy cover to the burned mound sites (Figure 8). The unburned mound plots differ from burned mounds mainly by the retention of fallen leaf-litter, which is represented by a significantly lower percentage of bareground (Figure 9). The unburned mounds were exploited by *Lygodactylus capensis* which is an arboreal species that feeds predominately on ants and termites (Simbotwe and Garber 1979, Branch 1998). This habitat type was also preferred by *Mabuya striata wahlbergii* which is a semiarboreal species that feeds on termites as well as grasshoppers, beetles, flies, moths and spiders that they are able to find in log piles, ditches and loose bark and leaf litter (Simbotwe and Garber 1979). The significant habitat preference of *Mabuya striata wahlbergii* for unburned mounds suggests that due to its arboreal nature it is a species that benefits from termitaria and cannot survive in the stunted trees of the matrix. *Ichnotropis* sp. is a terrestrial 'annual' species that preys on termites and other ground dwelling insects (Branch, 1998). The preference of *Ichnotropis* sp. found on burned mounds (Figure 7) is likely due to its close association with sandy soils rather than leaf litter (Simbotwe and Garber 1979).

Unburned matrix sites were dominated by *Hyperhenia filipendula* as well as other grass species often as high as 1.5 m that on average covered more than 95 percent of the plot areas. The study did not include grass as part of canopy cover which is a potential limiting factor as dense grass acts as canopy to terrestrial reptiles by preventing light from reaching ground level and creating a microclimate unique to the unburned matrix. This habitat type was favoured by *Panaspis* sp. and *Leptotyphlops longicaudus* both of which are burrowing reptiles that forage in grass tussocks and leaf litter (Branch 1998). Exposed ground as a result of fire can alter the soil structure and create hydrophobic conditions (Certini 2005). Changes to physical and chemical soil properties will vary with fire regime but undoubtedly have a bearing on burrowing reptiles. Previous studies of blind snakes suggest that they may be sensitive to a single incident of intense fire (Woinarski et al. 1999).

Burned matrix sites were characterized by high levels of bare ground with low percentages of other habitat features and therefore had less niche availability. The reptile species most commonly found here was *Nucras holubi* which is a terrestrial species that feeds around grass tussocks and has a diet that consists mainly of beetles (Branch 1998).

A combination of habitat and prey preference may explain why some species were found evenly in both burned mound and matrix sites. *Mabuya varia* is semiarboreal and can be drawn from protective tree cover to make short dashes after a diverse prey base (Branch 1998). *Gerrhosaurus nigrolineatus* is known to occupy rodent burrows and old termitaria and feeds on grasshoppers and beetles commonly found in grasslands (Branch 1998). Mortality was high (3 out of 4 specimens caught) for *Gerrhosaurus nigrolineatus*, and was most likely caused by overheating despite measures to prevent heat stress with shade cloth. This misfortune demonstrates the influence microclimate has on thermoregulation behaviour. Activity temperature is the range of

body temperatures in which a reptile can forage, breed and defend territories and is a principal driver behind habitat selection (Avery 1979).

It is presumptuous to identify distribution trends for species that were only represented once in the sampling. Three of these species (*Amblyodepsis polyepsis*, *Hemidactylus mabouia* and *Geochelone pardalis*) occur over a wide range of habitats and one (*G. pardalis*) has a home range that can reach 1-3 sq. km (Branch 1998). Nevertheless, the presence and absence of these species among habitat types fits a pattern of niche selection. Agamas are terrestrial lizards foraging largely on beetles and may supplement their diet with grass seed (Simbotwe and Garber 1979), which is abundant in the matrix environment where it was caught. Thread snakes are burrowing species that thermoregulate by moving up and down in the soil column and have adapted defence pheromones to protect against ants and termites; the specimen in this sample was caught near a mound burrow. *Amblyodepsis polyepsis* is another burrowing snake and feeds on sleeping lizards and blind snakes that are also associated with mounds; whereas *Hemidactylus mabouia* is an arboreal species and was caught on a densely vegetated mound.

This research shows a higher diversity and abundance of terrestrial species at Chizarira. Only four of the thirteen reptiles caught in this study are arboreal or semi-arboreal. This may be as a result of the change in vegetation structure from herbivory. If this theory holds then termitaria contribute to community resilience in miombo systems. The park may experience a succession in reptilian niche guilds from terrestrial to arboreal species overtime if elephant poaching continues. The absence of previous reptilian studies in Chizarira makes it impossible to make accurate inferences to the total impact elephants and fire has had on local reptilian diversity.

Study limitations

Many species that are known to occur in Chizarira including pythons, chameleons and several elapid species were not represented in the sampling. This stresses the importance of refining trap methods or catch effort to strengthen the current understanding of reptile distribution. The trap method used during this study is undoubtedly biased towards smaller reptiles. Because of the high concentrations of termitaria in Chizarira smaller reptiles were targeted to reveal trends of species with smaller home range requirements. Trapping methods support the findings of the time-area constrained searches, however the bare ground resulting from the fire may have aided the visual surveys and potentially biases the sampling towards higher abundance and richness in burned plots. Effort was taken to control this bias by allotting adequate yet equal search time for each plot to thoroughly cover the area while moving slowly and listening/looking for signs of reptiles. Another limit to this study is the low sample size resulting from a short duration of sample time and low number of replicates due to time constraints. Mark-recapture data yielded only two recaptures (both on the same mound where seven individuals were marked) of 40 marked reptiles. This data has been excluded from the results section as it is insufficient to draw conclusions, however extended sampling at each plot would yield data for local population sizes and dispersal patterns. Amphibians were excluded from this study as it was at the end of the dry season and most species are active during rainy periods (Carruthers 2001). Only one *Bufo* species was captured in this study and made its appearance within 24 hours of the first rain of the season along with *Amblyodepsis polyepsis*, *Agama armata* and *Geochelone pardalis*. This highlights the importance of continued sampling to study the seasonal effects on herpetofauna and how the role and importance of termitaria to reptiles changes throughout the year.

Conclusion

A review of worldwide studies of habitat change and herpetofauna cites continental Africa as a region with a 'near absence' of studies, yet extraordinary rates of habitat destruction (Gardner et al. 2007). Elephants and fire are two natural contributing factors to habitat transformation (Guy 1989, Mapaire 2001, Chafota and Owen-Smith 2009) in African savanna ecosystems. It is critical to thoroughly understand the ecological consequences of fire and elephants for decision makers to effectively manage biodiversity in a region that is increasingly threatened by anthropogenic disturbances. Large vegetated termitaria are a potential indicator of the impacts of fire and megaherbivores as they support a different suite of vegetation and appear to be less affected by burning compared to the surrounding matrix.

With the absence of large trees supported by termitaria, it is likely that Chizarira would experience a decline in arboreal reptilian species which represent 30% of species and 16% of the total reptilian abundance in this study. If the park managers exclude fire entirely, a similar fate would face terrestrial lizards, impacting nearly 58% of species present at Chizarira which contributed 84% of the total abundance. Frequent fires of anthropogenic origin observed throughout the duration of this study may have consequences for burrowing reptiles or grassland species and affect 23% of the species. Because herpetofauna are an important prey base for raptors and small carnivorous mammals, reptile population declines have potential to negatively impact other taxa. Reptilian species show a distinct and fine scale pattern of habitat selection in the patch mosaic created by termitaria, fire and elephants. This study provides baseline data that will be valuable for continued monitoring of biodiversity at Chizarira National Park.

Literature Cited

- Avery, R.A. 1979. Lizards -A study of thermoregulation. Studies in Biology 109. London.
- Braithwaite, R.W. 1987. Effects of fire regimes on lizards in the wet-dry tropics of Australia. *Journal of Tropical Ecology* 3(3): 265-275.
- Branch, B. 1998. Field Guide to snakes and other reptiles of southern Africa. Cape Town: Struik.
- Brown, G.W. 2001. The influence of habitat disturbance on reptiles in a Box-Ironbark eucalypt forest of south-eastern Australia. *Biodiversity and Conservation* 10: 161-176.
- Campbell, B., Frost, P. and Byron, N. 1996. Miombo woodlands and their use: overview and key issues. In: Campbell B. (ed), *The Miombo in Transition: Woodlands and Welfare in Africa*. CIFOR, Bogor, pp 1-10.
- Carruthers, V. 2001. Frogs and frogging in southern Africa. Cape Town: Struik.
- Certini, G. 2005. Effects of fire on properties of forest soils: a review. *Oecologia* 143: 1-10.
- Chafota, J. and Owen-Smith, N. 2009. Episodic severe damage to canopy trees by elephants: interactions with fire, frost and rain. *Journal of Tropical Ecology* 25: 341-345.
- Chidumayo, E.N., Gambiza, J. and Grundy, I. 1996. Managing miombo woodland. In: Campbell B. (ed), *The Miombo in Transition: Woodlands and Welfare in Africa*. CIFOR, Bogor, pp 175-194.
- Chidumayo, E.N. 1988. A re-assessment of effects of fire on miombo regeneration in the Zambian Copperbelt. *Journal of Tropical Ecology* 4: 361-372.
- Colli, G.R., Constantino and R., Costa, G.C. 2006. Lizards and termites revisited. *Australian Ecology* 31: 417-424.
- Cumming, D.H.M., Fenton, M.B., Rautenbach, I.D., Taylor, R.D., Cumming, G.S., Cumming, M.S., Dunlop, J.M., Ford, A.G., Havorka, M.D., Johnston, D.S., Kalcounis, M., Mahlangu, Z. and Portfors, C.V.R. 1997. Elephants, woodlands and biodiversity in southern Africa. *South African Journal of Science* 93: 231-236.
- Doan, T.M. 2003. Which methods are most effective for surveying rainforest herpetofauna? *Journal of herpetology* 37 (1): 72-81.
- Driscoll, D.A. and Henderson, M.K. 2008. How many common reptile species are fire specialists? A replicated natural experiment highlights the predictive weakness of a fire succession model. *Biological Conservation* 141: 460-471.

- Dufrene, M. and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345-366.
- Dunham, K.M. Mackie, C.S. Musemburi, O.C., Chipesi, D.M., Chiweshi, N.C., Taylor, R.D., Chimuti, T., Zhuwau, C. and Brightman, M.A.H. 2006. Aerial survey of elephants and other large herbivores in the Sebungwe Region, Zimbabwe, 2006. WWF-SARPO Occasional Paper No. 12 December, 2006, 90 pp. WWF-SARPO, Harare, Zimbabwe.
- Dunham, K.M. 2008. Detection of anthropogenic mortality in elephant *Loxodonta Africana* populations: a long-term study from the Sebungwe region of Zimbabwe. *Oryx* 42(1): 36-48.
- Fleming, P.A. and Loveridge J.P. 2003. Miombo woodland termite mounds: resource islands for small vertebrates? *Journal of Zoology*, London 259: 161-168.
- Frost, P.G.H. 1996. The ecology of miombo woodlands. Pages 11-57 in B.M. Campbell, editor. *The miombo in transition: woodlands and welfare in Africa*. Bogor, Indonesia, Centre for International Forestry Research (CIFOR).
- Gambiza, J., Bond, W., Frost, P.G.H. and Higgins, S. 2000. A simulation model of miombo woodland dynamics under different management regimes. *Ecological Economics*. 33: 353-368.
- Gardner, T.A., Barlow, J. and Peres, C.A. 2007. Paradox, presumption and pitfalls in conservation biology: The importance of habitat change for amphibians and reptiles. *Biological Conservation* 138: 166-179.
- Greenberg, C.H., Neary, D.G. and Harris, L.D. 1994. A comparison of herpetofaunal sampling effectiveness of pitfall, single-ended and double-ended funnel traps used with drift fences. *Journal of Herpetology* 28 (3): 319-324.
- Greenberg, C.H. 2001. Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. *Forest Ecology and Management* 148: 135-144.
- Guy, P.R. 1989. The influence of elephants and fire on a *Brachystegia-Julbernadia* woodland in Zimbabwe. *Journal of Tropical Ecology* 5: 215-226.
- Higgins, S.I., Bond, W.J. and Trollope, W.S.W. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88: 213-229.
- Holdo, R.M. 2003. Woody plant damage by African elephants in relation to leaf nutrients in western Zimbabwe. *Journal of Tropical Ecology* 19: 189-196.
- Holdo, R.M. and McDowell, L.R. 2004. Termite mounds as nutrient-rich food patches for elephants. *Biotropica* 36(2): 231-239.

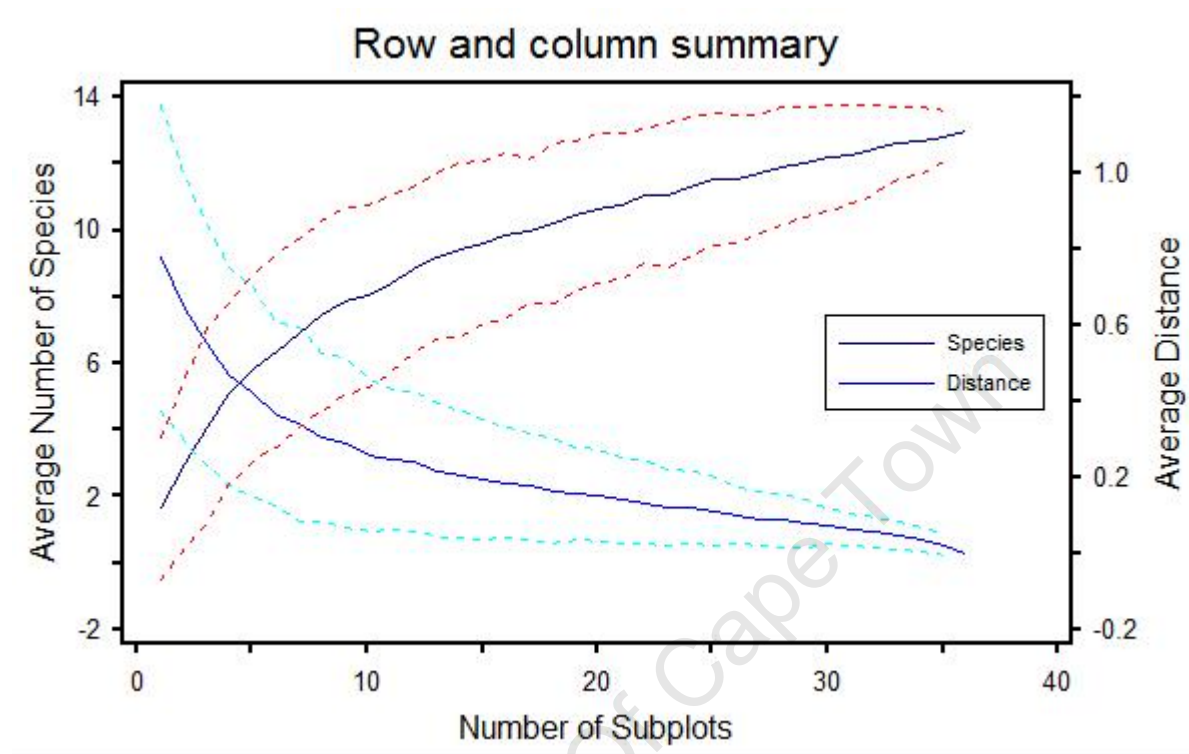
- Humphrey, G. 2008. Influence of large termitaria on species composition and tree height structure in a modified *Brachystegia/Julbernardia* miombo woodland in Chizarira National Park, Zimbabwe. MSc Conservation Biology. University of Cape Town
- Hutchinson, M.F., H.A. Nix, J.P. McMahon, and K.D. Ord. 1995. Topographic and Climate Database for Africa, Version 1.0. Centre for Resource and Environmental Studies, Australian National University, Canberra ACT 0200, Australia. <http://cres.anu.edu.au/outputs/africa.php>
- IUCN. 2006. Red list of threatened species 2006. International Union for the Conservation of Nature (IUCN). Gland, Switzerland. Available online www.iucn.org (accessed 13.01.10).
- Jones, C.G., J.H. Lawton and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69: 373-386.
- Joseph, G.S. 2008. Large termitaria provide refugia for cavity-using birds in a modified miombo woodland system. MSc Conservation Biology. University of Cape Town.
- Kikula, I.S. 1986. The influence of fire on the composition of miombo woodland of Southwest Tanzania. *Oikos* 46: 317-324.
- Kruskal, J.B. 1964. Nonmetric Multidimensional Scaling: a numerical method. *Psychometrika* 29: 115-129.
- Lawler, J.J., White, D., Sifneos and J.C., Master, L.I. 2003. Rare species and the use of indicator groups for conservation planning. *Conservation Biology* 17(3): 875-882.
- Lawton, R.M. 1978. A study of the dynamic ecology of Zambian vegetation. *Journal of Ecology* 66: 175-198.
- Legge, S., Murphy, S., Heathcoate, J., Flaxman, E., Augusteyn, J. and Crossman, M. 2008. The short-term effects of an extensive and high-intensity fire on vertebrates in the tropical savannas of the central Kimberley, northern Australia. *Wildlife Research* 35: 33-43.
- Levick, S.R., Asner, G.P., Kennedu-Bowdoin, T. and Knapp, D.E. 2009. The relative influence of fire and herbivory on savanna three-dimensional vegetation structure. *Biological Conservation* 142 (8): 1693-1700.
- Lindenmayer, D.B., Wood, J.T., MasGregor, C., Michael, D.R., Cunningham, R.B., Crane, M., Montague-Drake, R., Brown, D., Muntz, R. and Driscoll, D.A. 2008. How predictable are reptile responses to wildfire? *Oikos* 117: 1086-1097.
- Loveridge, J.P. and Moe, S.R. 2004. Termitaria as browsing hotspots for African megaherbivores in miombo woodland. *Journal of Tropical Ecology* 20: 337-343.

- Malaisse, F. 1978. High Termitaria, biogeography and ecology of Southern Africa. Vol 2: The Hague, Junk. pp 1279-1300.
- Mapaure, I. 2001. Small-scale variations in species composition of miombo woodland in Sengwa, Zimbabwe: The influence of edaphic factors, fire and elephant herbivory. *Systematics and Geography of Plants* 71(2): 935-947.
- Mapaure, I., and B.M. Campbell. 2002. Changes in miombo woodland cover in and around Sengwa Wildlife Research Area, Zimbabwe, in relation to elephants and fire. *African Journal of Ecology* 40(3): 212-219.
- Mather, P.M. 1976. Computational methods of multivariate analysis in physical geography. J. Wiley & Sons, London. 532 pp.
- McCune, B. and Grace, J.B. 2002. Analysis of Ecological Communities. Mjm Software Design, Gleneden Beach, Oregon, USA.
- McCune, B. and Mefford, M.J. 2006. PC-ORD. Multivariate Analysis of Ecological Data. Version 5. mjm Software, Gleneden Beach, Oregon, USA.
- Mielke, P.W., Jr. 1984. Meteorological applications of permutation techniques based on distance functions. Pp. 813-830. In P.R. Krishnaiah & P.K. Sen, eds., *Handbook of Statistics*, Vol. 4. Elsevier Science Publishers.
- Mittermeier, R.A., Mittermeier, C.G., Brooks, T.M., Pilgrim, J.D. Konstant, W.R., da Fonseca, G.A.B. and Kormos, C. 2003. Wilderness and biodiversity conservation. *PNAS* 100: 10309-10313.
- Moseley, K.R., Castleberry, S.B. and Schweitzer, S.H. 2003. Effects of prescribed fire on herpetofauna in bottomland hardwood forests. *Southeastern Naturalist* 2(4): 475-486.
- Pianka, E.R. 1973. The structure of lizard communities. *Annual Review of Ecological Systems* 4: 53-79.
- Pianka, E.R. 2000. *Evolutionary Ecology*. Addison Westley Longman Inc., San Francisco.
- Raxworthy, C.J. and Attquayefio, D.K. 2000. Herpetofaunal communities at Muni Lagoon in Ghana. *Biodiversity and Conservation* 9: 501-510.
- Rios-Lopez, N. and Aide, T.M. 2007. Herpetofaunal dynamics during secondary succession. *Herpetologica* 63 (1): 35-50.
- Rodgers, A., Salehe, J. and Howard G. 1996. The biodiversity of miombo woodlands. In: Campbell B. (ed), *The Miombo in Transition: Woodlands and Welfare in Africa*. CIFOR, Bogor, pp 12.

- Russell, K.R., Van Lear, D.H. and Guynn Jr., D.C. 1999. Prescribed fire effects on herpetofauna: review and management implications. *Wildlife Society Bulletin* 27(2): 374-384.
- Ryan, T.J., Phillippi, T., Leiden Y.A., Dorcas, M.E., Wigley, T.B. and Gibbons, J.W. 2002. Monitoring herpetofauna in a managed forest landscape: effects of habitat types and census techniques. *Forest Ecology and Management* 167: 83-90.
- Sileshi, G. and Mafongoya, P.L. 2006. The short-term impact of forest fire on soil invertebrates in the miombo. *Biodiversity and Conservation* 15: 3153-3160.
- Simbotwe, M.P. and Garber, S.D. 1979. Feeding habits of lizards in the genera *Mabuya*, *Agama*, *Ichnotropis* and *Lygodactylus* in Zambia, Africa. *Transactions of the Kansas Academy of Science* 82 (1): 55-59.
- StatSoft, Inc. 2007. Statistica (data analysis software system), version 8.0. www.statsoft.com
- Thomson, P.J. 1974. The role of elephants, and fire and other agents in the decline of *Brachystegia boehmi* woodland. *Journal of Southern African Wildlife Management Ass.* 5(1): 11-18.
- Trollope, W.S.W. 1982. Ecological effects of fire in South African savannas. *Ecology of Tropical Savannas* (eds B.J. Huntly & B.H. Walker), pp. 292-306. Springer-Verlag, Berlin, Germany.
- Valentine, L.E. and Schwarzkopf. 2008. Effects of weed-management burning on reptile assemblages in Australian tropical savannas. *Conservation Biology* 23(1): 103-113.
- Vallan, D. 2000. Influence of forest fragmentation on amphibian diversity in the nature reserve of Ambohitantely, highland Madagascar. *Biological Conservation* 96: 31-4
- Webb, G.A. 1999. Effectiveness of pitfall/drift-fence systems for sampling small ground-dwelling lizards and frogs in southern Australian forests. *Australian Zoologist* 31 (1): 118-126.
- Woinarski, J.C.Z., Brock, C., Fisher, A., Milne, D. and Oliver, B. 1999. Response of birds and reptiles to fire regimes on pastoral land in the Victoria District, Northern Territory. *The Rangeland Journal* 21: 24-38.
- Zolho, R. 2005. Effect of fire frequency on the regeneration of miombo woodland in Nhambita, Mozambique. MSc. University of Edinburgh.

Appendices

Appendix 1. Species Accumulation Curve (PC-ORD v 5.0)



13.0 = Number of species observed

17.9 = First-order jackknife estimate

22.6 = Second-order jackknife estimate

Appendix 2. Common tree species with > 6 cm basal diameter

Matrix species

Colophospermum mopane
Xeroderris stuhlmanni

Mound species

Berchemia discolor
Cassia abbreviata
Capparis tomentosa
Colophospermum mopane
Combretum hereroense
Diospyros quiloensis
Lanea schweinfurthii
Manilkara mochisia
Strychnos potatorum

University Of Cape Town

Appendix 3. Common tree species <6 m

Matrix species

Brachystegia boehmii
Catunaregum spinosa
Colophospermum mopane
Combretum apiculatum
Combretum collinum
Combretum molle
Combretum zeyheri
Crossopteryx febrifuga
Diospyros kirkii
Euclea divinorum
Julbernardia globiflora
Pericopsis angolensis
Pseudolachnostylis maprouneifolia
Terminalia sericea
Terminalia stenostachya
Xeroderris stuhlmannii

Mound species

Acacia nilotica
Capparis tomentosa
Cassia abbreviata
Combretum mossambicensis
Diospyros quiloensis
Erythroxylem zambesiacum
Euclea divinorum
Feretia aeruginescens
Flueggea virosa
Lannaea schweinfurthii
Lannea stuhlmannii
Manilkara mochisia
Strychnos potatorum
Terminalia stenostachya
Ximenia americana