Can MODIS NDVI measurements be used to predict zebra (*Equus burchelli*) foraging patterns?

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Declaration

I declare that this thesis is my own, unaided work. It is being submitted for the Master of Science degree at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree for examination at any other university.

(Signature of candidate)

16 July 2013

Abstract

As an indicator of above ground net primary productivity, the Normalised Difference Vegetation Index (NDVI) has been identified as important tool in understanding the resource requirements and distribution patterns of large herbivores. The efficacy of NDVI as an ecological tool is however, strongly contingent upon the scale of the foraging hierarchy at which data are interpreted. In this study I investigated whether vegetation greenness, as represented by MODIS NDVI 250 m resolution imagery, is a driver of zebra (*Equus quagga*) foraging patterns at three spatial/temporal scales, namely location within sixteen day home ranges, sixteen day home range within seasonal home range and seasonal home range within total home range, during both wet and dry periods. I also investigated how tree canopy cover influences the ability of MODIS NDVI to see the greenness at which zebra respond. During the wet season, the zebra clearly demonstrated evidence of selecting for greenness and a tendency to avoid areas of high woody canopy at all three scales. Conversely, during the dry season the zebra showed no preference for greenness and no consistent preference for or against woody cover across the three scales. I also noted that despite a positive relationship between ΔNDVI and woody canopy cover, the relationship is not significant and suggests that in savanna ecosystems tree densities may not be high enough to affect overall MODIS NDVI readings.

These results indicate that zebra foraging behaviour is complex and differs according to the scale of analysis, season, and even between individual zebra herds. The ability of MODIS NDVI to elucidate zebra movements is therefore limited to specific spatial and temporal scales and should be accompanied by an understanding of non-forage related factors.

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CHAPTER 1

Research aim

This study forms part of ongoing research conducted by the Centre for African Ecology (University of the Witwatersrand) into herbivore grazing ecology at different spatial scales. The aim of the study was to determine whether the foraging patterns of Burchell's zebra can be explained by MODIS NDVI greenness measurements at 250 m resolution.

Motivation for the study

In light of continued habitat degradation and transformation, the loss of biodiversity and the uncertain influences of global warming, the ability of ecologists to adequately forecast the ecological responses of plant and animal populations to environmental change is of increasing importance in conservation (Kerr & Ostrovsky 2003, Pettorelli et al. 2005, Berteaux et al. 2006). Until recently however, the ability of ecologists to assess and forecast such responses at large spatial and temporal scales has been limited by the inherent constraints of traditional, locally collected field data (Kerr & Ostrovsky 2003, Pettorelli et al. 2005).

As a means of overcoming these constraints, ecologists are increasingly using remote sensing data, such as the Normalised Difference Vegetation Index (NDVI) to study ecosystem dynamics (Pettorelli *et al.* 2005, Petrorelli *et al.* 2006). Greenness values, as derived from NDVI, are positively correlated to above ground net primary productivity and can be used to determine vegetation distribution, abundance and quality over large temporal and spatial scales (Verlinden & Masogo 1997, Pettorelli *et al.* 2005, Weigand *et al.* 2008). As herbivores adjust their foraging strategies based on *inter alia,* the availability and distribution of quality forage (Gordon and Lindsay 1990, Pettorelli *et al.* 2007, Bartlam-Brooks *et al*. 2011), NDVI greenness values have in turn, been coupled with herbivore distribution and movement patterns (Verlinden & Masogo 1997, Bro-Jorgensen *et al.* 2008, Mueller *et al.* 2007, Musiega & Kazadi 2004).

Marshal *et al.* (2011) indicate that the strength of coupling between vegetation greenness and herbivore distribution and movement is largely contingent upon the scale at which data are interpreted; with the influence of various environmental factors manifesting most clearly only at certain scales and levels of resource selection. Indeed, the element of scale, both temporal and spatial, is a fundamental conceptual challenge in ecology and cognisance of scale must be taken in all ecological research (Meyer *et al.* 2007).

From a foraging perspective, herbivores are confronted with a food resource that is not only highly variable in quantity and quality over time, but also widely and unevenly distributed over the landscape (Senft 1987). This temporal and spatial variance in forage availability has profound effects on how herbivores utilise the landscape, as they are required to make numerous foraging decisions at different scales in order to forage optimally (Senft 1987, Garcia *et al.* 2011). These range from broad scale decisions such as which vegetation community to use within a given landscape, to which feeding patch to feed in within a selected community, and finally through to fine scale decisions such as which plant or plant part to consume (Senft 1987). In such a framework selection occurs within a nested hierarchy of choices (Leblond *et al.* 2010, Marshal *et al.* 2011). Our ability to detect the underlying mechanisms or environmental cues that underpin herbivore distribution and movement patterns is thus highly contingent upon the scale or level at which foraging decisions are made.

Appreciation of scale is also a critical factor when using NDVI as an ecological tool. A single image of MODIS NDVI for instance, can cover an area of between 6.25 to 25ha depending on the image resolution. The spatial resolution of imagery may be recorded at 250 m, 500 m and 1 km (NASA MODIS Web 2011). This in a savanna environment will comprise greenness contributions from both the grass and the woody layer (Marshal *et al.* 2011). An inherent constraint of such an image is that it fails to differentiate between these plant forms, as many produce similar NDVI values or NDVI temporal trends (Pettorelli *et al.* 2005). Owing to differences in ability to store and access water, trees and grasses have different seasonal patterns of leaf display (Archibald & Scholes 2007), and as such, the contribution of greenness as measured by MODIS NDVI caused by these different functional types may vary substantially over time, and indeed from pixel to pixel (Marshal *et al.* 2011).

As trees and grasses represent fundamentally different foraging resources to herbivores, even at the finest scale drawing direct correlations between MODIS NDVI greenness and the foraging patterns of grazing or browsing herbivores may be limited (Marshal *et al.* 2011). Consequently Archibald & Scholes (2007) note that the problem of separating greenness contributions of trees and grasses has been inadequately addressed in many studies using MODIS NDVI.

In contrast to MODIS NDVI, greenness readings taken directly above the grass layer by a handheld NDVI sensor exclude any greenness contribution from the woody layer and thus represent a more appropriate measure of the greenness of the forage available to a grazer. However, due to practical constraints, such readings are inherently confined to small temporal and spatial scales and will therefore lack the landscape scale and temporal analysis capability of MODIS NDVI imagery.

It is clear that understanding the on-ground conditions that contribute to greenness in a MODIS NDVI image is of critical importance in developing a mechanistic explanation for herbivore distribution and movement patterns (Marshal *et al.* 2011) - a caveat which is supported by Verlinden & Masogo (1997), who following their study in the Kalahari, caution against the use of NDVI without detailed ground-truthing. Be that as it may, MODIS NDVI has the potential to greatly enhance our understanding of how free-ranging herbivores utilise the landscape which is of critical importance in ecosystem management.

In this study I aimed to determine whether vegetation greenness is a driver of foraging patterns by testing the relationship between zebra (*Equus quagga*) locations and MODIS NDVI 250 m resolution data at various levels of the foraging hierarchy and at different temporal scales. I also investigated how tree cover influences the ability of MODIS NDVI to see the greenness at which zebra respond, by correlating the difference in MODIS NDVI values and NDVI values obtained by a hand held sensor, with tree canopy cover.

Literature Review

Spatial scales and foraging hierarchies

All ecosystem processes take place at different scales and are associated with patterns at other scales (Meyer *et al.* 2007). Any conclusions as to the nature or mechanisms governing a particular ecological process are thus strongly contingent upon the scale at which phenomena are investigated (Marshal *et al.* 2011). Scale is therefore all important and forms an elementary conceptual challenge in ecology (Meyer *et al.* 2007).

Herbivore habitat selection in a heterogeneous landscape is a process that takes place at a hierarchy of scales (Leblond *et al.* 2010, Marshal *et al.* 2011), yet the extrinsic and intrinsic factors that determine the scales at which herbivores respond to plant resources are poorly understood (Garcia *et al.* 2011).

From a foraging perspective, herbivores are confronted with a food source of varying quality and abundance which is dispersed throughout the landscape (Senft *et al.* 1987, Marshal *et al.* 2011). These resource patches are the first level of spatial heterogeneity to which an herbivore is required to respond in order to meet their nutritive requirements (Garcia *et al.* 2011). Herbivores are thus required to make a number of foraging decisions based on their perceptive scale (Garcia *et al.* 2011). These range from the broad-scale decisions such as the selection of a preferred landscape within a particular region, through to which plant community to forage in and finally to proximal decisions, such as which feeding station to approach and which plant and plant part to actually feed on (Senft *et al.* 1987). Moreover, these decisions are not based on forage availability alone but are also influenced by other factors such as distance to water, predator avoidance, territorial constraints and topography (Leblond *et al*. 2010, Garcia *et al.* 2011). The factors that govern foraging decisions are often scale specific, with some having relevance only at a particular level of selection (Marshal *et al.* 2011). In addition, decisions are not mutually exclusive with decisions at higher scales often constraining options at finer scales (Senft 1987). Habitat selection is thus an exercise in trade-off management.

An inherent challenge faced by researchers when investigating scale-based resource selection is the paucity of landscape scale measurements. In remote areas for instance, rainfall data are often insufficient to allow for adequate habitat condition monitoring and subsequent herbivore distribution analyses (Verlinden & Masogo 1997). NDVI has been invoked as a landscape scale measurement of considerable importance which can provide a broad measure of habitat condition (Pettorelli *et al.* 2005). This notwithstanding the mechanisms that link actual vegetation greenness with NDVI greenness and herbivore movement at various levels of the foraging hierarchy remain vague, particularly in light of the confounding element introduced by the relative contribution of trees and grass to greenness measurements (Archibald & Scholes 2007, Marshal *et al.* 2011). Indeed, in a study conducted by Marshal *et al.* (2011) it was noted that the role of vegetation greenness in determining elephant distribution varied at both temporal and spatial scales, and additionally, between sexes.

NDVI

The Normalised Difference Vegetation Index (NDVI) is an index of vegetation greenness and is based on the ratio of red (RED) to near-infrared (NIR) reflectance [NDVI = (NIR-RED)/(NIR+RED)] captured by satellite sensors (Verlinden & Masogo 1997, Pettorelli *et al.* 2005). MODIS NDVI readings are derived from bands 1 and 2 of the Moderate-resolution Imaging Spectroradiometer which is aboard the Terra satellite operated by NASA. Readings are recorded at three spatial resolutions, namely 250 m, 500 m and 1 km.

Reflectance ratios are determined by plant chlorophyll levels, moisture and the leaf area index. As vegetation shows high reflectance in the near infrared and low reflectance in the red (Verlinden & Masogo 1997), high NDVI values are indicative of well-developed green vegetation while low NDVI values are characteristic of discontinuous or non-green vegetation (Van Bommel *et al.* 2006). MODIS NDVI greenness values range from 0 to 10 000 with larger values corresponding to greener vegetation (Pettorelli et al. 2005).

Indeed, NDVI has been shown to be strongly positively correlated to above ground net primary productivity and thus provides valuable information on *inter alia* vegetation distribution, abundance and quality (Tucker & Sellers 1986, Verlinden & Masogo 1997, Pettorelli *et al.* 2005, Mueller *et al.* 2007, Weigand *et al.* 2008). This is particularly applicable in savanna ecosystems where NDVI values rarely reach saturation (Verlinden & Masogo 1997). Owing to the coupling of herbivores to available forage, numerous studies have successfully linked animal habitat use with remote-sensing data (Van Bommel *et al.* 2006). Muisega & Kazadi (2004) and Mueller *et al.* (2007) for example found a significant relationship between NDVI and Mongolian gazelle and wildebeest occurrences respectively. In a more spatially explicit study, Marshal *et al.* (2011) found strong associations between elephant distribution and greenness, but only at specific spatial and temporal scales. These authors note that the role of vegetation greenness as measured by NDVI, varies with the scale of analyses and careful consideration of scale is thus required when utilising NDVI as a modelling tool (Marshal *et al.* 2011).

Study animal – Burchell's zebra

The Burchell's zebra is a medium-sized (weight 220-320 kg) ungulate occurring throughout the savanna regions of southern and east Africa (Estes 1997). Zebra's are non-territorial and gregarious, living in one-male harems of up to six females. Young adult male zebra live in bachelor herds ranging in size from two to 15 individuals (Estes 1997). Depending on local conditions, zebra are either sedentary, or migratory, moving vast distances in search of available forage with distinct wet and dry season home-ranges.

Zebra are the most abundant and widespread nonruminants among the African large grazing ungulates and along with wildebeest (*Connochaetes taurinus*) are the main participants in the large scale herbivore migrations in the Seregenti-Mara and Okavango-Makgadikgadi ecosystems (McNaughton 1985). Although these migrations are a response to seasonal variation in forage quality rather than absolute abundance, it is noted that the abundance of dry season forage is the overarching determinant of herbivore survival (Bartlam-Brooks et al. 2011). This is particularly relevant for the nonruminant zebra, which, owing to its comparatively lower digestive efficiency, requires larger quantities of forage and higher forage intake rates compared to ruminants in order to meet their nutritional demands (Owen-Smith 2005).

These physiological constraints have resulted in zebras being less selective foragers than ruminants (Bodenstein et al. 2000, Brooks & Harris 2008); a fact that is noted in the observation that zebra often select the tallest and most fibrous parts of the grass plant and as such subsist on a diet containing more fibre and less accessible nutrients than other ungulates (Janis 1976). Indeed, Groom & Harris (2009) and Brooks & Harris (2008) note that zebra prioritized selecting grass biomass and greenness over selecting grass of greater digestibility, with the latter authors observing that zebras often travel greater than expected distances in search of patches containing higher quantities of grass.

Based on this preference for patches displaying high grass biomass, it is reasonable to anticipate that zebra foraging patterns will correlate positively to above ground net primary productivity, which will in turn correlate with NDVI values.

Study area

The study area is located in the Manyeleti Game Reserve (MGR) in Mpumalanga Province, South Africa. The MGR is situated on the western boundary of the Kruger National Park (KNP), south of Orpen Gate. No boundary fence exists between the MGR and the KNP, and as such the MGR is part of a wildlife system (the greater KNP) comprising approximately 20 000 km^2 of Lowveld savanna. The greater KNP is characterised by a diverse range of habitats and a large assemblage of medium to large herbivores and predators.

The area receives a mean annual precipitation of between 500-700 mm, which mainly falls in the summer months of October through to April. Summers are characteristically hot, with temperatures often exceeding 40^{o}C. Winters are mild and generally frost free (Venter et al. 2003).

The MGR falls on the moderately undulating granitic plains of the Basement Complex (Venter *et al.* 2003). In comparison to soils originating on the eastern basalts, granitic soils tend to be highly leached creating a distinct catena characterised by nutrient poor uplands and the nutrient rich lowland's (Venter *et al.* 2003). The abiotic template strongly influences vegetation composition and structure. In comparison to the eastern basaltic plains, the vegetation of the study area is characterised by a high proportion of woody vegetation, including common species such as *Combretum apiculatum*, *Acacia exuvialis*, *Terminalia prunioides*, *Acacia nigrescens* and *Sclerocarya birrea* (Venter *et al.* 2003). The herbaceous layer is dominated by annual pioneers and wiry grasses including

Pogonathria squarrosa, *Schmidtia pappophoroides* and *Eragrostis rigidior* and various *Aristida* species (Venter *et al.* 2003).

The area is also characterised by Timbavati gabbro intrusions in the form of sills. These gabbro sills display similar properties to basalt derived soils and are characterised by comparatively lower woody vegetation density and a highly productive grass layer (Venter et al. 2003). Such areas represent important resource 'hot-spots' to grazers in the MGR.

In conjunction with the geological template, the wet and dry cycles associated with the areas rainfall pattern strongly influence grass cover, fire regime and animal population dynamics (Venter et al. 2003).

Research Design

Herd selection

Herbivore location data was obtained from three collared zebra. These individuals, each of which is part of a different herd, were fitted with a GPS/GSM collar sourced from Africa Wildlife Tracking (www.awt.ac.za) toward the end of 2009, and location data covering a one and a half year period were available for analyses. Owing to the gregarious nature of zebras, the movements of the collared individuals were used to represent the movement patterns of the whole herd. Data from the collars are transmitted to a GSM at hourly intervals and include the GPS location of the animal, the date and the time of the transmission, as well as other data such as temperature, movement direction and speed, and altitude.

In addition, location data derived through direct observations of non-collared animals were used. These data were collected by Melinda Boyers during the dry/wet transition period of 2010 and correspond to handheld sensor NDVI readings.

Data collection

Vegetation was represented by MODIS NDVI imagery and NDVI values obtained from a handheld sensor. The former data comprise 16 day composite images with a spatial resolution of 250 m (http://modis.gsfc.nasa.gov/). These data provide a landscape level measurement of vegetation quantity and quality. MODIS NDVI data for the period November 2009 to March 2011 was obtained. NDVI values from a handheld sensor for the dry season and the spring/summer transition period of August 2010 through to November 2010 were obtained from Melinda Boyers. These data comprise greenness values recorded in 0.5 m X 0.5 m quadrats at feeding stations (direct zebra observations) and randomly-selected non-feeding stations in landscape areas of 6.25 ha.

Zebra location data in the form of hourly GPS coordinates, as transmitted by the GPS collars fitted to three animals (AG198, AG199 and AG200), was obtained for the period of November 2009 to March 2011. These data were used to determine the total home range (broad scale), seasonal home range (intermediate scale) and sixteen day home range (fine scale) of the collared zebra. In addition aerial photographs taken in 2009 depicting vegetation structure and cover in the study area were obtained from the Chief Directorate: National Geo-spatial Information of the Department of Rural Development and Land Reform. These images were used to determine the percentage cover of woody vegetation in the study area.

Thesis outline

Chapter 1 provides a general overview of the field of research. In Chapter 2 I elaborate on the actual research I conducted, providing details on methods and data analyses. References cited in each chapter, are listed at the end of the applicable chapter.

Chapter 2 has been drafted in an article format, with an introduction, methods, results and discussion. In this study I aim to determine whether vegetation greenness as measured by MODIS NDVI 16 days composite dataset at 250 m resolution, is a driver of zebra foraging patterns. Accordingly, I have two primary objectives.

Objective 1: To determine at what spatial / temporal scale zebra respond to greenness as represented in a MODIS NDVI image and how the response varies with season.

Objective 2: To determine whether differences in MODIS NDVI greenness values and NDVI greenness values obtained from a hand-held sensor are dependent on tree canopy cover.

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CHAPTER 2

Can MODIS NDVI measurements be used to predict zebra (*Equus quagga*) foraging patterns?

Introduction

Large herbivore populations are in general decline throughout many of Africa's conservation areas – a fact primarily attributed to a lack of functional wet- and dry- season foraging resources (Fynn & Bonyongo 2010). Understanding the resource requirements and distribution patterns of large African herbivores is thus becoming increasingly important in wildlife management and conservation (Fynn & Bonyongo 2010).

The Normalised Difference Vegetation Index (NDVI) has been identified as important tool in modern ecology (Verlinden & Masogo 1997, Pettorelli *et al.* 2011). NDVI greenness values are strongly positively correlated to above ground net primary productivity and can be used to determine vegetation distribution, abundance and quality over large temporal and spatial scales (Verlinden & Masogo 1997, Pettorelli *et al.* 2005a, Weigand *et al.* 2008). In turn, these factors have been shown to correlate with the foraging behaviour of several herbivore species (Pettorelli *et al.* 2011)

This notwithstanding, Marshal *et al.* (2011) note that the strength of the coupling between vegetation greenness as represented by NDVI and herbivore distribution is contingent upon the scale at which data are interpreted. Herbivore foraging behaviour is based on optimising forage quality and quantity, and on minimising foraging cost and predation risk (Senft *et al.* 1987, Hopcraft *et al.* 2013). Across the landscape, these factors vary both spatially and temporally (Fryxell *et al.* 2005). In order to follow an energy maximising feeding strategy, herbivores are thus required to exploit landscape heterogeneity by actively making foraging decisions, the nature of which is determined by the scale in the ecological hierarchy at which they are made (Senft *et al.* 1987). Moreover, decisions are not necessarily consistent across all individuals and may depend on the reproductive state of individual herd members (Sundarsen *et al.* 2007). Appreciation of the underlying mechanisms that govern decision-making at each scale is therefore critical to our overall understanding of herbivore foraging patterns.

A complicating factor in applying NDVI to herbivore resource selection questions is that NDVI fails to differentiate between trees and grasses, as both have similar NDVI values and NDVI temporal trends (Pettorelli *et al.* 2005). Trees and grasses represent fundamentally different foraging resources to herbivores. It is therefore important that the on-ground conditions, most notably the degree of woody vegetation cover that contribute to NDVI greenness, are taken into consideration during the development of a mechanistic explanation for herbivore distribution and movement patterns (Marshal *et al.* 2011)

In this study I aimed to determine whether vegetation greenness, as represented by MODIS NDVI 250 m resolution imagery, is a driver of zebra (*Equus quagga*) foraging patterns at the landscape scale. The landscape scale is defined as levels of the foraging hierarchy above the foraging area - foraging area in turn being defined as a collection of feeding patches used during a feeding bout (Bailey *et al.* 1996).

I did this by testing the relationship between zebra locations, MODIS NDVI and tree canopy cover at different levels of the foraging hierarchy and at different temporal scales. I considered three explicit spatial/temporal scales, namely location within sixteen day home ranges (fine scale), sixteen day home range within seasonal home range (intermediate scale) and seasonal home range within total home range (broad scale), during wet and dry periods. I also investigated how tree cover influences the ability of MODIS NDVI to see the greenness at which zebra respond, by correlating the difference between MODIS NDVI images and NDVI obtained from a hand-held sensor, with tree canopy cover.

I expect zebra locations during the wet season to be positively correlated to MODIS NDVI greenness and this to be greatest at the broad scale, followed by the intermediate- and fine scales. I also expect a greater negative correlation between zebra locations and woody canopy cover at the fine scale, followed sequentially by the intermediate- and broad scales, during the wet season.

Conversely, during the dry season I expect the correlation between zebra locations and MODIS NDVI greenness to be most positive at the fine scale, followed sequentially by the intermediate- and broad scales. I expect no correlation between zebra locations and woody canopy cover at any scale during the dry season, as a loss of foliage by deciduous trees during the dry season improves visibility thereby reducing perceived predation risk. I also expect that differences between MODIS NDVI and NDVI obtained from a hand-held sensor are positively correlated to woody canopy cover.

Methods

Study Area

The study took place in the Manyeleti Game Reserve (MGR) on the western boundary of the Kruger National Park. The area receives a mean annual precipitation of between 500-700 mm

(Venter *et al.* 2003) and is characterised by moderately undulating granitic plains of the Basement Complex (Venter *et al.* 2003). The vegetation of the study area is characterised by woody plant species, most commonly *Combretum apiculatum*, *Acacia exuvialis*, *Terminalia prunioides*, *Acacia nigrescens* and *Sclerocarya birrea* and grasses including *Pogonarthria squarrosa*, *Schmidtia pappophoroides* and *Eragrostis rigidior* and various *Aristida* species (Venter *et al.* 2003).

Study animal

Burchell's zebra is a medium-sized (weight 220-320 kg) non-territorial ungulate occurring throughout the savanna regions of southern and east Africa (Estes 1997). Zebra's are primarily grazers although they do browse (Estes 1997). Indeed, Stanislaus (unpublished MSc. thesis) notes that as a consequence of higher herb diversity and abundance compared to grasses, Grevy's zebra (*Equus grevyi*) browse more than they graze in the Samburu community lands of Kenya.

Zebra are ruminants and therefore require large quantities of forage and high forage intake rates in order to meet their nutritional demands (Owen-Smith 2005). As a consequence, zebra are often forced to move vast distances in response to seasonal variations in forage quality and quantity (Bartlam-Brooks *et al.* 2011). Three zebra from separate herds were used in this study. These were captured by veterinarians using standard capture methods and fitted with GPS collars (African Wildlife Tracking, Pretoria) to monitor their spatial movements.

Data collection

Location data in the form of GPS coordinates from the three zebra representing three different herds was obtained from November 2009 to March 2011 (hereafter referred to as the study period). MODIS NDVI at 250 m spatial resolution and 16 days temporal resolution was used. For each 16 days composite the average NDVI across the study area was calculated to obtain a time series of mean NDVI values for the area starting from 2000. Values are higher in the wet season when it is green and lower in the dry season. I adapted the detection algorithm developed by White et al. (2002) to define start and end of wet season. For each year I selected the annual minimum and maximum area NDVI value and derived the midpoint between them. This was done for each year and then averaged across years. This long term average was used as the threshold value to identify the start and end of the growing (wet) season during the study period and therefore wet and dry season. NDVI values from a handheld sensor were obtained for the dry season period. These data comprise greenness values recorded in 0.5 m x 0.5 m quadrats at feeding stations within foraging areas where zebra were observed feeding. Aerial photographs taken in 2009 depicting vegetation structure and cover in the study area were obtained from the Chief Directorate: National Geo-spatial Information of the Department of Rural Development and Land Reform.

Data analysis

To investigate the relationship between MODIS NDVI, woody canopy cover and zebra foraging patterns at various levels of the foraging hierarchy, I selected three scales of analyses, namely fine-, intermediate- and broad scale (Figure 2.1). The finest scale was limited by the 16 day temporal resolution of NDVI imagery. At this scale, I compared observed use locations (GPS locations) with random use locations within each 16 day home range spanning the entire study period. Home ranges were determined using an estimated 95% adaptive kernel with least square cross validation (Marshal *et al*. 2011) with the home range tools for ArcGIS. A ratio of 1:2 used/random locations were selected, with used locations represented by the GPS locations of the zebra at 07h00 on each day of the 16 day period.

At the intermediate scale, I compared zebra locations within sixteen day home ranges with random locations from within wet and dry season home ranges at a ratio of 1:2. Wet and dry season home ranges were delineated using 95% adaptive kernel methods. Similarly, at the broad scale I compared zebra locations within wet and dry season home ranges with random locations within the total home range of each zebra. Subsequent analyses at the fine-, intermediate- and broad scales were based on NDVI values and woody canopy cover estimates for each random and used location.

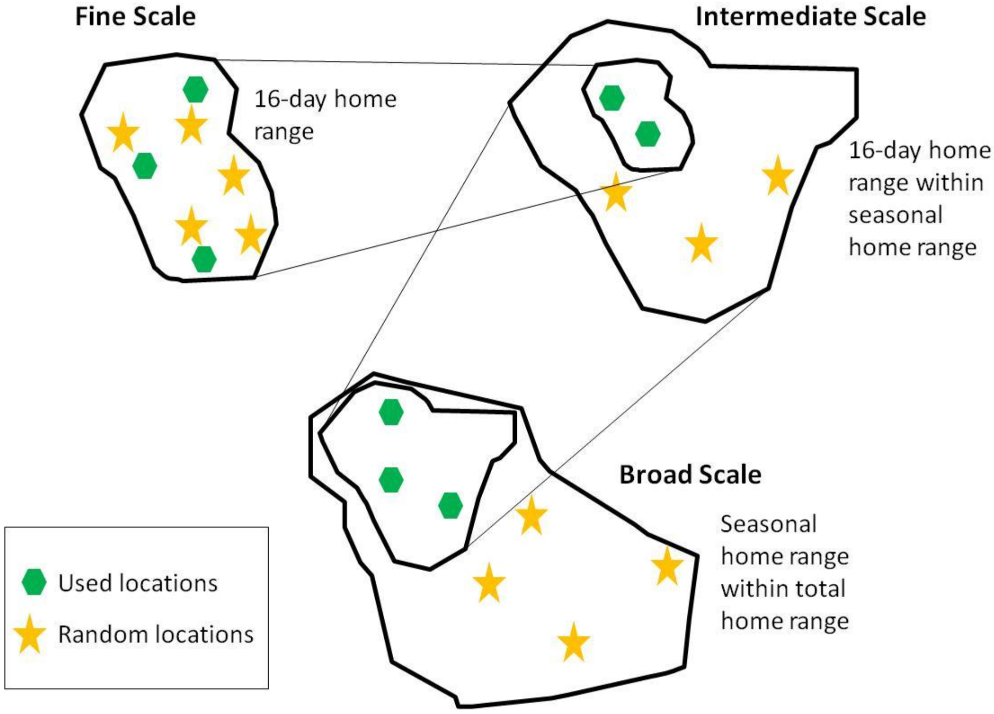

Figure 2.1: The three spatial scales used in this study.

To obtain woody canopy cover estimates, I superimposed a grid consisting of 200 m X 200 m blocks onto an aerial photograph of the study area using ARC GIS. Based on percentage of woody canopy cover, each block in the grid was scored into one of 3 classes (Table 2.1).

To test my research hypotheses regarding zebra foraging patterns and NDVI, I ran a range of logistic models using the lme4 package in R version 2.15.2. The lme4 package defines one set of a categorical predictor as a reference unit, against which other sets are compared. I tested each variable independently, as well as combinations thereof.

False convergences were encountered during the fitting of various models containing NDVI as an explanatory variable. According to Marshal *et al.* (2011) false convergences occur when there are discrete divisions in the frequency distribution of certain explanatory variables that result in the algorithms used for fitting models failing to converge on maximum likelihood estimates. To overcome this, when using NDVI in the resource selection function models, I converted the continuous NDVI data into categorical variables represented by five NDVI classes (Table 2.1). Explanatory variables used in the models were thus all categorical; NDVI (5 categories), woody canopy cover (3 classes) and season (wet and dry).

Table 2.1: Categorisation of the Normalised Vegetation Index (NDVI) and woody canopy cover in the Manyeleti Game Reserve, South Africa.

Variable	Class	Lower limit	Upper limit
NDVI	1	1170	2893
	2	2894	4617
	3	4618	6341
	4	6342	8065
	5	8066	9789
Woody canopy cover	1	0%	25%
	2	26%	50%
	3	51%	100%

I compared models using Akaike's Information Criterion (AICc). Models with the lowest AICc value were considered to be the most appropriate (Anderson 2008). Models were further compared by computing the relative likelihoods of each model (w_i). The model with the highest probability is considered to represent reality the closest (Anderson 2008).

To determine whether differences between MODIS NDVI and NDVI from a handheld sensor are attributable to woody canopy cover, I divided MODIS NDVI values by 10 000 so that they were on the same scale as hand held sensor NDVI values (-1 to +1). I then subtracted one from the other and ran a regression analysis between NDVI difference (Δ NDVI) and woody canopy cover.

Results

I analysed location data for three individual zebra - each from a different herd in the MGR. In total, the data set comprised 14 613 locations across the three animals, covering two wet seasons and one dry season.

At the fine scale of analysis, of the nine resource selection function models fitted to the data, the best model was one with only NDVI as a variable (Model 5, $w_i = 0.47$). At the intermediate scale, the model with the best fit contained NDVI, woody canopy cover and season as variables (Model 13, $w_i = 0.84$), while at the broad scale of analysis the model containing NDVI, woody canopy cover and their interaction with season was the best (Model 12, $w_i = 0.92$) (Table 2.2).

Table 2.2: Top four candidate resource selection function models showing explanatory variables and their interactions at the fine-, intermediate- and broad scales.

Model #	**Variables**	**K**	**AICc**	**ΔAIC**	w_i
Fine Scale					
Model 5	NDVI	5	6138	0	0.47
Model 6	NDVI+season	6	6138	0	0.47

Model #	Variables	K	AICc	ΔAIC	w_i
Model 7	NDVI+cover	6	6143	5	0.04
Model 13	NDVI+cover+season	7	6144	6	0.02
Intermediate Scale					
Model 13	NDVI+cover+season	7	9406	0	0.84
Model 12	NDVI+cover*season	7	9410	4	0.11
Model 6	NDVI+season	6	9413	7	0.03
Model 2	Season+cover	3	9414	8	0.02
Broad Scale					
Model 12	NDVI+cover*season	7	1843	0	0.92
Model 4	Season*cover	3	1849	6	0.05
Model 7	NDVI+cover	6	1867	8	0.02
Model 13	NDVI+cover+season	7	1868	9	0.01

From the results it is clear that zebra were responding to vegetation greenness (NDVI) at all scales, with woody canopy cover also affecting distribution patterns at the two higher scales. This notwithstanding, when the location data of the three zebra were analysed separately, it is evident that each individual zebra and by extension each zebra herd, showed variable and herd-specific responses to NDVI and woody canopy cover at different scales during the wet and dry seasons.

Dry season: In general, all three zebra showed no preference for greenness during the dry season at any scale and appeared to move randomly across their home range (Figure 2.2 - 2.4). In terms of woody canopy cover, Zebra 198 showed neither selection for nor against woody cover at all three scales. Zebra 199 selected for areas with higher woody canopy cover at the broad scale, but showed no selection for or against at the lower scales. Conversely, Zebra 200 showed no preference at the broad scale, but selectively avoided areas of high woody canopy cover at the intermediate and fine scales (Figure 2.5 - 2.7).

Wet season: During the wet season Zebra 198 showed a positive selection for greenness at all three scales. Zebra 199 did not select for greenness at the broad and intermediate scales, but selected for greenness at the fine scale. Similarly, Zebra 200 showed no selection preference for greenness at the broad scale, but selected for greenness at the intermediate and fine scales range (Figure 2.2 - 2.4).

In terms of woody canopy cover, Zebra 198 selected against areas of high woody cover at the broad scale, but then showed neither selection for nor against woody cover at the two lower scales. Zebra 199 actively selected against woody cover at all three scales, while Zebra 200 showed no preference for or against woody cover at any scale (Figure 2.5 - 2.7).

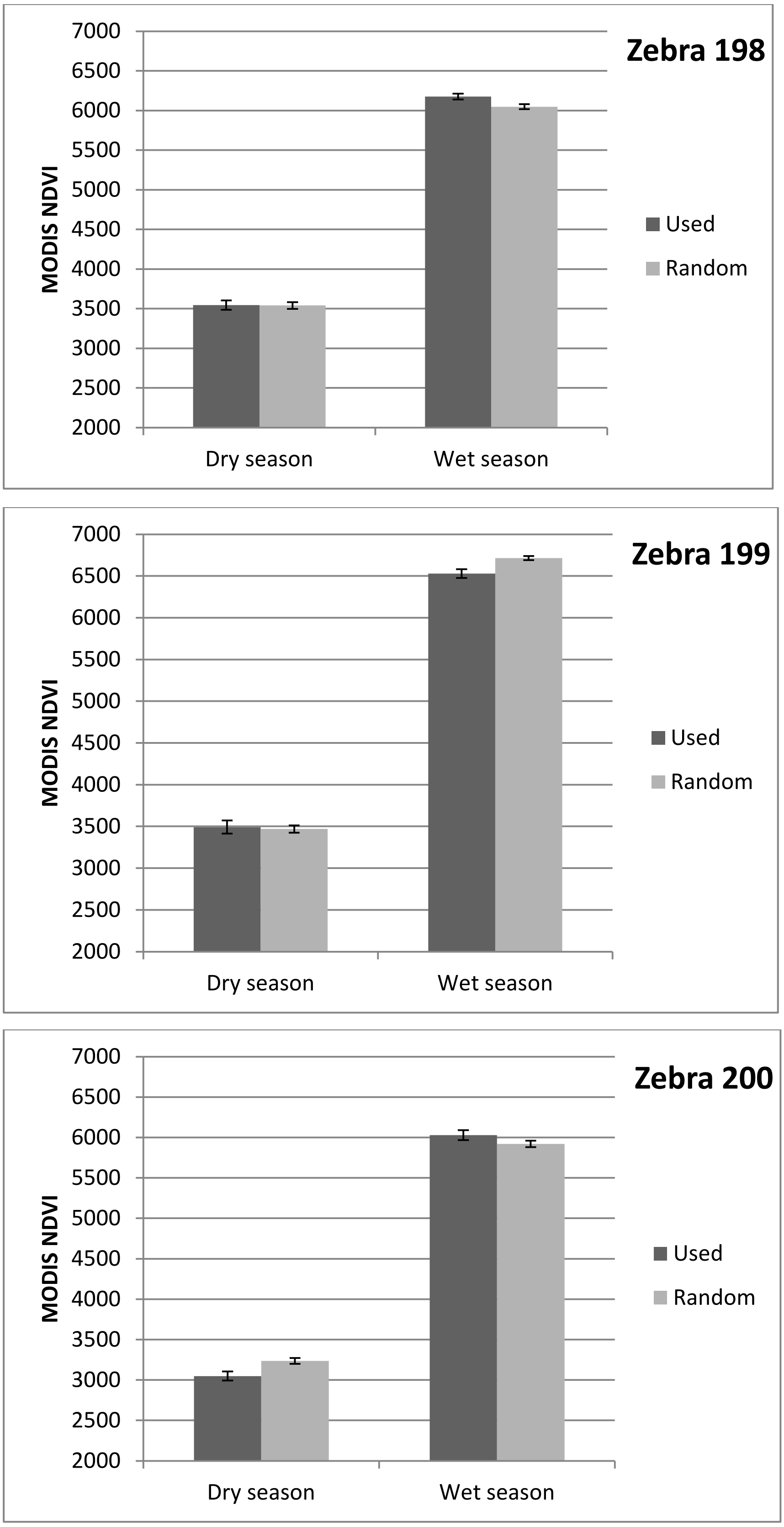

Figure 2.2: Comparison of NDVI readings at Used and Random locations during the wet and dry season at the **fine scale** of analyses.

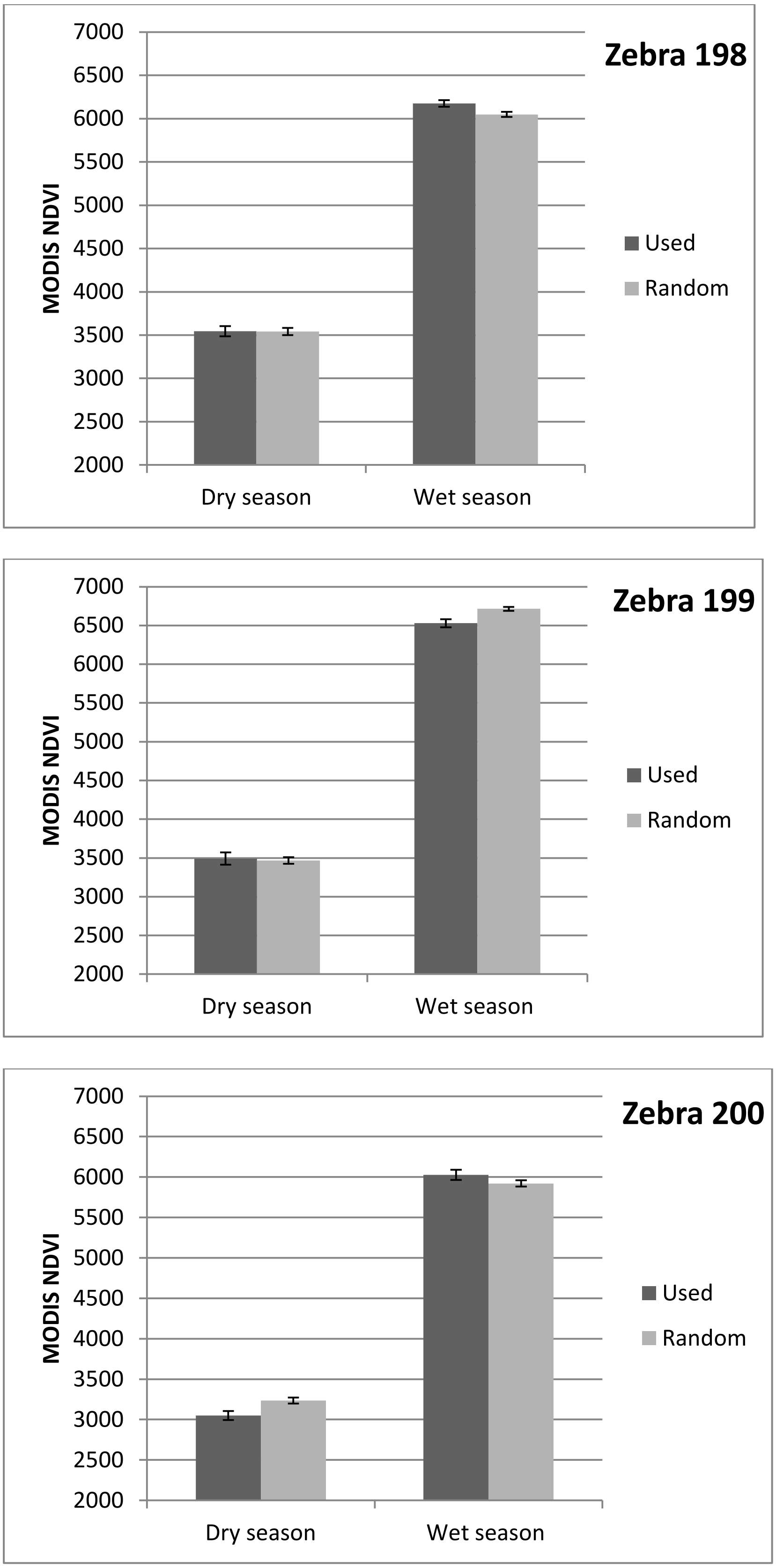

Figure 2.3: Comparison of NDVI readings at Used and Random locations during the wet and dry season at the **intermediate scale** of analyses.

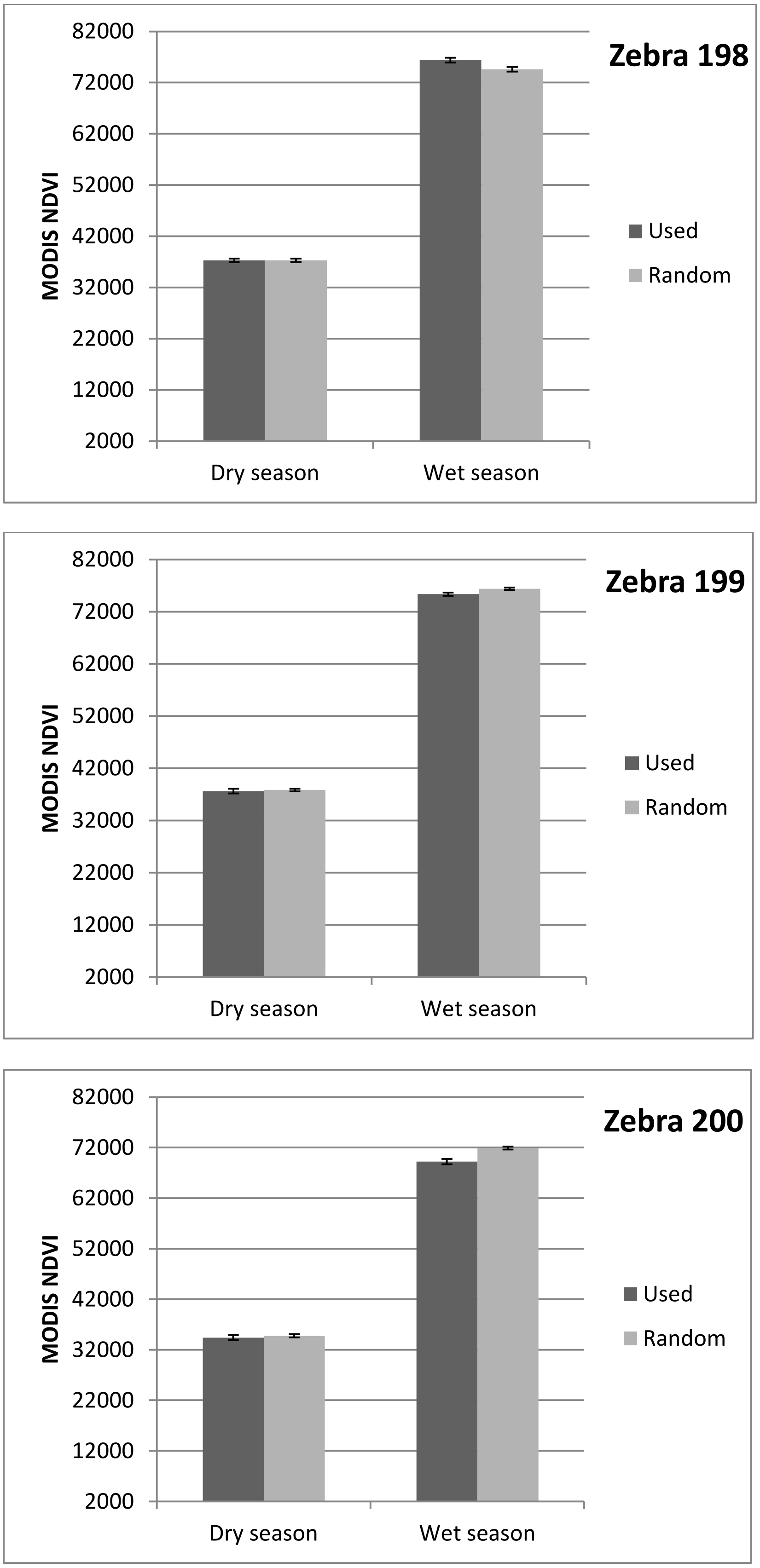

Figure 2.4: Comparison of NDVI readings at Used and Random locations during the wet and dry season at the **broad scale** of analyses.

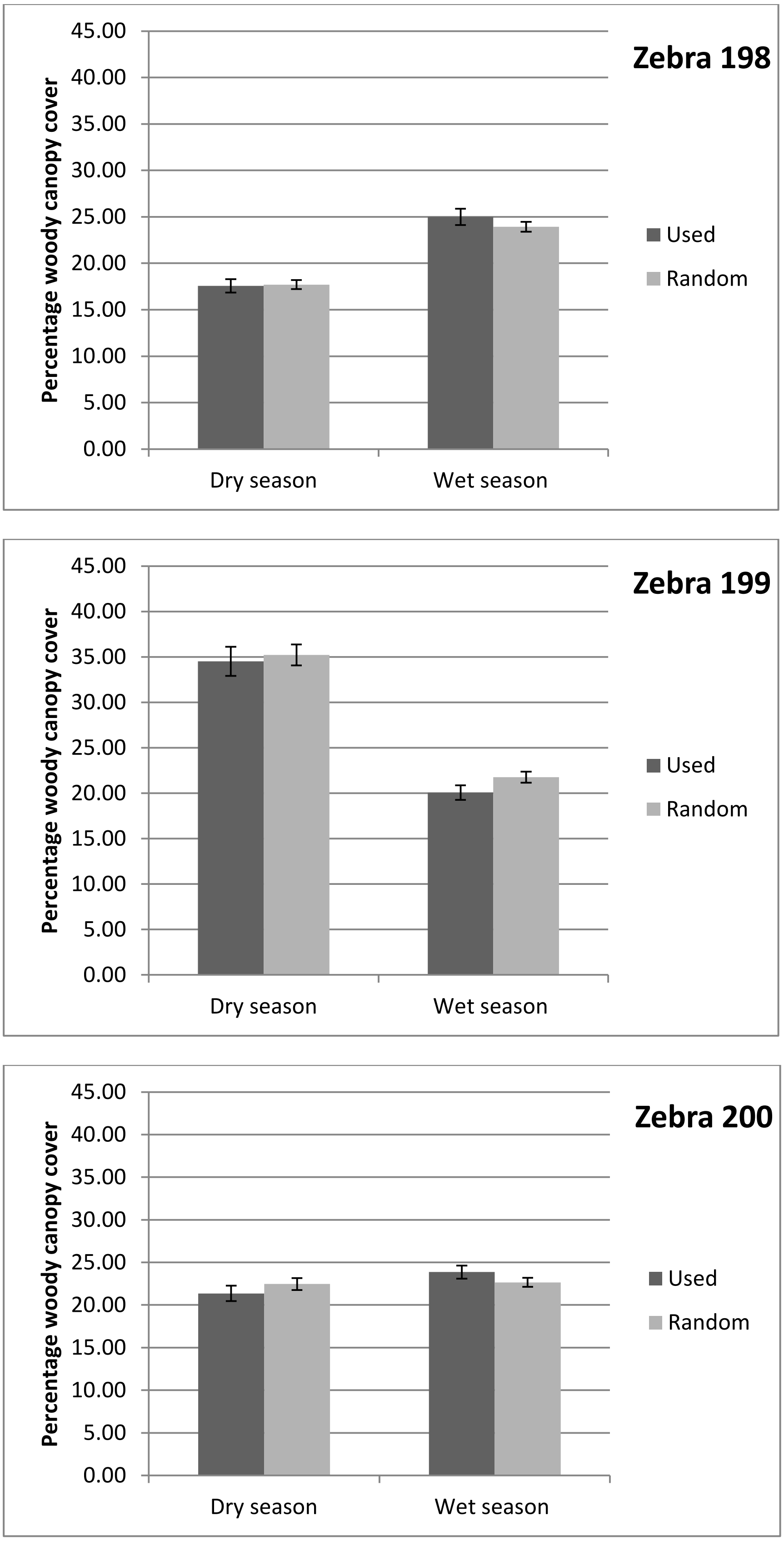

Figure 2.5: Comparison of woody canopy cover (%) at Used and Random locations during the wet and dry season at the **fine scale** of analyses.

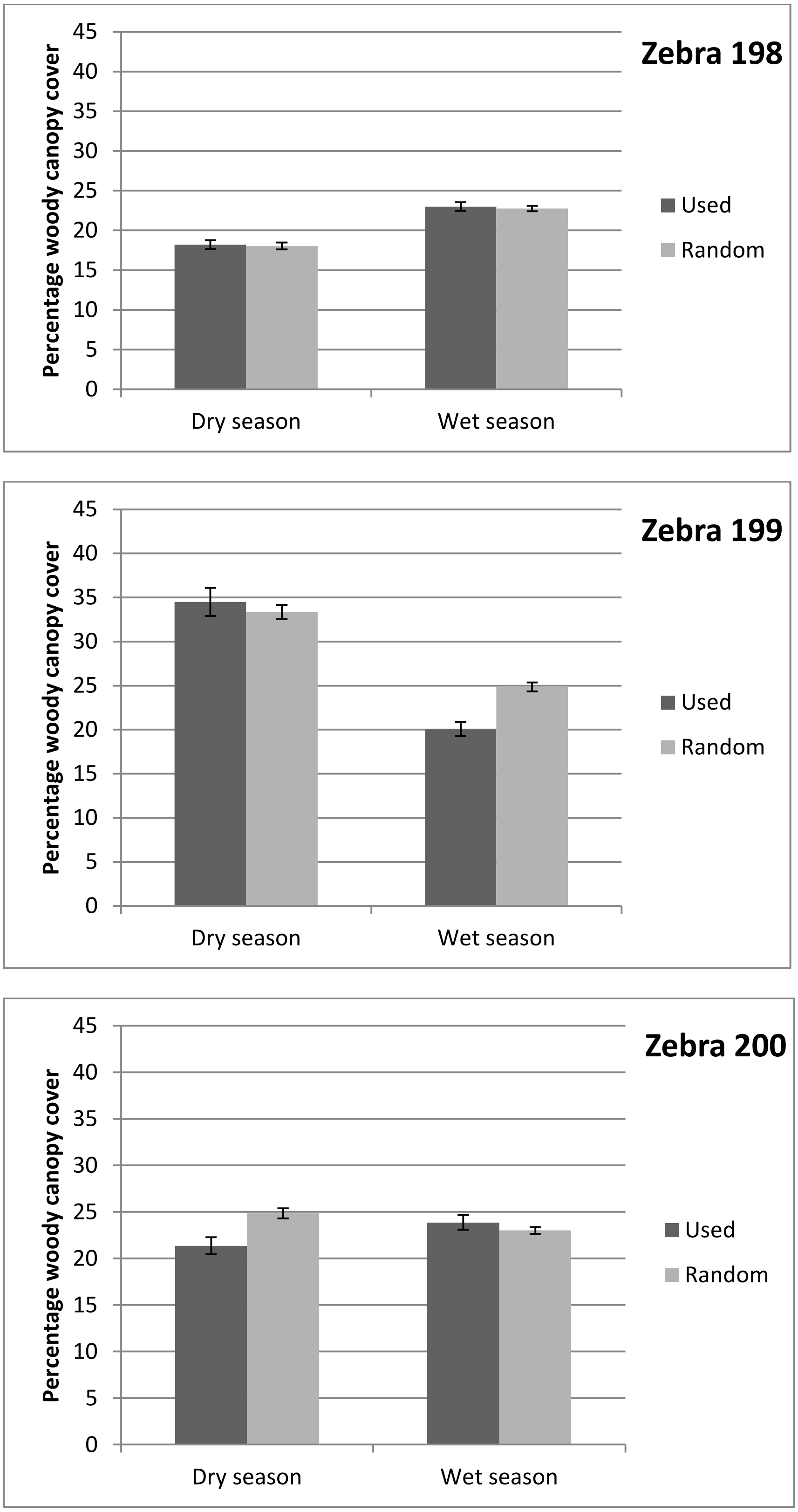

Figure 2.6: Comparison of woody canopy cover (%) at Used and Random locations during the wet and dry season at the **intermediate scale** of analyses.

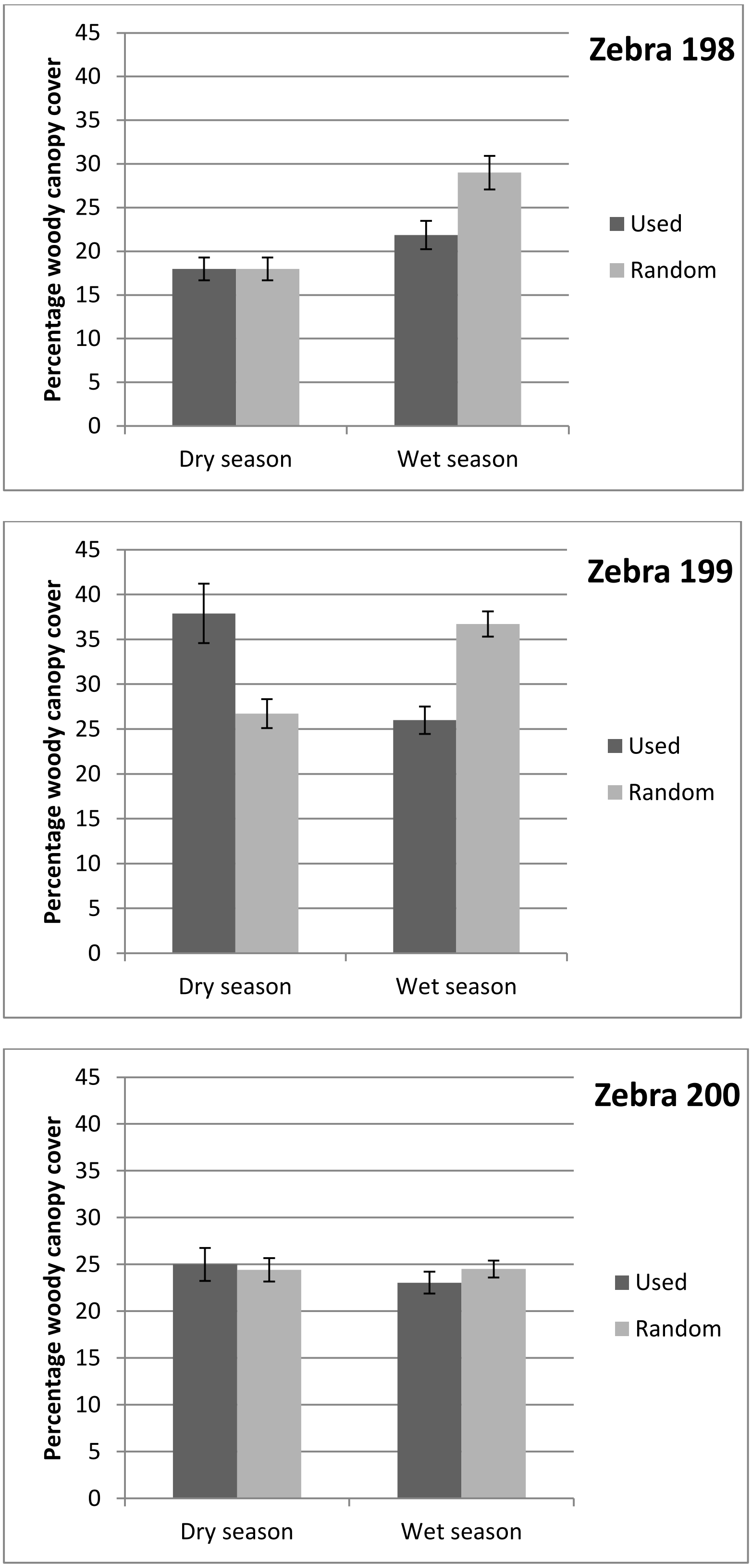

Figure 2.7: Comparison of woody canopy cover (%) at Used and Random locations during the wet and dry season at the **broad scale** of analyses.

The analysis as to whether the difference between MODIS NDVI values and NDVI values from a hand held sensor (Δ NDVI) can be attributed to woody canopy cover, indicated that although there was a positive relationship between Δ NDVI and woody canopy cover, this relationship is not significant (R^2 = 0008)(Figure 2.8).

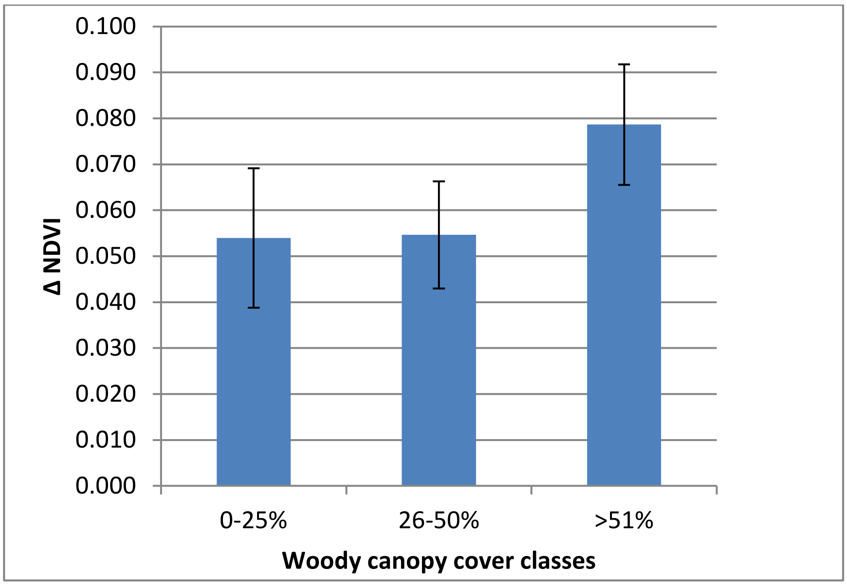

Figure 2.8: Difference between MODIS NDVI and hand held sensor NDVI in relation to percentage woody canopy cover.

Discussion

This study set out to determine whether vegetation greenness (NDVI) is a driver of zebra foraging patterns. I also investigated whether tree cover influences the ability of MODIS NDVI (250 m resolution 16 days composite imagery,) to see the greenness at which zebra respond.

In terms of the first objective, the results indicate that zebra foraging behaviour is highly complex and differs according to the scale of analysis, season, and even between individual zebra herds. The underlying determinant of the relationship between MODIS NDVI and zebra movements appears to be season. During the wet season, the zebra clearly demonstrated evidence of selection for greenness at all scales. This was most apparent at the fine scale. However, even at higher scales where this was not overtly explicit, I note that the MODIS NDVI values of both used and random locations were appreciably higher (>6500) than in cases where greenness was actively selected for by zebra. I postulate that in these cases, the greenness of forage available to zebra at any given time is greater than a threshold requirement needed to satisfy metabolic demands. Invoking optimal foraging theory (Schoener 1971), I suggest that the energy costs associated with leaving a current feeding location and searching for a neighbouring ‘greener’ patch may exceed the energy gains of feeding in a ‘greener’ patch. The zebra is therefore be best served by continuing to feed at its current location.

The selection preference for greenness during the wet season is consistent with a number of studies including Marshal *et al.*’s (2011) study on elephants, Verlinden & Masogo’s (1997) study on ostrich and wildebeest, Musiega & Kazadi’s (2004) study on wildebeest, and a study conducted by Boyers (unpublished data) on zebra.

Unlike the wet season, zebra did not show evidence of selecting for greenness at any scale during the dry season. This is contrary to a similar study on impala conducted by Van Der Merwe & Marshal (2012). A possible explanation for this is that unlike ruminants such as impala, zebra are non-ruminants and must obtain large quantities of forage in order to survive (Owen-Smith 2005). In the dry season green grass is limited and zebra may be forced to graze less selectively in order to meet their nutritional demands. Other possible explanations are that alternate factors such as the presence of predators is influencing zebra foraging patterns during the dry season, or simply that MODIS NDVI cannot discern the greenness at which zebra are responding to during the dry season. In her study, Boyers (unpublished data) found that during the dry season zebra selected for greenness at both the feeding station and grass tuft level. These levels are both lower in the foraging hierarchy than the fine scale defined in my study. It is thus probable that selection for greenness during the dry season is indeed occurring, but at scales beyond the sensitivity of MODIS NDVI.

In the wet season, zebra showed a tendency to avoid areas of high woody canopy – a possible anti-predator response. Interestingly however, the scale at which this was manifest differed between herds. Some herds selected against woody canopy cover at the broad scale, while others only showed a preference at the lower scales. In contrast, during the dry season woody canopy cover did not seem to be as critical factor, with some zebra selecting for high woody canopy cover at the broad scale, but others actively avoiding it at the lower scales.

Predation pressure is an important influence in the distribution of animals (Fischoff *et al.* 2007, Van Der Merwe & Marshal 2012) and may be influencing wet season habitat selection by zebra in this study. Zebra in the Serengeti for example, have been shown to actively distribute themselves so as to avoid predators yet still maximise their quality forage intake (Hopcraft *et al*. 2013). According to Fischoff *et al.* (2007) lions prefer to hunt in more wooded areas and these authors note that the zebra in their study consequently frequented grassland habitat more than they did woodland areas. It is possible therefore that the zebra in my study are actively selecting against woody cover during the wet season to lower the predation risk.

Conversely, during the dry season I suspect that habitat selection by zebra may not be as heavily influenced by predation pressure as it is during the wet season, and may in fact be determined by the foraging requirements of zebra moving though a resource strained landscape. During the dry season high quality protein is limiting and herbivores are forced to leave short nutritious grasslands and move into areas of high forage production, such as floodplains or open vleis (Fynn & Bonyongo 2011). These areas have inherently low woody canopy cover as a consequence of the high soil moisture and this may explain the presence of zebra herds in areas of low tree density.

Similarly, selection by zebra of areas of high woody canopy cover in the dry season may also be a consequence of zebra attempting to feed on high quality forage. *Acacia* trees for example, have a large positive effect on the nutrient content of vegetation growing beneath them, particularly grass species such as *Panicum maximum* (Van Der Merwe & Marshal 2012). During the dry season this grass becomes an important grazing resource and by selecting wooded areas, zebra may thus also be attempting to maximise access to high quality forage.

In term of my second objective - whether tree cover influences the ability of MODIS NDVI to see the greenness at which zebra respond – I note that despite a positive relationship between ΔNDVI and woody canopy cover, the relationship is not significant and indicates that in savanna ecosystems tree densities may not be high enough to affect overall MODIS NDVI readings. As such, contrary to the contention of Archibald & Scholes (2007), it may not be necessary to separate the greenness contributions of trees and grasses when using MODIS NDVI in savannas.

Conclusions

Although MODIS NDVI is a valuable tool in modern conservation, the results of this study highlight the complexity of herbivore foraging patterns. Various ecological factors, both forage-related and non-forage related, may determine herbivore movements and distribution. The importance of these factors varies at both temporal and spatial scales, and indeed between individual zebra.

Forage-related factors include grass quality and quantity which depend on *inter alia* stochastic and patchy rainfall patterns (Senft *et al.* 1987, Hopcraft *et al*. 2013), edaphic factors (Fynn & Bonyongo 2011) and fire (Fuhlendorf *et al.* 2008). Foremost amongst non-forage related factors is predation pressure. Indeed, abandonment of patches even very green patches may be unrelated to any nutritional demand, and may purely be a response to the presence of predators, such as lions (Fischoff *et al.* 2007).

The results of this study indicate that both forage-related factors and non-forage related factors determine zebra movements. The relative importance of these factors is contingent upon season and level of the foraging hierarchy, and it is therefore important to consider both when investigating herbivore spatial organisation (Fischoff *et al.* 2007, Bro-Jørgensen *et al.* 2008).

In savanna ecosystems, MODIS NDVI at a resolution of 250 m is an important and useful tool in studies relating to herbivore grazing ecology. It seems however, that this is limited to specific spatial and temporal scales and moreover should be accompanied by an understanding of other factors, such as *inter alia*, the presence of predators.

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