Modelling of the response of sable antelope (*Hippotragus niger niger*) to trophy hunting: A GIS and remote sensing approach

By

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Dedication

This thesis is dedicated to the three most important people in my life. All continue to play a unique but large part in my life.

To my wife Pertunia for your patience and support, you have always been there for me.
To my daughters Michelle Natalie and Brielle Yaretzi for the long days I was never there to see you grow to be the beautiful little ‘angels’ you are today.

Declaration 1: Originality

By submitting this Master of Philosophy thesis to the University of Zimbabwe, I declare that the entirety of the work contained therein is my original work and that I have not previously in its entirety or in part submitted it for obtaining any qualification. I further declare that all sources cited or quoted are indicated by means of a comprehensive list of references.

Ndaimani Henry

Declaration 2: Publication

Details that form part and/ or include research presented in this thesis include publications in preparation, submitted, in pres and published and give details of the contributions of each author to the experimental work and writing of each publication.

Publication 1: Ndaimani H[1], Murwira A[2] and Kativu S[3](2013) *Comparing terrain and vegetation-based visibility for explaining sable flight behaviour in a Southern African savanna.* Geocarto International **28**(2): 130-143

This work was done by the first author under the guidance and supervision of the second and third authors.

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Publication accepted and in press 2: Ndaimani H[1], Murwira A[2] and Kativu S[3]
(In review at Geocarto International Journal) *Predicting the spatial distribution of hunted and non-hunted sable antelope (Hippotragus niger niger) using remotely sensed woody cover in a Southern African savanna.*

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Certification by supervisor Dr A Murwira…………………………………………………….

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Abstract

The main objective of this study was to test the impact of hunting on sable (*Hippotragus niger niger*) habitat selection using a combination of satellite remotely sensed data and GIS based spatial analysis. Firstly, we used remotely sensed vegetation cover estimated by the normalised difference vegetation index (NDVI) to test whether hunted sables selected more closed woodland habitats, i.e., an uncharacteristic habitat for sable, while those not exposed to hunting selected more open woodland habitats, i.e., characteristic habitat for sable. Secondly, we tested whether terrain based visibility modelled from remotely sensed data explains sable Flight Initiation Distance (FID), an indicator of fearfulness in hunted animal species, better than vegetation based visibility measured in the field. We tested these hypotheses in a study area consisting of one hunting area and one non-hunting area of north-western Zimbabwe. Our results show that hunted sables significantly ($P < 0.05$) selected more closed woodland than those not exposed to hunting. Our results also show that remotely sensed Advanced Spaceborne Thermal Emission and Reflection Radiometer Digital Elevation Model (ASTER DEM) derived visibility could explain FID of sable better than field measured vegetation based visibility. Results of this thesis open new ground in spatial ecological understanding of wildlife species such as the threatened sable antelope.

List of acronyms

ANCOVA	Analysis of Covariance
ASTER	Advanced Spaceborne Thermal Emission and Reflection Radiometer
AUC	Area Under Curve
DEM	Digital Elevation Model
FID	Flight Initiation Distance
GIS	Geographic Information Systems
GPS	Global Positioning System
MODIS	Moderate Resolution Imaging Spectroradiometer
NDVI	Normalised Difference Vegetation Index
ROC	Receiver Operating Characteristic
SPSS	Statistical Package for the Social Sciences
SRTM	Shuttle Radar Topography Mission
ZPWMA	Zimbabwe Parks and Wildlife Management Authority

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Chapter 1: General introduction

1.1 Introduction

Regulated trophy hunting of wildlife such as sable antelope (*Hippotragus niger niger*) has been identified as a major driving force for its conservation (Duriez, Eraud et al. 2005) in Southern Africa as it provides the funding needed for conservation. However, whether regulated trophy hunting promotes conservation of the target species or not is a critical question as hunting has been associated with species extinction in Africa and elsewhere in the world (Grignolio, Merli et al. 2011). For example, it is known that hunting contributed to reductions in the populations of dorcas gazelle (*Gazella dorcas*) and total extirpation of the Nubian bustard (*Neotis nuba*) in the Sahel region of Africa (Newby 1990). It is important to focus on sable antelope because it is generally considered endangered in most parts of Southern Africa(Skinner, Fairall et al. 1977; Harrington, Owen-Smith et al. 1999; Pitra, Hansen et al. 2002; Ogutu and Owen-Smith 2003) owing to continued population decline that has mainly been attributed to overhunting (Ginsberg and Milner-Gulland 1994). Therefore, the continued success of trophy hunting as a conservation strategy relies mainly on our understanding of the factors that not only directly but also indirectly indicate the existence of hunting pressure on the hunted species.

In order to develop stress indicators in hunted animals, there is need to understand how animals that are subjected to hunting react. For instance, animals subjected to hunting are expected to either change habitats as a hunter avoidance strategy or engage in behaviour that minimises contact with hunters such as initiating flight earlier than normal in the face of approaching hunters. An understanding of such shifts in sable habitat choice and behaviour will help to establish whether and to what extent sables are under threat of hunting pressure.

Sables are grazers hence they are known to select open woodland habitats in landscapes where hunting levels are non-existent or even negligible (Wilson and Hirst 1977; Perez-Barberia, Gordon et al. 2001; Jenkins, Corti et al. 2002). Open woodland habitats are associated with high grass biomass thus provide the sable with ideal conditions for maximum foraging while scattered trees provide shade during warmer hours of the day (Fischer, Zerger et al. 2010). Although the typical habitat for sables is well documented (Gagnon and Chew 2000; Macandza, Owen-Smith et al. 2012), the amount of vegetation cover they select in the face of hunting risk remains largely unknown. However, our understanding of how other animals select habitats in landscapes where hunting takes place may help to generate hypotheses for use in predicting sable habitat selection in similar landscapes. Observations made in hunting areas show that animals select habitats they would not normally select in landscapes where hunting levels are low (Kilgo, Labisky et al. 1998; Tchabovsky, Krasnov et al. 2001). For instance, wildebeest studied in hunting areas have been shown to select tall grass habitats instead of short grass habitats they typically select in undisturbed landscapes as a strategy for hunter avoidance (Tambling and Du Toit 2005). Similar responses have been recorded in impala (Setsaas, Holmern et al. 2007) and avifauna (Newberry and Shackleton 1997; Bregnballe, Madsen et al. 2004; Casazza, Coates et al. 2012) among many other animal species. These studies all suggest a possible shift in the habitat selected by the hunted animals as a strategy for hunter avoidance. However, how a species shifts from its typical habitat when confronted with the risk of hunting is expected to differ from the next species. Some species may select more closed woodland habitat (Davidson, Valeix et al. 2011; Grignolio, Merli et al. 2011) while others select open habitats (Schmidt, Ver Hoef et al. 2007). Thus, knowing how sables select habitats in response to hunting pressure is critical for their conservation

In addition to understanding whether sables change habitat when hunted, the success of trophy hunting as a conservation strategy also depends on our understanding of stress levels in the hunted population (Olsson, Willebrand et al. 1996). In this regard, the development of metrics that quantify stress levels within hunted animal populations, particularly on a landscape scale, are central in studies that investigate potential indicators of overhunting of any wildlife species such as the sable antelope. Flight behaviour, particularly flight initiation distance (FID), is a well known and important indicator of stress levels in animals (de Boer, van Breukelen et al. 2004). For example, early flight is indicative of high stress levels, whereas delayed flight could indicate low stress, and is often associated with longer periods of energy acquisition through herbivory. However, good data on habitat factors explaining FID is important. Overall, flight is an important ecological process that determines chances of survival of prey in a landscape with predators. Thus, an objective quantification of FID, together with factors that relate to it, is an important precursor to the understanding of stress levels in a wildlife population.

Ecological hypotheses investigating the impact of hunting pressure on target species are best tested at large spatial extents. This allows for the measurement of predictor variables like habitat visibility within landscapes spanning large spatial extents without the need for extensive field work. As such, ready availability of satellite remotely sensed data in addition to other ancillary spatial data has seen a shift in habitat factor characterisation from field based measurements taken at particular points to ecological modelling covering larger landscapes. Applicability of satellite remotely sensed data in ecological modelling studies is well known. However, its use in studies testing how wildlife species such as sables respond to hunting remains largely rudimentary. Thus, testing whether satellite remotely sensed data, in addition to other ancillary data could be useful for understanding the response of sable to hunting is critical. This is more so when such hypotheses are tested in large landscapes where field data collection is time consuming and expensive.

1.2 Thesis objectives

The main objective of this thesis was to model sable response to hunting using a GIS based modelling approach that combines satellite remotely sensed data and field based sable data. Firstly, we tested whether hunted sables selected more closed woodland habitat (estimated by remote sensing derived NDVI) than those not hunted. Secondly, we tested whether terrain based visibility derived from the remotely sensed ASTER DEM explains the FID of sable better than vegetation based visibility measured in the field

1.3 Organisation of the thesis

This thesis is divided into five chapters;

Chapter 1 is an outline of the main objectives and hypotheses pursued in this study. The chapter also provides a background to the importance of vegetation cover in sable habitat studies within hunting landscapes. It further explores the role of terrain and vegetation based visibility in explaining the FID of sables.

Chapter 2 outlines the materials and methods used to answer our hypotheses. The chapter explains how we used a two factor logistic regression analysis to predict the probability of sable occurrence within our study sites. Moreover the chapter details the ANCOVA analysis used to test the importance of remotely sensed terrain based visibility as a predictor for sable FID.

Chapter 3 is a presentation of results of the comparison of sable probability of occurrence predicted by woody cover between the hunting and non-hunting study sites, as well as the relationship between remotely sensed woody cover and NDVI. A discussion of the results concludes the chapter.

Chapter 4 presents results on the comparison of terrain and vegetation based visibility for explaining sable flight behaviour in both study sites. The chapter further provides a discussion of the results.

Chapter 5 is a synthesis and general discussion of the findings made in Chapter 4 and 5. In particular the chapter discusses findings on the comparison of sable habitat selection in the hunting and non-hunting area. It further provides a general discussion on whether and to what extent terrain based visibility could be used as a predictor for sable FID. The chapter ends by providing a general conclusion to the discussion.

Chapter 2: Materials and methods

2.1 The study area

The study was carried out in hunting and non-hunting areas of north-western Zimbabwe, between 25°30' - 26°30' longitude and 18°10'- 18°45' latitude (Figure 2.1). The study sites are ideal for testing our hypotheses since trophy hunting has been the sole land use in the hunting area for thirty seven years, whereas non-consumptive tourism has been the major land use in the non-hunting area over an equal length of time (PWMA 2000).

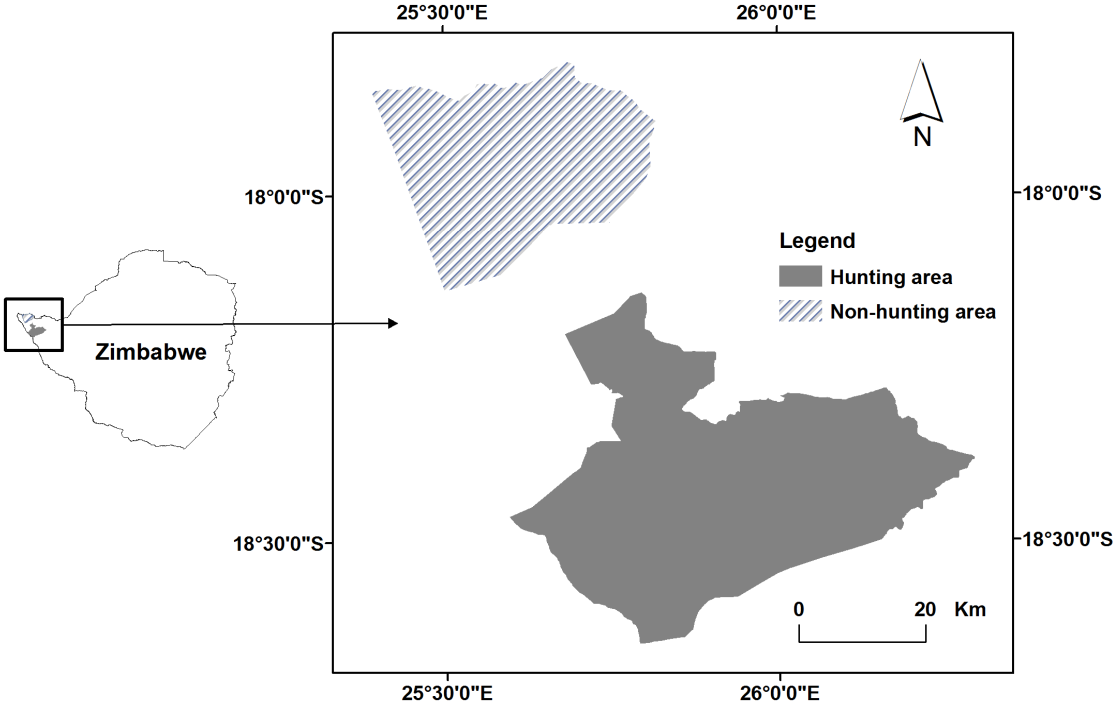

Figure 2.1 - Location of the study sites in Zimbabwe

The hunting area covers c. 2,000 km², while the non-hunting area covers c. 1000 km². The study sites are characterized by flat to gently undulating terrain between 600-1200 m above mean sea level in elevation. The climate is subtropical savannah with a mean annual rainfall of 650mm, most of it falling during a single rainy season between November and March

(Childes and Walker 1987). Mean monthly temperatures range between 32.5°C and 27.5°C in October and July respectively (Chenje, Sola et al. 1998). The main soil type in both study sites are lithosols and regosols developed on karoo volcanic and Kalahari hydrogeological formations respectively (Chenje, Sola et al. 1998). The major woody vegetation type on the regosols are dry early deciduous trees dominated by *Baikiaea plurijuga* which occurs in association with *Pterocarpus angolensis* and *Guibortia coleosperma* (Chenje, Sola et al. 1998), while *Colophospermum mopane* and *Terminalia sp*, dominate the lithosols (Chamaille-Jammes, Fritz et al. 2006).

2.2 Sable presence/absence data

Data on sable presence/absence were collected at 120 randomly selected sample sites located in both the hunting and non-hunting area. Of the total 120 sample sites, 79 were selected in the hunting area while 41 were visited in the non hunting area. The number of sampling sites allocated in each study site depended on the total surface area of the site. The hunting area was about double the size of non-hunting area hence the number of sampling points allocated in the hunting area was about double that of the non-hunting area. Selection of sampling sites was done in a GIS using the random point generating tool.

We collected sable presence/absence data in September 2010 since the month records most hunts and thus represents the period of peak hunting. It is expected that September is the month when sable response to hunting is most profound. Thus, the choice of September facilitated the evaluation of the effect of hunting on sable habitat selection.

A hand-held Global Positioning System (GPS) receiver was used to navigate to each randomly selected point. At each random site, a plot measuring 250 by 250 metres was then marked with the point being the centre of the plot. The plot size used in this protocol coincides with the spatial resolution of the MODIS satellite imagery used in the calculation of NDVI. Sable presence was recorded where evidence of sable was observed whereas absence was recorded where no evidence of sable existed in the plot. In each plot, observers searched for sable evidence in strips of width 2 metres in order to ensure that every part of the plot was covered. Each time, the same observes were used so as to minimise variations in observations associated with the use of different observers.

Presence was recorded in a plot if sable spoor or droppings were seen. Sable droppings were identified based on the knowledge of park rangers and where necessary cross-confirmation with samples collected from dead animals was done. In no circumstance did we come across live sables in any of the plots although we saw some on our way to and from the plots. These live sable sightings were ignored in our analysis since they were not part of our random sampling procedure. Therefore it should be emphasised that in this study sable spoors and droppings were used as proxies for sable presence since real presence was never detected. Sixteen presence and 25 absence locations were recorded in the non-hunting area whereas 37 presence and 42 absence locations were recorded in the hunting area.

2.3 Remote sensing of woody cover

We used a MODIS based NDVI as a proxy for vegetation cover. A MODIS based NDVI was used since MODIS imagery is offered at a moderate spatial resolution of 250m which is several times smaller than the sable home range size of about 890 ha (Wilson and Hirst 1977). In addition MODIS imagery is made freely available via http://ladsweb.nascom.nasa.gov/). In general the spatial resolution of the imagery used must be of a size several times smaller than the home range of the animal under study (Murwira and Skidmore 2005). In this case the MODIS spatial resolution of 250m is about 142 times smaller than sable typical home range sizes in African savannas. Measurements of NDVI and woody cover obtained at 14 randomly selected points on satellite imagery were correlated in order to establish the nature of the relationship between the two variables. Random points were created using the random point generator function within a GIS. The random point generator tool generates spatially explicit random points within selected themes. The MODIS image used to calculate NDVI was acquired in September 2010 to coincide with the time when we collected sable presence/absence data.

Next, we needed to test whether and to what extent NDVI is related with tree crown cover. In doing this, we assumed that areas with dense tree crown cover would reduce the field of view of the sable thus putting it to more risk of death through hunting. For this we followed several steps. First, tree crowns were digitized in Google Earth (http://earth.google.com)(Knorn, Rabe et al. 2009) within 14 randomly selected plots measuring 250m by 250m . In digitising tree crowns in Google Earth, we tried as much as possible to exclude tree crown shadows which normally result from the fact that images are taken at times when the sun is not overhead.

The plot size was selected to match the spatial resolution of the MODIS image used in the calculation of NDVI. Second, the digitized crowns were imported into a GIS in order to calculate the total area covered by tree crowns. Third, the total area covered by crowns was calculated in a GIS using the area calculation algorithm. NDVI values at each plot centre were later extracted using the cross function of overlay analysis in a GIS. The cross function compares values found at pixels occupying the same locations in space from two input maps, and in this case, the NDVI and the percentage crown area maps were the two input maps. Finally, the relationship between percentage tree crown area and NDVI was established using regression analysis. The significance of the regression models was tested at alpha equal 0.05

2.4 Comparison of the hunting and non-hunting area

To ensure that variations in habitat selection and flight behaviour of sables between the hunting and non-hunting area were not a result of differences in the biophysical environment between both sites, we performed a comparison of NDVI in both sites. We also compared sable densities in the study sites. NDVI was first calculated based on a MODIS image acquired in September 2010. NDVI values were then extracted for every pixel occurring in both study sites. The 95% confidence interval of NDVI within each site was then compared and where overlap was detected, we concluded that the NDVI values for both sites were the same. A similar comparison of confidence intervals between both study sites was also done for sable densities calculated using Distance 5 software (Buckland, Anderson et al. 1993). The Distance Sampling analysis used in this study follows the example in Valeix *et al.* (2007). Since we found no significant difference in NDVI and sable density between the hunting and non-hunting area, we assumed that conditions prevailing in both study sites could be similar.

2.5 Modelling the probability of sable presence in the hunting and non-hunting area

The probability of sable occurrence in both study sites was estimated using a two factor logistic regression. Sable presence/absence was used as the response variable while NDVI and site were used as the predictor variables. We used the global Moran’s I index to test for spatial autocorrelation in the NDVI values at the sites selected. Site was classified as either hunting or non-hunting area. Our reduced model comprised NDVI and site as the main effects while the maximal model had an added NDVI x site interaction. Thus we were able to compare the predictive ability of the interaction above and beyond the main effects. We later performed a stepwise regression analysis using the enter method in SPSS 13.0 (2004).

Selection of the best model was done based on the following criteria: the -2 Log likelihood value, variability of the response variable explained by the explanatory variables (estimated by the Nagelkerke R^2) and the model's predictive power evaluated by the receiver operating characteristic (ROC) area under the curve (AUC) measure. Models with AUC values closer to 1 have close to perfect discrimination ability while those with values closer to 0.5 have discrimination ability no better than random. Classification tables displaying the number of correct and incorrect predictions made for the current data set, using a selected cutoff value of 0.5 were also presented. The classification results were calculated based on the data points used for modelling since the sample size could not allow setting aside of a sample set for testing the predictive power of the final model. For this reason, the classification tables are presented for the purpose of describing the model. The nature of relationship between sable probability of presence and the explanatory variables was determined using EXP (B). The relationship is positive when Exp (B) > 1 and negative when Exp (B) lies between 0 and 1. Exp (B) represents the odds associated with a unit change in the value of the predictor variables.

2.6 Sable FID data

Data on the FID of sables were collected along five road-transects in the hunting area and two in the non-hunting area. The road-transects averaged (± CL at 95% confidence level) 76.11±10.38 km in length and were covered by the same vehicle to minimise the confounding effect of vehicle type on sable flight behaviour. We collected data on FID in 2008 and 2010, during the peak of the hunting season in September so as to take account of the effect of hunting on the flight behaviour of the target species.

When a sable herd or a single sable was sighted, we stopped the car and turned off the engine immediately (Setsaas, Holmern et al. 2007). An observer then carefully opened the car door, and started to approach the sables in a direct line at a constant speed of 1 step per second following the method of (Fernández-Juricic and Schroeder 2003), simulating a hunter approach. To ensure consistency in approach speed, the observer was trained to 95% accuracy before starting data collection. When approaching a herd, the observer focused on a single individual identified before the approach approximately at the centre of the herd. Once the focal animal took flight, the approach was stopped and the distance between the observer's current position and the focal animal's position at the commencement of flight was measured using a rangefinder. Where necessary, the position of the focal animal was memorized from visual landscape signs according to the method by Wolf and Croft (2010). However, in cases where sables started running before the car moved into view, no FID measurements were taken, and such cases were not included in this analysis.

In order to minimise variations in measurements associated with the use of different observers, we used the same observer throughout the whole data collection protocol. We also made sure the observer continued wearing the same clothes following the method by Diego-Rasilla (2003). In addition, we minimised the potentially confounding effect of time of the day on sable flight behaviour by driving along transects at similar times (in the morning between 6 am and 10 am, and in the afternoon between 2 pm and 6 pm). More so, we avoided driving along the same transect within a period of less than five days in order to minimise habituation of sables to frequent disturbance.

2.7 Vegetation based visibility

We estimated vegetation based visibility by positioning an observer at the point where the focal sable stood before approach commenced during the FID measurement protocol. The observer maintained an eye level of 150 cm above ground, simulating a sable’s eye height (Estes 1991). The observer used a calibrated stick of similar height in order to ensure consistency in eye height. Another person then walked away from the observer in a straight line toward a random compass bearing until the stationary observer could no longer view them. At this point, the moving person was signalled to stop by whistling and the distance between the two people was measured using a rangefinder to the nearest meter. Three other measurements of similar nature were then taken in successive directions adding 90° to each previous bearing, and mean visibility was calculated for each point. The mean visibility represented openness of the habitat as estimated by the average distance the focal sable could see in all directions.

2.8 Terrain based visibility

The area that was visible to the focal sable (occupying the centre position in the herd) at each point was simulated using the Viewshed Analysis tool based on an ASTER Digital Elevation Model (DEM) at a nominal spatial resolution of 30 metres. The Viewshed analysis tool is a GIS based application which predicts the total area that is visible from an observation point based on a terrain model (Cooper 2005; Domingo-Santos, Fernández de Villarán et al. 2011). Since the sable’s region of sight is not limited, both in vertical and horizontal directions, we set the scan angles to obtain 180° vertical and 360° horizontal scan. We then used an offset value of 150 cm, corresponding to the average eye height of adult sables. More so, we limited the maximum search radius at 330 metres to coincide with the maximum non-outlier FID recorded for sable in this study. Figure 2.2 illustrates the results of viewshed analysis based on the already discussed parameters within the hunting area.

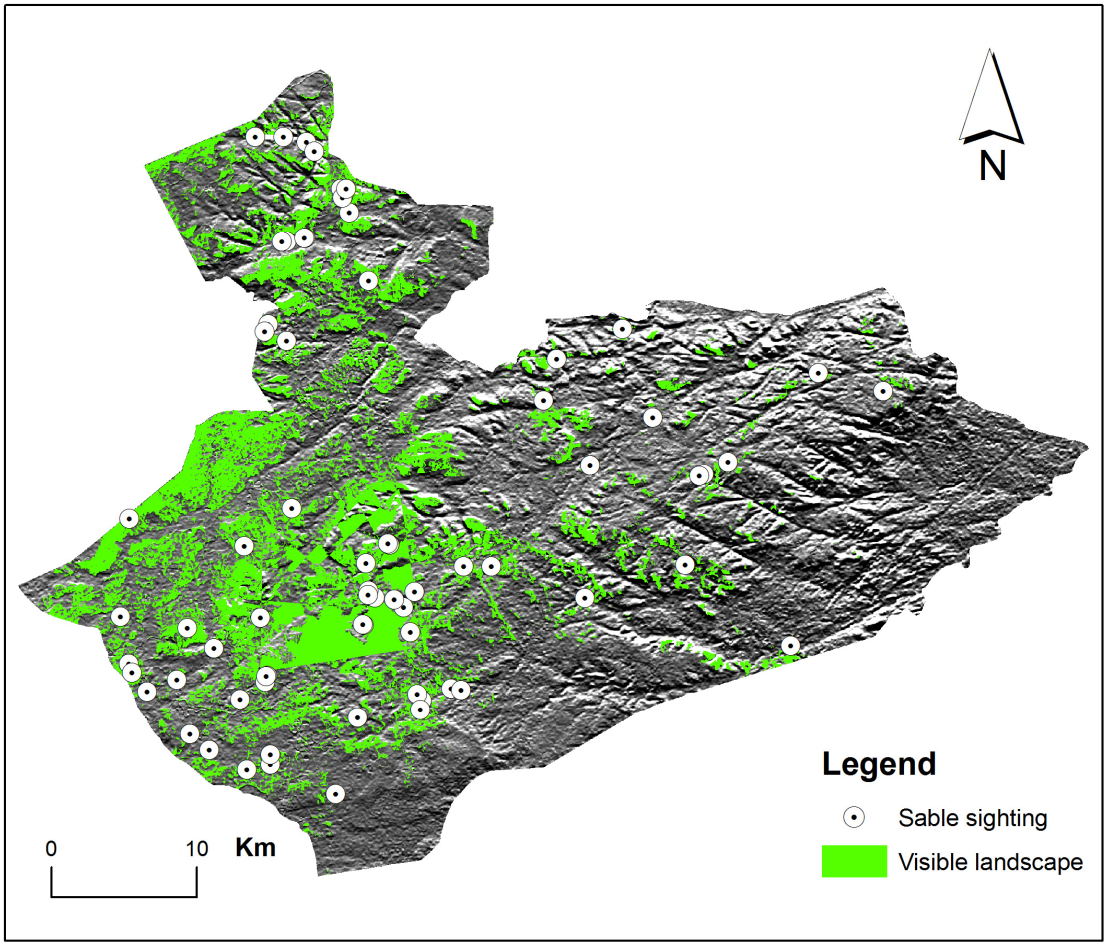

Figure 2.2 – Variation in sable viewshed in the hunting area (overlaid on a 3D terrain model)

2.9 Hunting pressure

To test the influence of hunting on sable flight behaviour, we compared models relating visibility to FID in both the hunting and non-hunting study sites. However, for the purpose of testing the influence of hunting pressure, we only considered sable sightings in the hunting area. First, we produced a point map of the locations where hunters killed or wounded any animal within a period of two weeks or less before the FID protocol was carried out. When considering a period of two weeks, we assumed that it is the maximum period within which the memory of a kill is still fresh in sables. Hence, any response to threat exhibited by sables within this time could be related to the kill. Second, we calculated the distance away from the kill location using the distance calculation algorithm in a GIS. Locations closer to the kills represented areas of high hunting pressure which decreases with increasing distance from the kill location (Figure 2.3). The median distance from the kill locations was used to divide the hunting area into high and low hunting pressure areas with those at a distance of less than the median being categorised as high hunting pressure areas. The sable locations recorded during measurement of FID were then overlaid on the distance map, and their distance from the nearest kill location extracted using overlay analysis in a GIS.

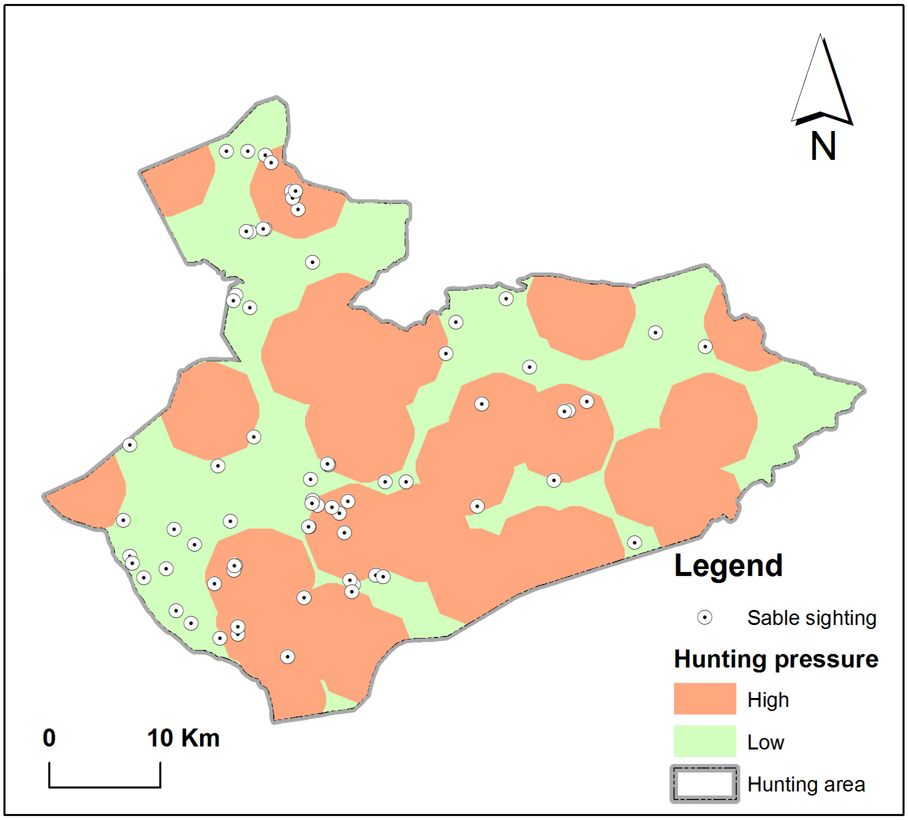

Figure 2.3 – Variation of hunting pressure in the hunting area (note that the distance from kill locations was used as a proxy of hunting pressure)

2.10 Comparison of vegetation and terrain based visibility as predictors of sable FID

We used linear regression modelling to investigate the nature of relationship between FID and both measures of visibility (vegetation and terrain based visibility). To test for the most important predictor of FID between both measures of visibility, we first standardised the measurements so that they varied within the same scale and later compared their coefficients. The variable with a larger coefficient thus represented the most important predictor of FID. We also compared the coefficients of determination (r^2) for both models where the variable with the larger r^2 explained more variance in FID and was thus the better predictor of FID. To further support this result, we also compared the Akaike Information Criteria values associated with inclusion of each of the predictor variables in the linear model. The AIC value of another linear model with standardised values of both measures of visibility was also used in the comparison. To establish contribution of the interaction of both measures of visibility over and above the main effects of vegetation and terrain based visibility, the AIC of the maximal model was also produced and compared to that of the reduced models.

We later used analysis of covariance (ANCOVA) to investigate whether hunting and hunting pressure influenced the relationship between both measures of visibility and FID. In addition, slopes of the relationships between visibility and FID densities were found to be statistically different if their confidence intervals did not overlap.

However, in all cases where linear regression modelling was used, we first tested whether the response variable did not significantly deviate from a normal distribution using both the Shapiro-Wilk test and the histogram method. Equality of variance was tested using the Levene’s test for homogeneity of variance while linearity was verified using visual inspection of the scatter plots relating the response and the predictor variables. Where the majority of the above conditions were met, we proceeded with linear modelling. Transformation of FID data was not necessary since it did not significantly deviate from a normal distribution.

Results and Discussion

Chapter 3: Predicting the spatial distribution of hunted and non-hunted sables using remotely sensed woody cover

3.1 Results

Our results show a significant exponential relationship (F = 28.107, df 1 = 1, df 2 = 12, R^2 = 0.701, $p<0.001$, SEE =0.347) between NDVI and percentage tree crown area (Figure 3.1). For this reason, NDVI was used as a proxy for woody cover subsequent analyses.

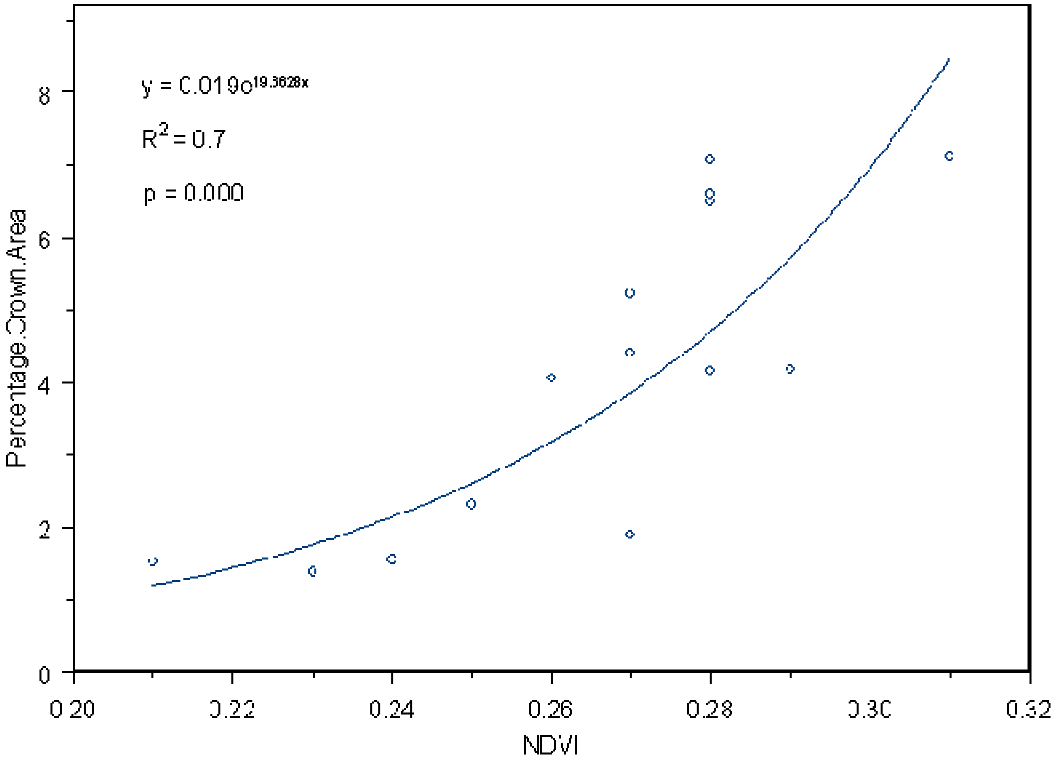

Figure 3.1 - Significant exponential relationship between percentage tree canopy area and NDVI (n = 14).

Results of our analysis also show that there was no significant difference in mean NDVI between the hunting (0.452) and non-hunting area (0.489) (Figure 3.2 (a)). The 95%

confidence interval of NDVI for the hunting area was (0.360; 0.522) while that for the non-hunting was (0.394; 0.574). Overlap of NDVI values for both study sites is also illustrated by the overlapping distribution histograms (Figure 3.2 (b)). We also observed an overlap (Figure 3.2 (c)) in the density of sable in both the hunting and non-hunting area (hunting area; density = 1.844 and 95% confidence interval (0.591; 5.753), non-hunting area; density = 1.545 and 95% confidence interval (0.331; 7.214).

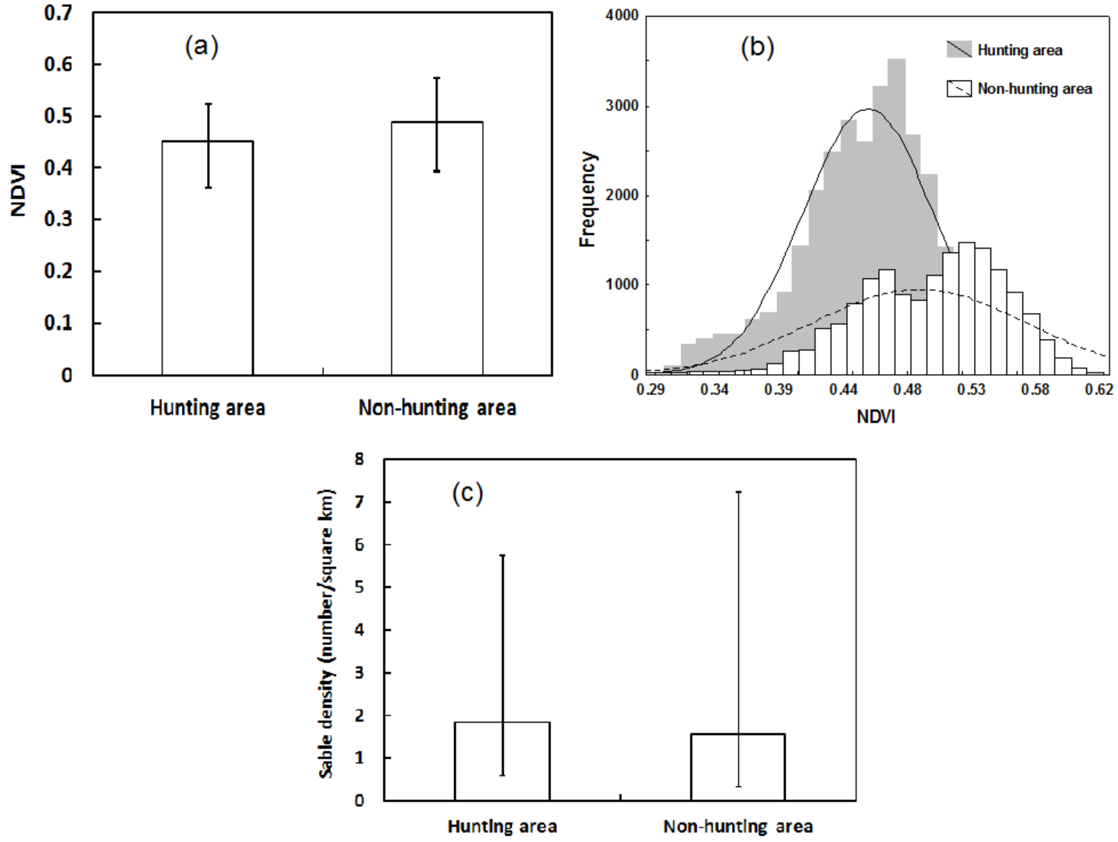

Figure 3.2 - Comparison of (a) mean NDVI, (b) NDVI distribution histograms and (c) sable density between the non-hunting and hunting area.

Spatial data analysis showed lack of spatial autocorrelation in NDVI at sites where sable presence/absence was recorded, both in the hunting (global Moran's I = 0.04, Z = 0.63, p>0.05) and non-hunting area (global Moran's I = 0.04, Z = 0.63, p>0.05).

In both study sites, 120 site visits were made. Seventy nine sites were visited in the hunting area while 41 were visited in the non-hunting area. Sixteen presence and 25 absence locations were recorded in the non-hunting area whereas 37 presence and 42 absence locations were recorded in the hunting area. In this study, sable spoors and pellets were used as proxies for sable presence. Mean NDVI in the hunting area was 0.16 +/- 0.06 (mean +/- SD) while in the non-hunting area it was NDVI 0.19 +/- 0.07 (mean +/- SD).

Results for logistic regression show significant relationships between probability of sable presence and NDVI in both the hunting (Wald = 8.971, $p<0.05$) and non hunting area (Wald = 11.868, $p<0.05$) (Table 3.1). The relationship was positive in the hunting area (Exp (B) > 1) while negative in the non-hunting area (0 < Exp (B) < 1) (Figure 3.3).

Table 3.1 – Variables for the model relating sable probability of presence to tested predictors based on multi-factorial logistic regression

Variables	**Coefficient**	**Standard Error (SE).**	**Wald**	**df**	**P-value**	**Exp (B)**
Reference category: Non-hunting area						
NDVI	-59.822	19.973	8.971	1	0.003	1.05 E - 26
SITE	-24.419	5.611	18.937	1	0.000	2.48 E - 11
SITE:NDVI	134.553	29.487	20.822	1	0.000	2.73 E + 58
Constant	10.949	3.887	7.933	1	0.005	56891.77
Reference category: Hunting area						
NDVI	74.731	21.692	11.868	1	0.001	2.85 E + 32
SITE	24.419	5.611	18.937	1	0.000	4.03 E + 10
SITE: NDVI	134.553	29.487	20.822	1	0.000	3.67 E - 59
Constant	-13.470	4.047	11.080	1	0.001	1.41 E - 06

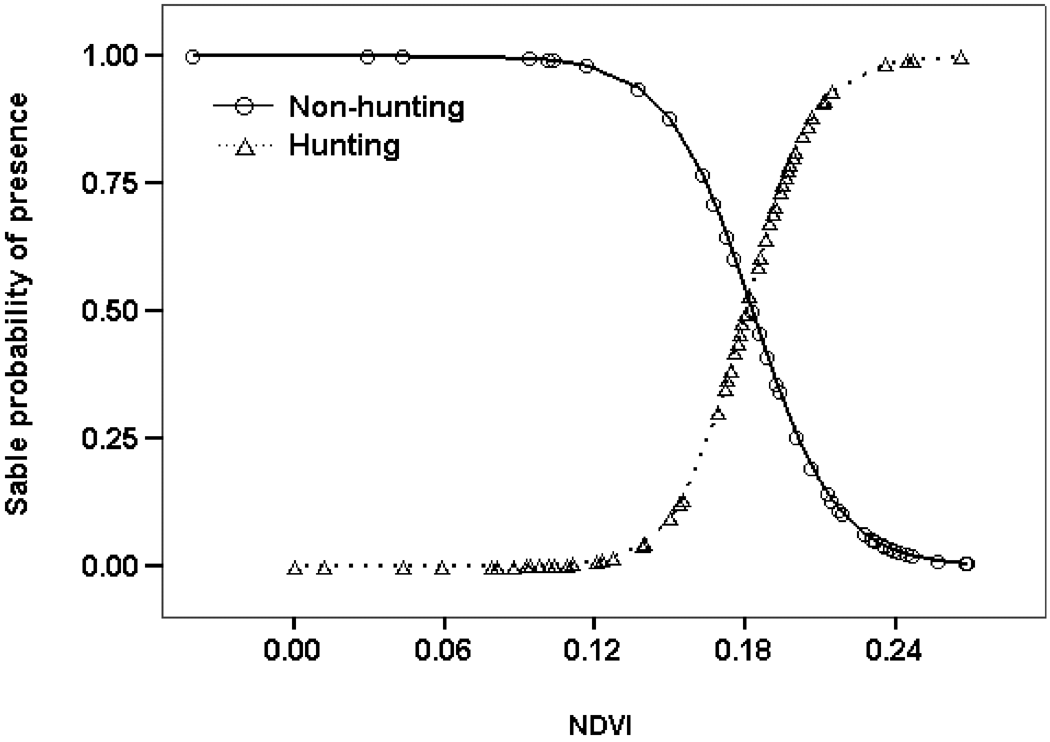

Figure 3.3 - Probability of sable presence as a function of NDVI in the non-hunting and hunting area based on the results of logistic regression (data points on curves are model-generated predictions of probability of sable presence)

The final logistic regression model had an overall classification success of 93.3%, misclassifying only four of 53 sites where evidence of sables was actually observed (Table 3.2). In addition, the model misclassified 4 of 67 sites where sables were actually recorded as absent. A Receiver Operating Characteristic (ROC) plot showed that Area Under Curve (AUC) was 0.949 (95% CI = 0.903; 0.995, SE = 0.023, p<0.001), indicating that the model was successful in predicting sable presence/absence (Figure 3.4). The addition of a site and NDVI interaction to a reduced model with site and NDVI as the only predictor variables increased the Nagelkerke R^2 from 0.03 to 0.67 at the same time reducing the -2 Log likelihood value by half from 162.15 to 81.94.

Table 3.2 - Predictive power of final logistic regression model (with all three predictors).

	Predicted		Percentage correct
	Absent	Present	
Logistic regression classification table			
Observed			
Absent	63	4	94.0
Present	4	49	92.5
Overall percentage			93.3

Note: cutoff value = 0.5

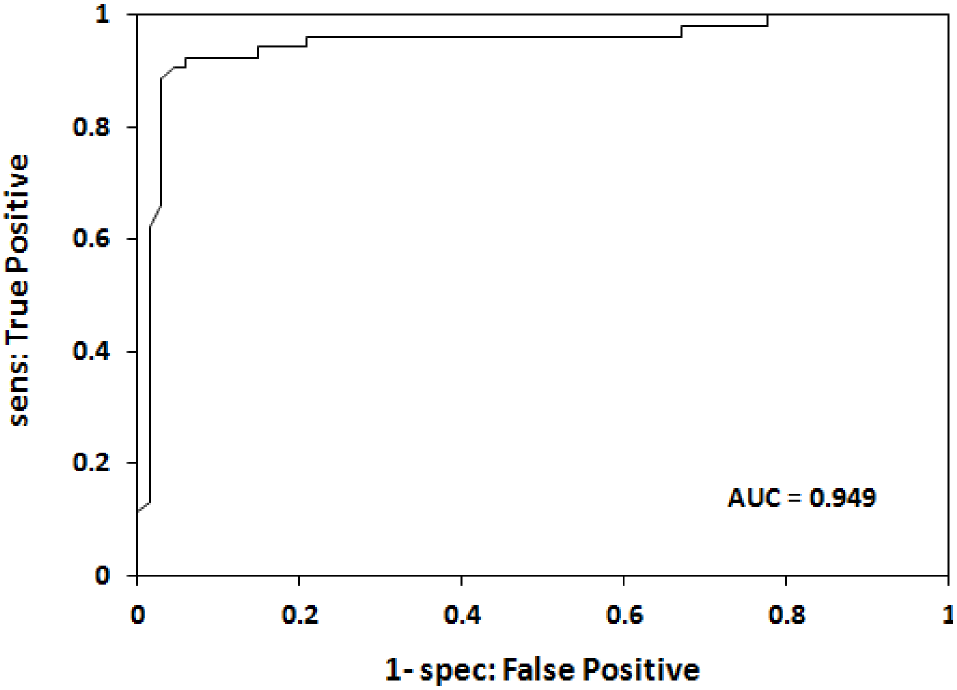

Figure 3.4 - Receiver Operating Characteristic plots for logistic regression models.

3.2 Discussion

Results of our study suggest that in savanna ecosystems and only during the dry season NDVI can be used as a proxy for tree canopy cover in studies testing how animals change cover types as a strategy for hunter avoidance. Several studies that test how animals make use of different vegetation cover types when confronted with the risk of hunting have used field measured vegetation cover (Setsaas, Holmern et al. 2007; Ndaimani, Murwira et al. 2012). Field based measurements of vegetation cover are often expensive, time consuming and limit observation to smaller landscapes. The freely available satellite data measuring vegetation vigour over large spatial extents like MODIS has made the establishment of empirical relationships possible. For instance the relationship between remote sensing derived vegetation indices and field measured tree cover is well known (Franklin, Davis et al. 1991; Carreiras, Pereira et al. 2006). However, the applicability of remote sensing derived vegetation indices as a proxy for ground vegetation cover in studies that test how hunted animals change habitats as a strategy for hunter evasion has mainly been untested especially in savanna landscapes. The fact that we could successfully test cover preference by hunted and un-hunted sable using remotely sensed vegetation cover validates the utility of remote sensing in wildlife ecology. To our knowledge, our results are among the first to emphasize application of the empirical relationship between NDVI and ground vegetation cover to explain how hunted animals switch habitats in the face of hunting threat.

Mean tree canopy cover was observed to be the same in both the hunting and non-hunting areas as depicted by similarity in NDVI. These results suggest that any differences in sable cover selection reported in this study are not confounded by differences in vegetation cover between the study sites. Similarly, a comparison of sable densities between the hunting and non-hunting area seem to suggest that the densities do not significantly differ between both study sites. We therefore assert that the observed differences in sable cover selection in both the hunting and non hunting area are not a result of differences in sable density. Although we have not compared all environmental variables existing in both study sites, these results confirm that both study sites are similar and any differences in sable habitat selection observed in our analysis could be attributed to the effect of hunting.

In this chapter, we tested whether sables facing the threat of hunting selected more closed woodland habitats than those in non-hunting areas. Our results suggest that in the hunting area sables selected habitats exhibiting closed tree canopy cover whereas in the non-hunting area they selected habitats with open tree canopy cover. This phenomenon can be explained by the fact that sables exposed to the risk of hunting tend to select closed vegetation cover as protection (Cassini and Galante 1992; Whittingham and Evans 2004; Wilson, Rayburn et al. 2012) against detection by hunters. Conversely since no hunting is permitted in the non-hunting areas, sables occurring there face limited risk of hunting therefore they select more open woodland. Open woodland is known to be typical sable habitat (Sekulic 1981; Gagnon and Chew 2000). The behaviour where hunted animals change habitats as a strategy for hunter evasion has also been observed in blue wildebeest (Tambling and Du Toit 2005), impala (Setsaas, Holmern et al. 2007), domestic fowl (Newberry and Shackleton 1997) and many other animals. However, up to now little has been known on how sables facing the risk of hunting may switch habitats. While this hunting risk driven change in habitat selection is well known for certain species (Isaac and Cowlishaw 2004), we make a claim that our study is amongst the first attempts to show that sables faced with the risk of hunting appear to select more closed habitats as a survival strategy.

Chapter 4: Comparing effectiveness of terrain and vegetation based visibility in explaining sable flight behaviour

4.1 Results

A total of 100 FID measurements were taken in both the hunting and non-hunting areas. Of these 100, seventy two were measured in the hunting areas while the other 28 were measured in the non-hunting area. Mean FID in the hunting area was found to be 164 +/- 155.2 (mean +/- SD) while in the non-hunting area it was found to be 120 +/- 120.5.

Linear regression modelling showed significant ($p < 0.01$) relationships between FID and standardized coefficients for both vegetation and terrain based visibility (Table 4.1). Vegetation based visibility explained 24% of the variance in FID ($F_{1,98} = 31.26$, SE = 8.07, adjusted $r^2 = 0.24$) whereas terrain based visibility explained 29% ($F_{1,98} = 40$, SE = 7.81, adjusted $r^2 = 0.29$).

Table 4.1 - Results of linear regression of FID as a function of the standardized coefficients of vegetation and terrain based visibility.

Parameter estimate	Vegetation	Terrain
β1	45.1114	49.3928
df	98	98
p	0.000	0.000
Multiple R^2	0.2419	0.2898

The reduced model with standardised vegetation based visibility as the sole predictor of FID produced an AIC value of 1165 while that with standardised terrain based visibility had an AIC value of 1158. Inclusion of both predictors in the linear model reduced the AIC value to

1135 while addition of an interaction of both predictors to the model with both predictors as the main effects further reduced AIC to 1131.

Vegetation based visibility significantly influenced FID in both the non-hunting ($p = 0.000$, $b = 2.34$, $df = 26$ and multiple $r^2 = 0.43$) and hunting area ($p = 0.000$, $b = 1.26$, $df = 70$ and multiple $r^2 = 0.16$). For both areas, the relationship between FID and vegetation based visibility was positive (Table 4.2 and Figure 4.1(a)). Similarly, there were significant positive relationships between FID and terrain based visibility in both the non-hunting ($p=0.000$, $b = 0.0010$, $df = 26$ and multiple $r^2 = 0.36$) and hunting area ($p=0.000$, $b = 0.0007$, $df = 70$ and multiple $r^2 = 0.28$) (Table 4.2 and Figure 4.1(c)).

Table 4.2 - Variables for the models predicting FID from vegetation and terrain based visibility in non-hunting and hunting areas based on ANCOVA

Visibility measure	Parameter estimate	Non-hunting area	Hunting area
Vegetation based visibility	Intercept	-12.6894	67.6628
	$\beta 1$	2.3404	1.2573
	F-statistic	19.31	13.68
	df	26	70
	p	0.000	0.000
	Multiple R^2	0.4262	0.1635
Terrain based visibility	Intercept	-84.4449	4.2405
	$\beta 2$	0.0010	0.0007
	F-statistic	14.68	27.74
	df	26	70
	p	0.000	0.000
	Multiple R^2	0.3608	0.2838

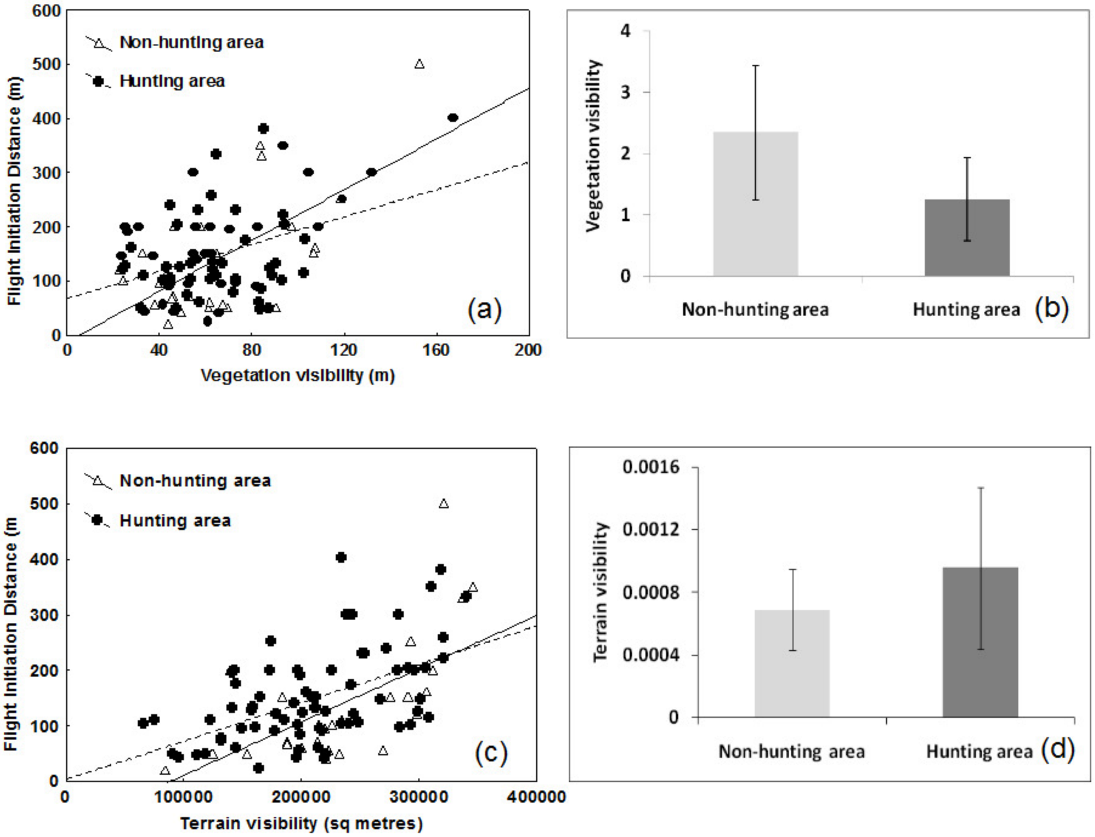

Figure 4.1 - Relationship of FID to vegetation based visibility in the hunting and non hunting area (a) no significant difference (p = 0.079) in the slope coefficients of vegetation based visibility in the hunting and non hunting area (b) Relationship of FID to terrain based visibility in the hunting and non hunting area (c) and no significant difference (p = 0.299) in the slope coefficients of terrain based visibility in the hunting and non hunting area (d).

The slopes of vegetation based visibility did not significantly ($p > 0.05$) differ between the non-hunting and hunting area (Figure 4.1(b)). The slope for the non hunting area was however steeper (b ± CL = 2.34 ± 1.10) than that of the hunting area (b ± CL =1.26 ± 0.68). We also found no significant ($p = 0.299$) difference in the slopes for terrain based visibility in both areas (Figure 4.1(d)). Terrain based visibility in the non-hunting area however, exhibited more influence on FID than in the hunting area (non-hunting area: *b* ± CL = 0.00096 ± 0.0052, hunting area: *b* ± CL = 0.00069 ± 0.0026).

Moreover, we observed that vegetation based visibility had a significant effect on FID in high hunting pressure areas ($p < 0.01$, $b = 1.664$, $df = 33$ and multiple $r^2 = 0.30$) whereas it exhibited no significant effect on FID in the low hunting pressure areas ($p = 0.231$, $b = 0.463$, $df = 35$ and multiple $r^2 = 0.04$) (Table 4.3 and Figure 4.2(a)). Furthermore, FID increased with increasing vegetation based visibility in both areas (Figure 4.2(a)).

Table 4.3 – Variables for the models predicting FID from vegetation and terrain based visibility in areas of low and high hunting pressure based on ANCOVA.

Visibility measure	Parameter estimate	Low hunting pressure	High hunting pressure
Vegetation based visibility	Intercept	83.5519	77.8606
	β1	0.4629	1.6642
	F-statistic	1.486	14.06
	df	35	33
	p	0.231	0.000
	Multiple R^2	0.04	0.299
Terrain based visibility	Intercept	59.2358	-19.4394
	β2	0.0003	0.0009
	F-statistic	3.974	23.64
	df	35	33
	p	0.102	0.000
	Multiple R^2	0.05404	0.4174

When analyzed in relation to hunting pressure variation in the hunting areas, terrain based visibility influenced FID in areas of high hunting pressure ($p <0.01$, $b =0.0009$, $df = 33$ and multiple $r^2 = 0.42$) while its influence in the low hunting pressure area was not significant ($p = 0.102$, $b = 0.0003$, $df = 35$ and multiple $r^2 = 0.05$). Long FIDs were observed in highly visible terrain areas in both areas (Figure 4.2(c)). Vegetation based visibility explained 30% and 4% of the variance in FID respectively, within the high and low hunting pressure areas (Table 4.3). Forty two percent of the variance in FID was explained by terrain based visibility within areas of high hunting as compared to 5% in areas of low hunting pressure (Table 4.3).

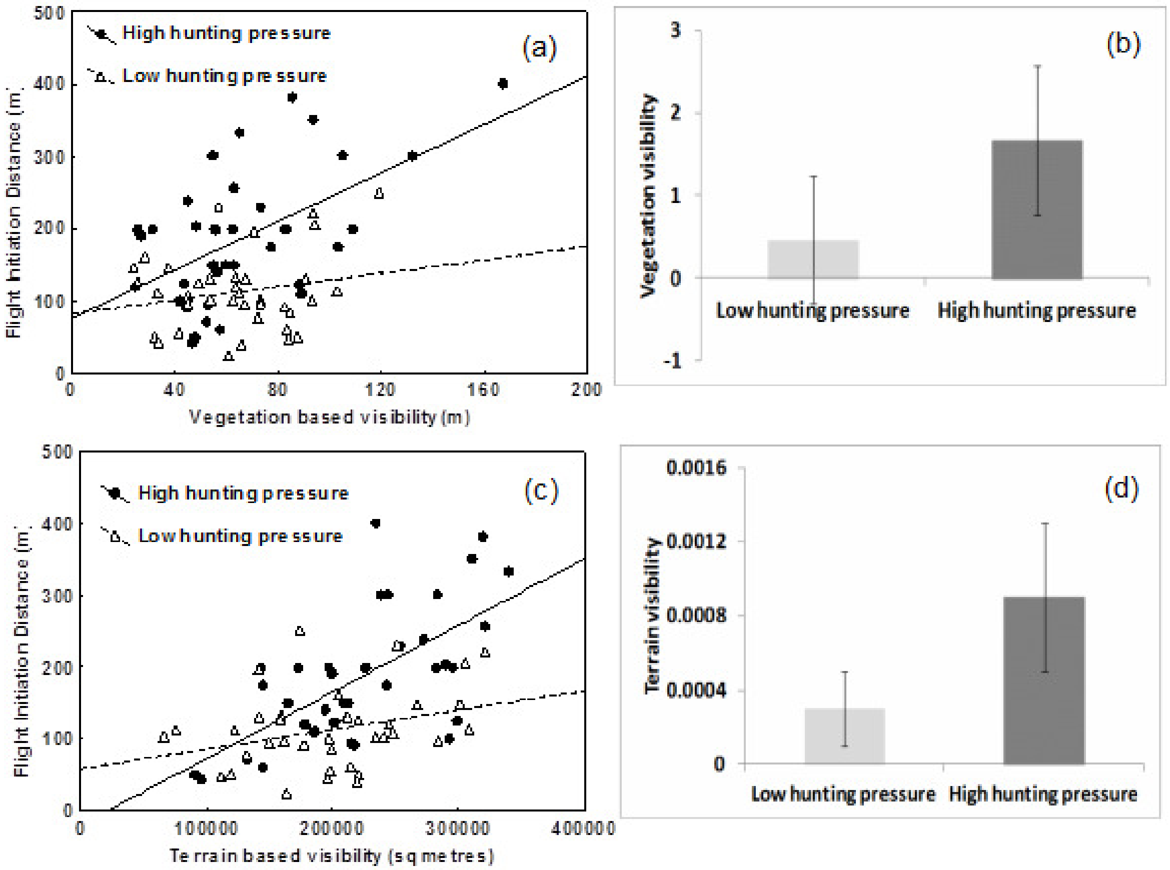

Figure 4.2 - Relationship of FID to vegetation based visibility in low and high hunting pressure areas within the hunting area (a) no significant difference ($p = 0.052$) in the slope coefficients of vegetation based visibility in low and high hunting pressure areas (b) relationship of FID to terrain based visibility in the low and high hunting pressure areas (c)

and significant difference (p = 0.006) in the slope coefficients of terrain based visibility in the low and high hunting pressure areas (d).

The slope of vegetation based visibility was not significantly (p > 0.05) steeper in areas of high hunting pressure compared with areas of low hunting pressure (Figure 4.2(b)). In both areas however, FID increased with increasing vegetation based visibility. Similarly, terrain based visibility had a significantly (p = 0.006) stronger influence on FID in areas of high hunting pressure than in areas of low hunting pressure (Figure 4.2(d)). In addition, FID increased with increasing terrain based visibility in both areas.

4.2 Discussion

Our results suggest that remotely sensed terrain based visibility predicts the FID of sable better than vegetation based visibility. Specifically, we suggest that sables in our study area appear to rely more on terrain than vegetation cover in detecting hunters and to initiate flight. Previous studies on the influence of visibility on the flight behaviour of animals mainly used visibility estimated by vegetation cover. For example, a study by Setsaas *et.al.,* (2007) used vegetation cover to estimate visibility and found that hunted impalas avoided open areas. As a result, vegetation based visibility had become the most acceptable surrogate for cover in most animal behavioural studies (Balme, Hunter et al. 2007; Setsaas, Holmern et al. 2007). Thus, our study improves on previous studies by showing that terrain based visibility may explain flight behaviour even better than vegetation based visibility.

Although interest has grown on the use of terrain as a visibility measure to explain the flight behaviour of animals (Frid 2003; Ripple and Beschta 2006; Grignolio, Merli et al. 2011), most of these studies have used field measured terrain to explain the flight behaviour of selected animal species. The launch of space-borne earth observation sensors like ASTER (Stevens, Garbeil et al. 2004) and the Shuttle Radar Topography Mission (SRTM) (Rabus, Eineder et al. 2003) in the early 2000s improved DEM availability for virtually any location on earth. Before then, DEMs were of limited availability in many regions because they were being produced from expensive photogrammetric methods as in Marzolff & Poesen (2009). The improved availability of DEM data has thus provided enhanced opportunities to model terrain based visibility for specific applications in spatial ecology. In the present study, we demonstrate this improvement by showing that ASTER based DEM derived visibility performs better than vegetation based visibility in explaining sable FID. Thus, for the first time in African savanna landscapes, our results indicate that terrain based visibility derived from an ASTER DEM explains flight behaviour better than vegetation based visibility.

Where our study differs from previous studies is in our use of fine resolution remotely sensed DEM data to model terrain based visibility. Traditionally, viewshed data have been used extensively in landscape planning (Baerenklau, Gonza´lez-Caban et al. 2010; Brabyn and Mark 2011) and highway design (Castro, L et al. 2011) but rarely in the study of the effect of terrain on animal flight behaviour. A DEM based terrain model calculated in a GIS allows for continuous modelling of the landscape over vast spatial extents with comparatively high levels of accuracy unlike field measured terrain which can only be done at limited localities. We therefore conclude that remotely sensed DEM, especially from ASTER can be an important data source for use in explaining the flight behaviour of sable. In particular, we managed to show that remote sensing based terrain visibility explains sable FID better than the well studied vegetation based visibility. We thus conclude that remotely sensed terrain based visibility better explains the flight behaviour of sable.

Chapter 5: A synthesis: Remote sensing and GIS approaches enhance understanding of habitat selection by sables in hunting and non hunting landscapes.

5.1 Introduction

The main objective of this thesis was to understand sable response to hunting using a GIS based spatial modelling approach based on a combination of satellite remotely sensed data and sable field data. Firstly, we tested whether hunted sables selected more closed woodland habitat (estimated by remote sensing derived NDVI) than those not hunted. Secondly, we tested whether terrain based visibility derived from the remotely sensed ASTER DEM explains the FID of sable better than vegetation based visibility measured in the field.. Overall, this thesis tests the importance of remote sensing derived data in the characterisation of both vegetation and terrain based visibility for use in studies modelling the spatial response of animals to hunting.

Previous studies testing the selection of land cover types by hunted animals have mainly used field measured vegetation cover which is often restricted to selected localities. In this thesis, we used remote sensing derived data to estimate vegetation cover for use in modelling the response of sables to hunting. Our results are amongst the first to observe significant difference ($P<0.05$) in woody cover types (estimated by remotely sensed data) selected by sables in hunting and non-hunting landscapes. To date, most studies testing the importance of landscape visibility as a predictor for FID in hunted animals have mainly used vegetation based visibility measured in the field. As a result, applicability of remote sensing derived terrain based visibility in most of these studies remained largely unknown. The results of this thesis are amongst the first to observe significance of remote sensing derived terrain based visibility as a predictor for the FID of sables..

5.2 Hunted sables select more closed woodlands

Sables are grazers that are known to select open woodland habitats in landscapes where hunting is not a permitted landuse (Wilson and Hirst 1977). In this study we found that hunted sables selected more closed woodlands. While shift in habitat by hunted populations is well documented in other species (Tambling and Du Toit 2005; Setsaas, Holmern et al. 2007), how sables would react in similar conditions had until this study had remained largely unknown. Thus, the finding that sables select closed woodland in hunting areas provides critical evidence for the estimation of hunting pressure. The shift in habitat to more closed woodland could also imply compromised foraging opportunities for sables. In this thesis this novel finding lays the foundation for future directions in understanding of the indirect impacts of hunting on sables. Understanding of the effect of hunting on sable is especially important given the fact that sable populations are declining in southern Africa and thus need protection. This thesis for the first time shows that in an African savanna, we can assess sable habitat change induced by hunting using remotely sensed data and spatial analysis. Overall, adoption of a remote sensing and GIS spatial analytical approach allows measurement of habitat factors, in this case habitat visibility, over larger landscapes as opposed to point based visibility measurements obtained from field work.

5.3 Terrain based visibility is a better predictor of sable FID than vegetation based visibility

Flight initiation distance has been used as a measure of fear in hunted populations (de Boer, van Breukelen et al. 2004). For instance shorter FID has been known to be exhibited by fearless animals while on the other side longer FID has been known to be common in hunted animals that live in constant fear of death or capture.. Thus, FID is an important parameter that can be used to measure the impact of hunting on hunted animals. Moreso, the identification of the predictors for FID is a critical step in understanding FID dynamics in hunted populations. While vegetation based visibility, often measured in the horizontal direction in the field has been widely used as a predictor for FID (de Boer, van Breukelen et al. 2004; Boyer, Hass et al. 2006), landscape visibility derived from remote sensing data has received little attention. Moreover, whether terrain based visibility is a better predictor of FID than vegetation based visibility has also remained largely rudimentary. Therefore in protected landscapes of Zimbabwe, the importance of DEM derived landscape visibility was tested against well known vegetation based visibility as predictors of sable FID. In this thesis, we found that terrain based visibility is a better predictor of sable FID than vegetation based visibility. This is despite the wide use of vegetation based visibility as a predictor of FID in studies testing fear in hunted populations (Frid 2003; Grignolio, Merli et al. 2011). This finding is amongst the first to prove that terrain based visibility and specifically viewshed is a better predictor of FID in hunting landscapes. While the importance of viewshed has been acknowledged in other fields (Baerenklau, Gonza´lez-Caban et al. 2010; Castro, L et al. 2011), its application in animal behaviour studies is largely unknown. We therefore emphasise utility of remote sensing in testing the impact of hunting on hunted animals since it allows for measurement of visibility over larger spatial extents. Future formulation of hypotheses testing the influence of visibility on FID could thus combine both vegetation and terrain based visibility as predictors since we have proven that remotely sensed terrain based visibility is an important predictor of FID.

5.4 Summary of findings

In this thesis, we have demonstrated that hunted sables select more closed woodland habitats than those found in non-hunting areas which select more open woodland habitat. In this thesis, we also demonstrated that NDVI can be used as a proxy for woody cover in studies that test the effect of hunting on habitat selection of target species. We therefore conclude that remote sensing data specifically NDVI, can successfully be used in studies comparing habitat selection of hunted and non-hunted sables. Finally, the results of this study imply that selection of closed woodland habitats by hunted sables can successfully be used as an indicator for overhunting. An effect of hunting on habitat use opens the possibility of hunting-induced indirect effects on the sable population, and such an effect would potentially indicate the need for further research to assess whether overhunting may be occurring. The thesis also shows that remote sensing based terrain visibility explains sable FID better than the well studied vegetation based visibility.

Spatial modelling of sable presence as a function of vegetation cover in this thesis was based on sable presence/absence data collected in September to coincide with the period of peak hunting. Thus, the models produced can only be used to predict sable response during periods of high hunting pressure and should be used with caution when applied to periods of low hunting pressure. Modelling of sable presence in hunting landscapes during periods of low hunting pressure should therefore form the basis of future research. In addition, our spatial modelling was based on sables only thus future spatial modelling should include other hunted animal species in the study site to establish whether the findings we made are not specific to sables. Moreover, replication of the study in several other study sites could help answer the question whether the reported pattern is not site-specific. Finally, a comparison of forage quality in the areas selected by sables both in the hunting and non-hunting sites could also form the basis for formulation of hypotheses for future research. Testing this could help establish whether the habitats selected by sables in hunting landscapes are optimal for fitness of sables compared to those selected in non-hunting sites.

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