AN ABSTRACT OF THE THESIS OF

Cathleen Anna Dora for the degree of Masters of Science in Environmental Sciences presented on July 28, 2004.

Title: The Influences of Habitat Structure and Landscape Heterogeneity on African Buffalo (*Syncerus caffer*) Group Size in Hluhluwe-iMfolozi Game Reserve, South Africa.

Abstract approved:

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David A. Lytle

This study aimed to connect habitat and landscape scale variation, through time and space, to wildlife population dynamics. I studied African buffalo (*Syncerus caffer*) group size according to habitat structure, landscape heterogeneity, forage quality, and water availability in Hluhluwe-iMfolozi Game Reserve, South Africa. I used two approaches to study grouping behavior of buffalo – daily field observations and digital vegetation classification and mapping home range areas to quantify seasonal and geographic changes.

Daily buffalo observations included a record of tree and shrub density within habitat patches and buffalo group counts. I concluded that buffalo occurred in smaller groups during the dry season. During both seasons, buffalo maintained larger groups in more open habitat and in the dry season, group size also depended on grass quality.

To examine landscape heterogeneity, a Landsat Enhanced Thematic Mapper (ETM) satellite image was classified into structural vegetation types and radio tracking data from ten herds were used to calculate and delineate home range area. Vegetation

structure and water availability were summarized in each home range area and an average buffalo group size was calculated for each herd in each season. During the dry season, average vegetation density was the only significant influence on group size. Again, buffalo maintained larger groups in more open areas. During the wet season, vegetation density did not affect group size, but the heterogeneity of vegetation types within the home range did. Buffalo were found in larger groups in more heterogeneous home range areas. The total size of the herd was also a significant influence in the wet season. Larger herds maintained larger average groups.

I also determined the influence of vegetation structure and landscape heterogeneity on group size variability within herds. During the dry season, variability was affected by home range heterogeneity, total herd size, and, marginally, by water availability. In the dry season, more variability was observed in heterogeneous areas and areas with more permanent water. Larger herds also had more group size variability than small herds. In the wet season variability was determined by total herd size only. Larger herds had more variability than small herds.

This study has important implications in terms of wildlife management. I have shown that habitat structure, forage availability, and landscape heterogeneity significantly affect buffalo population dynamics. I have also presented a method to quantify vegetation factors on a landscape scale and determine how those factors can influence wildlife populations. The map of structural vegetation can also be used to examine the effects of landscape change, yearly burning regimes, and large herbivores on the reserve's ecosystem.

The Influences of Habitat Structure and Landscape Heterogeneity on African Buffalo (*Syncerus caffer*) Group Size in Hluhluwe-iMfolozi Game Reserve, South Africa

by
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Cathleen Anna Dora, Author

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The Influences of Habitat Structure and Landscape Heterogeneity on African Buffalo (*Syncerus caffer*) Group Size in Hluhluwe-iMfolozi Game Reserve, South Africa

1. Introduction

1.1 Overview

In the last ten years, advances in satellite imagery and geographic information systems (GIS) technology have enabled ecologists to study animal populations from an entirely new perspective. Landscape patterns and other broad scale environmental factors can be detected and measured using remote methods that combine field collected data with satellite or aerial imagery. These remote sensing methods promise new insights to classic animal behavior problems such as group foraging dynamics (Charnov 1974, deBoer and Prins 1989, Belisle 1998), social behavior and predation (Festa-Bianchet 1988, Clutton-Brock et al. 1999, Ruckstuhl and Festa-Bianchet 2001), and the influence of the landscape on population dynamics (Dempster and Pollard 1986, Bailey et al. 1996, With et al. 1997, Hanski and Ovaskainen 2000, Hiebeler 2000, Lawes et al. 2000, Kie et al. 2002).

In natural ecosystems, living organisms are not uniformly or randomly distributed, but aggregate in patches or groups, form gradients, or other kinds of spatial patterns (Legendre 1989). The challenge facing many ecological and biological studies is to quantify environmental pattern and to determine its effect on the processes, dynamics, and biota of the ecosystem. Remote sensing, digital image processing, and GIS allow us to examine the environment on a broader and more complete scale than ever before.

The landscape structure and broad scale patterns found in the environment are not simply the background upon which organisms live and ecosystems function. Wiens et al. (1993) introduced the concept that landscape matrices of vegetation patches are not ecologically neutral, but an active influence on the biotic processes of the ecosystem. They emphasized that matrix properties such as edge contrast, vegetation structure, and land use influence animal movement. Structural patterning of the vegetated environment influences the spatial organization of organisms. Belisle (1998) demonstrated that the spatial distribution of forage constrains group size. A combination of remotely-sensed parameters such as structural vegetation properties and forage distribution may be useful for understanding the social dynamics of herbivores that live in groups.

Real and McElhany (1996) presented the question of which biological and ecological processes produce measurable patterns of spatial organization. Spatial questions present problems which are often solved disconnected from biology or ecology (i.e. parametric statistical analysis of spatial pattern). Advances in GIS and modeling technologies are poised to connect spatial dynamics to the disciplines that the variable of space once confounded. Technology is beginning to allow us to embrace the complexity of landscapes rather than impose artificial simplicity on them (Wiens 1999). With these tools it is easy to detect when environmental and biological variables may be linked to one another sharing the same spatial structuring (Borcard et al. 1992).

Spatial heterogeneity is found at many different scales across landscapes. Kareiva (1994) challenged the future of ecology to correct past oversimplification as a result of neglecting spatial variation on many different scales. He insisted that investigation of space should become a fundamental theme around which we base our study of nature and its processes. Merriam (1991) agreed that landscape heterogeneity has a functional importance in ecosystems. O'Neill et al. (1986) stressed the importance of representing the world on a scale of time and space at which the environment and organisms respond. Heterogeneity has been widely studied in terms of the effects of habitat fragmentation on biodiversity, animal movement, and population dynamics (Burgess 1988, Saunders et al. 1991, Johnson et al. 1992, Pulliam et al. 1992, Diffendorfer 1995, Bjornstad et al. 1998). There is a growing interest to study heterogeneity in terms of spatial grain, vegetation structure and landscape organization (Ives et al. 1998, Hiebeler 2000, Kie et al. 2002). This study outlines digital and field methods to measure landscape heterogeneity and determine its effects on animal group size.

In order to study large herd animals, it is most sensible to measure and observe environmental variables on the scale of home range areas. Home range can be defined as "the area, usually around a home site, over which the animal normally travels in pursuit of its routine activities" (Leuthold 1977). Representing and examining the area within which animals live and travel is critical to ecological questions ranging from behavioral to environmental (Getz and Wilmers, in press). Various methods have been developed to determine the size and relative use of home range areas (Anderson 1982, Samuel and Garton 1985, Samuel and Green 1988, Worton 1989, Harris et al. 1990, Moorcroft et al. 1999, Kenward et al. 2001, Blundell et al. 2001, and Selkirk and Bishop 2002). Getz and Wilmers (in press) examine many home range methods and connect their local nearest-neighbor convex-hull method to an ArcView script, introducing the groundwork for a whole new set of ecological questions. With animal populations placed in a spatial context, we are able to connect various aspects of their environment to the area in which they live and interact.

Addicott et al. (1987) pointed out that conclusions about one scale of environmental heterogeneity may be invalid if transferred to another scale. It is important then to consider appropriate scales of response. The first scale in this study refers to a daily influence of vegetation structure and forage availability on buffalo group size; the second examines seasonal averages and variability based on water and average vegetation measures within herd home range areas. Buffalo maintain home range areas that do not significantly overlap between herds and spatially shift both yearly and seasonally.

Home range area relates positively with body size for many large herbivores and there is likely to be a similar relationship between herd size and home range area. Lindstedt et al. (1986) detailed this relationship between animal body size and home range area. They concluded that animals select and use home ranges to meet their metabolic needs; larger animals utilizing larger home range areas. Polo and Carrascal (1999) linked body mass, both evolutionarily and ecologically, to habitat use. Herd animals must then, on some level, select and utilize areas that can sustain their entire group. Home range areas must be suitable for the total size of the herd and daily habitat choices must influence daily grouping dynamics within that larger herd.

African buffalo herds are not static entities, but often split into smaller splinter groups and eventually rejoin into the same larger herd (Prins 1989). Prins argued that this herd grouping dynamic was dependent on the original size of the herd. Large herds split more frequently than small herds; however, a herd's total size is not the only driver of group dynamics. Other factors including, forage quality and availability, habitat structure, water availability, and landscape heterogeneity, may play a role. In the context of this study, I defined landscape heterogeneity after McGarigal et al. (2002) as a measure of the spatial grain of discrete patches of structural vegetation rather than functional habitat.

This study synthesized remotely-sensed landscape-level data and field observations of animal groups in order to examine group dynamics on multiple spatial and temporal scales. I hope to broaden the scope of basic ecological questions concerning foraging strategies and group dynamics and provide information that may aid in managing large herbivores on the scale of entire ecosystems.

1.2 Objectives

The following is an investigation of how vegetation structure, landscape heterogeneity, and forage quality influence African buffalo (*Syncerus caffer*) group size. Buffalo herds return to previously grazed patches in order to best utilize nutritionally rich re-growth (deBoer and Prins 1990, Mugangu et al. 1995). Large grazing herbivores rely on spatial memory to improve foraging efficiency and could use previous grazing experiences to develop a routine of habitat utilization (Bailey et al. 1996). Within this framework, buffalo could effectively develop a grazing routine within their home range that is both nutritionally rich and energetically efficient. The driving forces behind the creation and maintenance of such a routine remain largely unknown but, habitat structure, forage availability, and the degree of heterogeneity of a herd's physical environment could play a role.

In order to measure and study the effects of the physical structure of vegetation on buffalo herds, a vegetation map depicting such an environment is necessary. The following includes a method to map and analyze structural vegetation in southern African savannah ecosystems and applies these techniques to Hluhluwe-iMfolozi Game Reserve in KwaZulu-Natal, South Africa. Hluhluwe-iMfolozi is a park dedicated to wildlife management of large herbivores such as African buffalo, elephant, white and black rhinoceros, kudu, giraffe and predators such as lion, leopard, hyena, wild dog, and cheetah. Supplemental to game management, an understanding of vegetation pattern can improve the decision-making process and increase the longevity and effectiveness of the reserve. With a map of structural vegetation and buffalo home range areas, managers will be able to quantify vegetation variables on a landscape scale and determine how some of these factors affect animal group size, which could help managers decide where animals should be introduced or removed. A vegetation map could also be used to monitor broad scale changes in vegetation that occur due to yearly burning regimes and grazing and browsing of large herbivores.

Apart from the study of Hluhluwe-iMfolozi's buffalo population, the park supports projects investigating predator movement and population dynamics, elephant ecology and management, wild dog reproductive behavior, the effects of fire on grasslands, and a long term study on large herbivores and grazing patch size. Management decisions based on the ecological and biological data of these studies can be placed into a spatial context. A map of basic vegetation types can be used as a template to compile and analyze field data on animal movement, group size, habitat utilization, and landscape change as a result of prescribed burning.

The goals of this study were first to generate a digital map of structural vegetation within Hluhluwe-iMfolozi Game Reserve, then to calculate and delineate African buffalo home range areas for ten study herds over two and a half years and to summarize structural vegetation within those home range areas. Third, I examined seasonal and geographic variation in buffalo group size and group size variability. I wanted to determine how habitat structure and landscape heterogeneity, in terms of the spatial grain of vegetation patches, influenced group size using two approaches. To examine group size data at a fine temporal scale, I analyzed daily buffalo tracking data in terms of tree and shrub density, grass quality, and presence of water. Next, at a coarser, seasonal scale, I summarized home range characteristics of vegetation density, area covered by water, and landscape heterogeneity to determine how broad scale geographic variation affects seasonal average size and variability within herds.

2. Methods

2.1 Study Area

Hluhluwe-iMfolozi Game Reserve is located in KwaZulu-Natal, South Africa (28° S, 31-32° E). The fenced reserve covers about 900 km^2. High hills, large open grasslands, and dense broadleaf forests characterize the northern Hluhluwe sections of the park while the southwestern iMfolozi sections are dominated by lower, relatively flat *Acacia* spp. bush land. Rainfall in Hluhluwe-iMfolozi occurs seasonally (November through April) and on a north/south gradient. The northern sections receive roughly 980mm annually, while the southwestern sections receive approximately 650mm (Jolles 2004). This gradient in rainfall along with widely diverse soil and topography contribute to the park's diversity of vegetation species and structure. Yearly prescribed burning and effects of large herbivores such as elephants, buffalo, and kudu are also likely contributors to landscape heterogeneity and maintenance of vegetation diversity. Heterogeneity observed over the landscape led to the hypothesis that animal behavior and population dynamics may also display changes related to these geographic gradients. There is one paved road running north/south and several dirt roads providing vehicle access to a large majority of the reserve (Fig. 1).

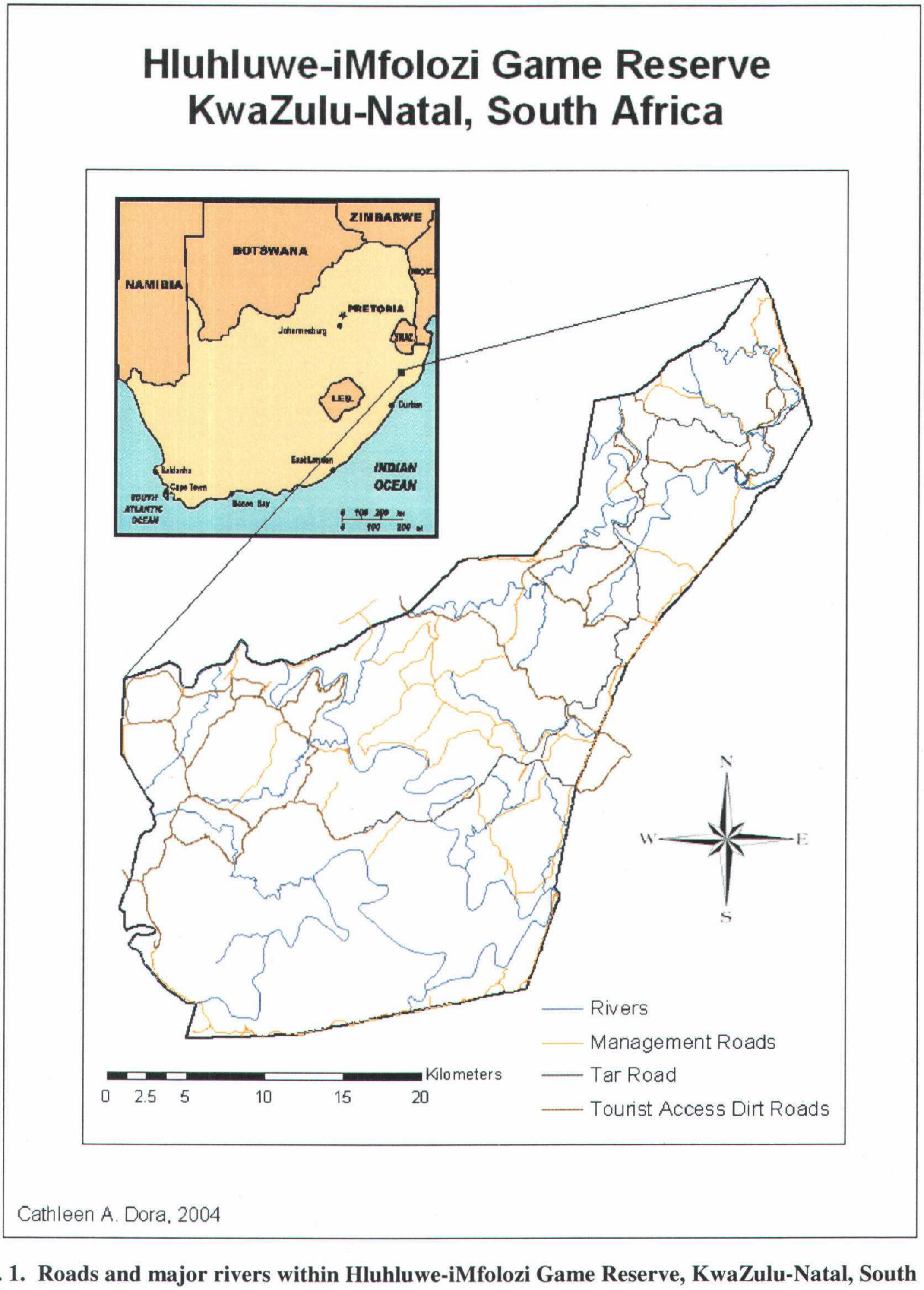

Fig. 1. Roads and major rivers within Hluhluwe-iMfolozi Game Reserve, KwaZulu-Natal, South Africa.

2.2 Study population

The study population consisted of ten radio collared buffalo herds (one to three collared adult females per herd) in the park's Nqumeni, Masinda, and Mbuzane management sections (Fig. 2). The herds varied in size from 45 animals to 270 animals and were marked with herd-specific brands at yearly tuberculosis testing. Select herds also have individuals marked with color-coded ear tags. These markings allowed observers to identify uncollared splinter groups of known herds.

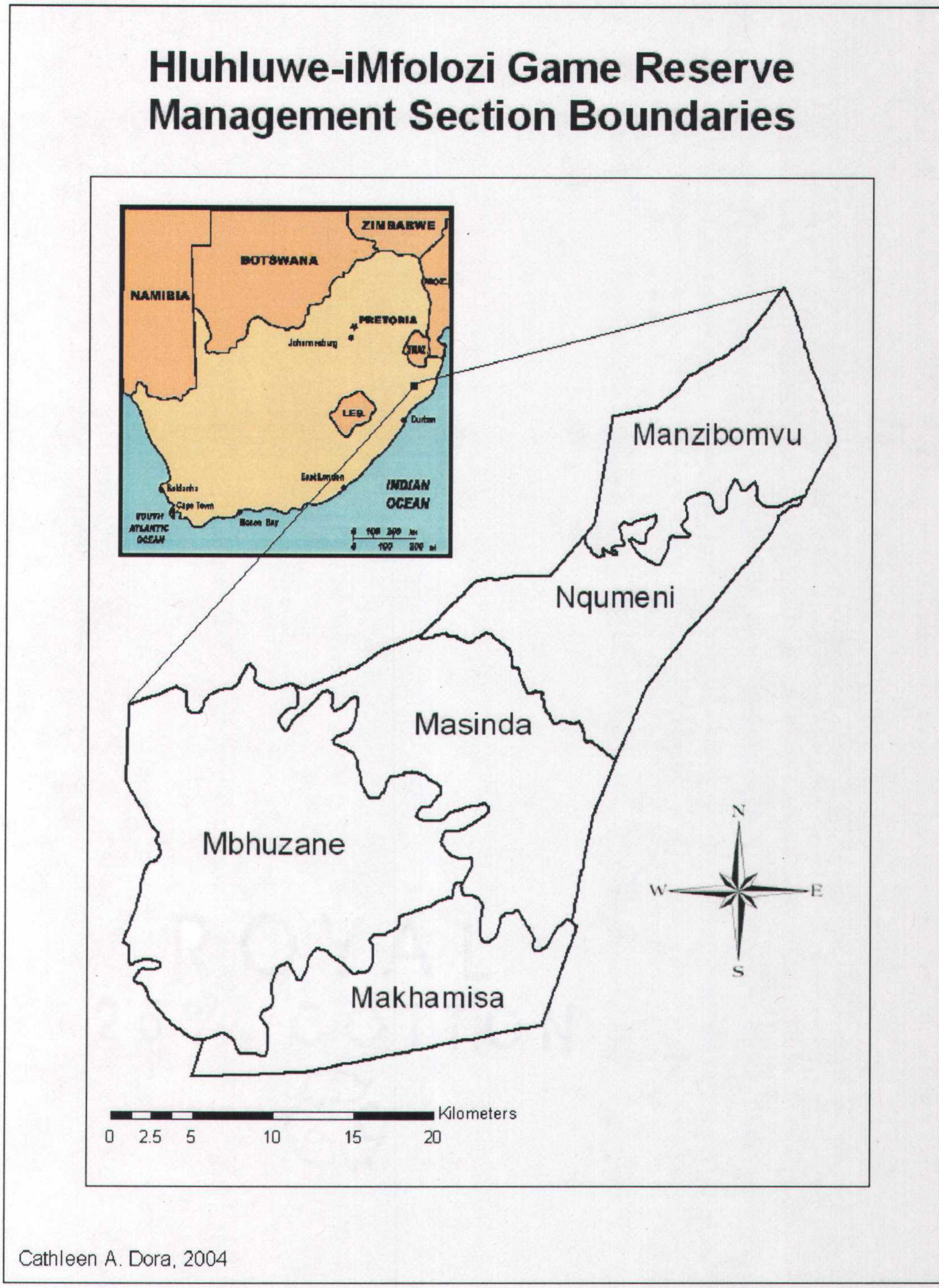

Fig. 2. Map illustrating management sections in Hluhluwe-iMfolozi Game Reserve.

2.3 Habitat Data Field Collection

Recording of habitat was consistent with a method devised for an ongoing study of tuberculosis in the buffalo population (Jolles et al. 2004) and is a simplified version of the habitat definitions described by Mugangu et al. (1995). Seven habitat classifications were devised characterizing physical vegetation structure (Table 1). Each habitat type definition depended on two physical characteristics – canopy tree cover and thicket stem density. These characteristics concern the physical structure of habitat patches so canopy and thicket were defined simply by size, not by species. Woody plants over a height of 4 meters were classified as canopy and all other woody plants as thicket. For each habitat type a number 0 through 4 was assigned to quantify canopy and underbrush. Underbrush values were determined according to stem density below 4 meters (Walker 1976).

Table 1. Field definitions of vegetation types. Percentage values reflect visual interpretation of vegetation within the area occupied by the buffalo group at each sighting. Canopy and underbrush values were assigned to group vegetation types into generalized classes.

Vegetation Type	% Canopy Cover	Canopy Value	% Stem Density	Underbrush Value
Open Grassland	0	0	0	0
Open Thicket	0-25	0-1	0-50	1-2
Med. Dense Thicket	0-25	0-1	51-75	3
Dense Thicket	0-25	0-1	76-100	4
Open Woodland	26-50	2	0-100	0-4
Med. Dense Woodland	51-75	3	0-100	0-4
Dense Woodland	76-100	4	0-100	0-4

Dominant species information for woody plants was also noted. Other habitat information collected included percent green of grass cover (a measure of forage quality) and presence of a water source in the animals' immediate area. The grass quality percentage was given a rank 0-7 (Walker 1976) for data analysis. Rank definitions are as follows.

Rank	Percent Green
0	0
1	1-10
2	11-25
3	26-50
4	51-75
5	76-90
6	91-99
7	100

The patch of land considered in recording these habitat data was the area occupied by the buffalo group at the time of each sighting.

2.4 Vegetation Classification from Satellite Imagery, Unsupervised

Unsupervised vegetation classifications can be used to find patterns in an image when the user cannot define cover classes prior to the classification process. The unsupervised classification detects similarities in the image and allows examination of what such similarities may represent. An unsupervised classification was performed using the iterative self-organizing data analysis method (ISODATA) on bands 2 (green), 3 (red), and 4 (infrared) of the Landsat ETM image (Jensen 2000). Parameters were set at the following values to allow the widest variety of vegetation classes while not allowing clumps to appear in patches smaller than 60 m^2, four Landsat ETM pixels (Table 2).

Table 2. Parameters set for unsupervised classification of Landsat ETM image.

Isodata Parameters	Description	Value Set
Number of classes	Minimum and maximum number of classes allowable	Minimum = 5 Maximum = 50
Maximum iterations	The classification process stops when either the maximum number of iterations or the number of pixels in each class changes by less than the change threshold	20
Change Threshold		5%
Minimum number of pixels per class	Clusters contain no less than this number of pixels	4
Maximum class standard deviation	If the standard deviation (of spectral values) within the class is more than this value the class is split	1
Minimum class distance	If the distance between class means (of spectral values) is less than this value classes are merged	5
Maximum number of merge pairs	The number of classes allowed to be merged	4

I defined clumped pixel groupings post classification into dense, medium dense, open vegetation and open grassland by image examination and field knowledge. Unsupervised classification methods do not require any field collected data points. I present this method as a possible alternative to a supervised classification to detect very broad scale trends in the landscape.

2.5 Vegetation Classification of Satellite Imagery, Supervised

The supervised vegetation classification process transforms the red/green/blue spectral values of pixels into land and water classification polygons. The process depends on the relationship of each pixel's digital color space value and the values assigned to the field collected training areas (Ma et al. 2001).

Landsat ETM bands 2, 3, and 4 were used because they measure chlorophyll absorption and therefore vegetation cover (Jensen 2000). Band 1 is used to measure water reflectance. This band was not used in this study because of the course resolution of the data (30 m x 30 m). Large rivers and streams were mapped from topographic and field collected data (Hluhluwe Research Centre, unpublished). Water layers were incorporated into the vegetation map post-classification. Bands 5 and 7 are used to measure leaf moisture content which can detect seasonal changes in vegetation but not amount of cover. Bands 6 and 8 of Landsat ETM are at different spatial resolutions (60 m x 60 m and 15 m x 15 m respectively)

The maximum likelihood classification method is based on the normal probability function (Jensen 1996). The algorithm views the image in various dimensions as probability surfaces in what is referred to as the color space of the image. The color space is built upon the value of each pixel in each color band of the satellite sensor. The Landsat ETM satellite has eight bands meaning each pixel has eight color values and can potentially be viewed in eight dimensions of color space. Each pixel of the image is analyzed and assigned to the class to which it has the highest probability according to the training area data.

The maximum likelihood method was preferred to other supervised classification methods due to its ability to dimensionally contour the color space of the image according to the training data values. Other methods classify pixels according to their value relative to other pixels, while the maximum likelihood method relies on the training data and a probability threshold. The maximum likelihood method classifies areas outside the probability threshold as 'unclassified' rather than interpolating from similar pixels. The user is then able to interpolate unclassified pixels in geographic space (incorporated into a GIS) rather than the color space of the image. In terms of vegetation classification, interpolation in geographic space makes the most sense because isolated pixels often can easily be defined by their surrounding space (i.e. one isolated pixel within a large defined polygon).

GPS points were collected at the approximate center of 60 m x 60 m homogenous habitat areas with a hand held Garmin GPS unit set to World Geodetic System 1984 datum in latitude and longitude (Tanser and Palmer 2000). This first set of vegetation training points consisted of twenty points in each of the seven defined habitat types. The training points were incorporated into tables and converted to decimal degrees using a script written for that purpose (Tchoukanski 2003, Appendix A).

Using the Interactive Data Language/Environment for Visualizing Images (IDL/ENVI 4.0, 2003) field training points were used to create “regions of interest”. From each point a small homogenous area was delineated (Fig. 3). Mapping vegetation types requires a careful definition of scale (Wang et al. 2001) and single points are not a reasonable scale from which to define habitat types in areas. Homogenous training areas were delineated from image examination rather than a buffer function that would create a circular area around points because some data points were located on the border of their vegetation type. A buffer would have included pixels outside the homogeneous area.

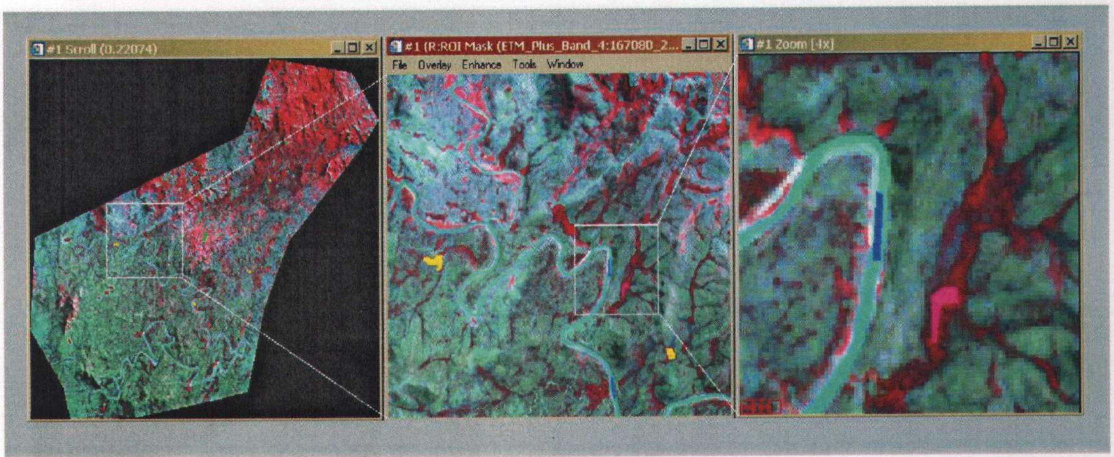

Fig. 3. Defined training areas for supervised classification in IDL/ENVI. At the far right a dark blue area of water and a pink area of dense thicket are visible.

The training areas were then used to perform a supervised classification on bands 2, 3, and 4 of the Landsat ETM image. The maximum likelihood method was used to generate a class map at 50% threshold probability. A 50% classification refers to the probability of any pixel belonging to its assigned class. This study aims to delineate relatively coarse vegetation types; therefore, 50% is an appropriate classification level. A greater probability would result in large unclassified areas and a lesser probability would misclassify types with similar spectral reflectance.

The resulting classification image was then post-processed by sieving to remove isolated pixels within larger polygons (Fig. 4). The sieved image was then clumped to eliminate the isolated unclassified pixels (Fig. 5). Sieving removes isolated pixels by defining them as unclassified depending on the class value of the eight neighboring pixels. Isolated pixels are unreasonable because, for the purposes of this study, I defined vegetation types in areas on the order of 60 m^2 which is equal to four Landsat ETM pixels. Clumping interpolates classification of isolated pixels from the value of its eight surrounding pixels and eliminates borders between classified polygons of the same value.

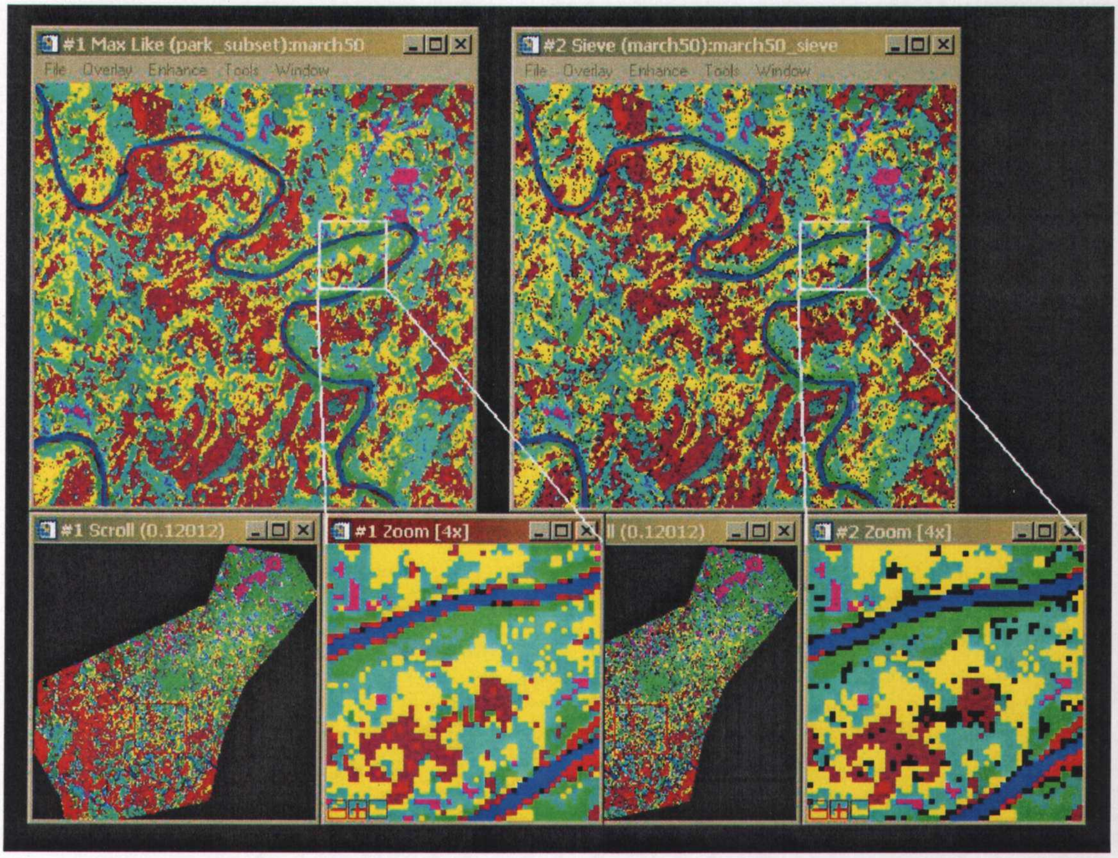

Fig. 4. IDL/ENVI screen shot illustrating a supervised classification (left) and the same area after a post processing sieve (right).

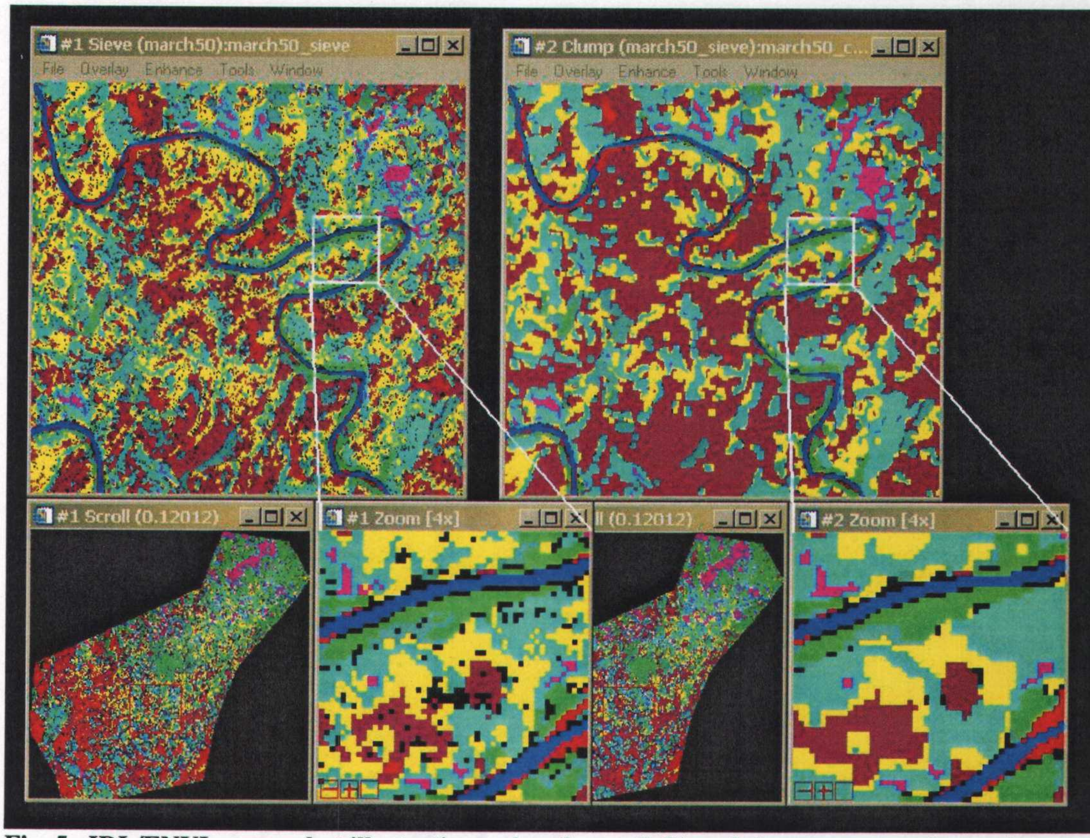

Fig. 5. IDL/ENVI screen shot illustrating a sieved area (left) and the same area after a clump (right).

The resulting polygon coverage was then converted into a shapefile and incorporated into an ArcView 8.3 project.

2.6 GIS Methods

The geographic information system (GIS) layers were built upon park infrastructure and river shapefiles provided by Hluhluwe Research Centre. The supervised classification layer was clipped to the exact park boundaries and a union was performed on the river and vegetation layers combining them into one coverage. The union layer was then dissolved to join adjacent polygons of the same class.

The vegetation layer was ground-truthed using 111 vegetation points collected throughout the Manzibomvu, Nqumeni, Masinda, and Mbuzane sections of the reserve

(Fig. 6). Field collected points of known vegetation were incorporated into the GIS and compared to the computer generated vegetation data.

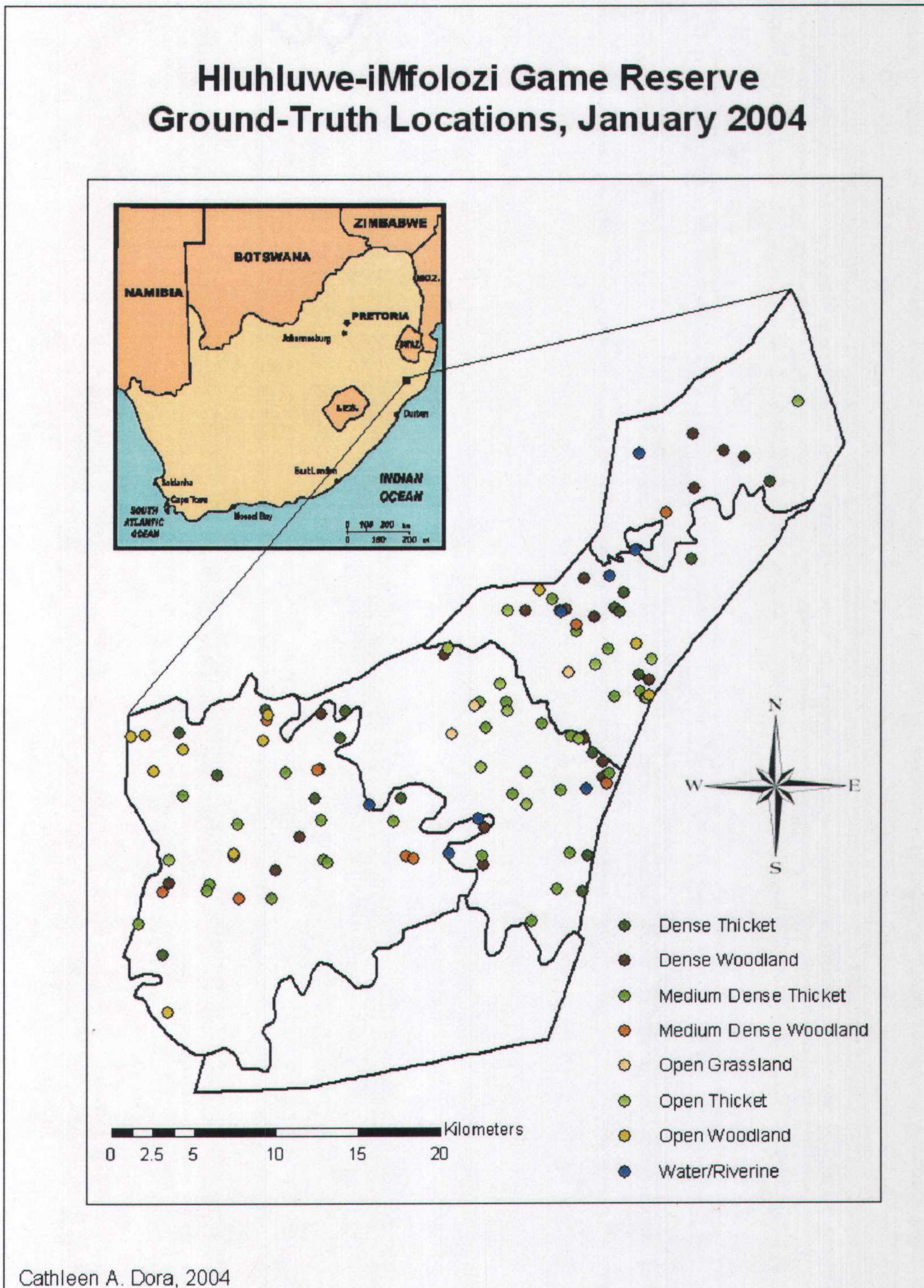

Fig. 6. Hluhluwe-iMfolozi Game Reserve vegetation ground-truth point locations, January 2004.

2.7 African Buffalo Home Range Mapping

For ten study buffalo herds home range areas were calculated in Arc View using the local, nearest-neighbor, convex, hull method (Getz and Wilmers, in press) with a script written for this purpose (Andy Lyons, personal communication; appendix A). This method is based on the construction of animal utilization distribution areas from a union of minimum convex polygons associated with each herd location point and its neighboring points. Getz and Wilmers compared their results to commonly used home range measures such as the minimum convex polygon (Rurik and Macdonald 2003), the bivariate kernel (Worton 1989), and α-hull methods (Burgman and Fox 2003). They concluded that their method, an extension of the simple minimum convex polygon, performed better than the kernel method in fitting home ranges with distinct boundaries and better than the α-hull method at incorporating all location points into the home range area. The home range areas were calculated for three consecutive wet seasons (November through April) and two corresponding dry seasons (May through October) from November 2000 through April 2003. I compared home range areas across years and seasons and between herds using analysis of variance (ANOVA) where total home range area (m^2) was the response variable to determine if ranges varied between herds, seasons, and years.

2.8 Animal Observation Data Collection

Buffalo group size and daily habitat data collection consisted of one to three weekly sightings of each collared buffalo herd. Two field crews of two people spent roughly 19,200 person hours collecting about two hundred observations of each herd over three wet seasons and two dry seasons. Telemetry equipment was used to locate collared groups. The herds were observed through binoculars and a spotting scope from the closest possible point without disturbing the animals. Location was recorded using a Garmin GPS unit and 1:50,000 topographic maps. During each herd sighting the number of animals present, vegetation type, and location were recorded. For observations where the collared herds were split into smaller splinter groups a complete sighting record was made for all uncollared groups that could be located within known home range areas. These groups were considered splinters of the collared herd that regularly occupies that home range area. It was also noted if tagged or branded animals were seen thus confirming that the uncollared groups were part of known herds. The number of animals present was recorded after a series of one to five counts of the herd depending on the herd's location and activity. At each sighting the counts were evaluated on a qualitative scale from poor to excellent depending on an estimate of how many animals could have been missed or counted twice, depending on animal activity and herd visibility. Counts rated poor to medium (plus or minus over 15 animals) were eliminated from the data analysis presented here. Counts of the same herd occurring less than two days apart were also eliminated. On the basis of several hundred observations where group size changed from day to day or even within one day, I conservatively estimated that herds were able to reorganize into new subgroups in a matter of two days or longer. Therefore, sightings spanning that time-frame are considered to be serially-independent data points.

The southern-most portion of the reserve is designated wilderness and has no vehicle access. For this reason no animal observations were recorded in that section of the reserve. The northern-most section of the reserve is characterized by steep terrain and dense woodland. As animal observation is extremely difficult in this section of the reserve, it was omitted from the field data collection area. All other areas of the reserve are accessible either by four-wheel drive vehicles or on foot.

3. Statistical Methods

I analyzed group size and vegetation data in three sections. First I examined variables of daily habitat choice using vegetation data collected at daily buffalo sightings. Next I analyzed data on the scale of seasonal home range areas. Vegetation variables were measured in each home range area from the GIS and tested against group size average within season. Finally to analyze influences on group size variability I tested the same home range variables against group size standard deviation within season. The analysis aimed to explain grouping behavior on various spatial and temporal scales. The daily habitat data allowed examination of habitat choice within herds' home range area. The average seasonal vegetation variables allowed for a geographic range of examination; how the spatial grain of vegetation patches affects grouping behavior. The temporal variation came between seasons when changes in water and forage availability forced the animals to adapt.

3.1 Influences of Habitat Structure on Daily Group Size Choice

The independent variables measured on a per-sighting basis were tree density, shrub density, grass quality as a percentage of green cover, and waterhole presence. Vegetation structure was determined from tree and shrub density and therefore not an independent variable. I tested the vegetation factors separately (tree and shrub density instead of vegetation structure) to investigate which individual measure may be the more important driver. An analysis of variance (ANOVA) was performed with individual counts of buffalo group size as the response variable and four factors of habitat measures (Table 3). The ANOVA assumptions of normality and equal variances were met or nearly met by all datasets. The wet season dataset consisted of 589 independent buffalo sightings and the dry season consisted of 505 independent sightings.

Table 3. ANOVA factors testing influences on buffalo group size on a daily time scale.

Buffalo Group Size =	Factor Description
Tree Density	Rank of 0-4 indicating percentage of canopy cover (>4m)
Shrub Density	Rank of 0-4 indicating ground cover percentage of stem density (<4m)
Grass Quality Rank	Rank of 0-7 indicating quality in terms of relative greenness (Walker 1976)
Waterhole Presence	Binomial variable present or absent

3.2 Influences of Home Range Vegetation Density and Heterogeneity on Average Group size and Group Size Variability

The group size average from approximately 20 to 150 separate sightings was taken for each herd each season. Variability was measured as the standard deviation of these counts. ANOVA was used to determine whether group size and variability in group size differed significantly between season and among herds. The data were then analyzed separately for wet and dry seasons.

The home range areas were overlaid with the structural vegetation layer to determine a variety of larger scale vegetation factors. Variables of landscape heterogeneity (after McGarigal 2002) were measured for each of the 50 home range areas for the ten herds in three wet seasons and two dry seasons (Table 4). ArcGIS 8.3

has a functional error and a supplemental script was used to calculate area and perimeter of vegetation patches (Sawada 2003; Appendix A).

Table 4. Measures of landscape heterogeneity.

Landscape Measure	Equation	Limitations
Average Patch Size (m^2)	total area (m^2)/number of patches	Does not indicate any information about individual patches.
Patch Density (patches/m^2)	Number of patches/total area (m^2)	Averages over the entire area and potentially loses small scale variations.
% of Dominant Patch	(Largest patch (m^2)/total area (m^2)) * 100	Dependant upon vegetation within the area.
Edge Density (m/hectare)	(Total edge (m)/ Total area (m^2))* 10,000	Places importance on borders between vegetation types and ignores the "fuzziness" between patches.

I also measured square meters covered by permanent water sources, and average vegetation density. Vegetation density was measured by first ranking each habitat type. Preliminary investigation of the results of daily buffalo group size data suggested that tree density was the most significant structural habitat influence. The delineation of shrub density in the GIS was also found to be too generalized. Thicket was defined for the algorithm training data as any woody vegetation under the height of 4m. Therefore, areas dominated by thicket stems under 0.5m were classified in the same way as areas dominated by thicket between 1m and 4m. Stems under 0.5m had very little structural significance. In the field, areas such as this appear almost identical to open grassland (pers obs). Vegetation classification of a Landsat ETM image has no robust way to separate very short thicket from other thicket heights because image processing depends solely on spectral reflectance, so the following vegetation density ranks were assigned according to those results. All thicket vegetation types received a rank of 1 which overestimates density importance in some cases (areas dominated with very small stems), and underestimates importance in others (areas dominated by 1-4m stems) but more realistically reflects the significance of all vegetation types.

Vegetation Type	Density Rank
Open Grassland/Bareground	0
Open Thicket	1
Medium Dense Thicket	1
Dense Thicket	1
Open Woodland	2
Medium Dense Woodland	3
Dense Woodland	4

All heterogeneity measures (Table 4) were based on similar analyses of vegetation patches and could not be considered independent. Based on the limitations of each measure, edge density was chosen a priori as the most reasonable and consistent variable of spatial grain of vegetation patches. Edge density measures how much transition area between habitat types is present in the environment (meters per hectare). A totally homogeneous environment would have an edge density of zero; more heterogeneous environments have higher edge density values. The limitation of edge density, that it ignores the fuzziness of transition area, is not a problematic limitation for the purposes of the study. I was interested in structural vegetation and the variety and pattern of the landscape rather than the functionality of habitat types (Fig. 7).

Fig. 7. Photograph illustrating vegetation boundaries between dense woodland and open grassland in Hluhluwe-iMfolozi Game Reserve, May 2002.

An analysis of variance (ANOVA) test was performed to determine the significance of edge density, permanent water, average vegetation density and the significance of interactions between these factors on average group size (Table 5). The ANOVA assumptions of normality and equal variances were met or nearly met by all data sets. The wet season dataset consisted of 30 independent home range areas and the dry season dataset consisted of 20 independent home range areas.

Table 5. ANOVA factors testing group size and variability influences on the scale of home range area.

Average Group Size/Variability =	Factor Description
Permanent Water (m^2)	Area of home range (m^2) covered by rivers and streams
Average Vegetation Density	Sum of the area of each vegetation type (m^2) * density rank/total home range area (m^2)
Edge Density (m/hectare)	(Total perimeter of all patches within home range area (m)/total home range area (m^2)) * 10,000
Total Herd Size	An estimate, based on several herd sightings, of the total number of animals associated in each herd.

A second ANVOA was used to test the influence of environmental structure on the variability of group size against the same factors (Table 5). Standard deviation of the buffalo herd counts was used as a relative measure of variability between herds.

4. Results

4.1 Unsupervised Vegetation Classification

In post image processing of the unsupervised classification, vegetation density was defined but vegetation type was not. The unsupervised classification was not able to separate woodland from thicket (Fig. 8). Although the image was eliminated from home range mapping and ecological analysis, a visual analysis of the map shows the northeastern sections of the reserve are dominated by denser vegetation than the more open southwestern sections. The unsupervised classification method would be a good alternative if field data collection were impossible due to cost or time constraints. If a supervised method is possible the product is more precise.

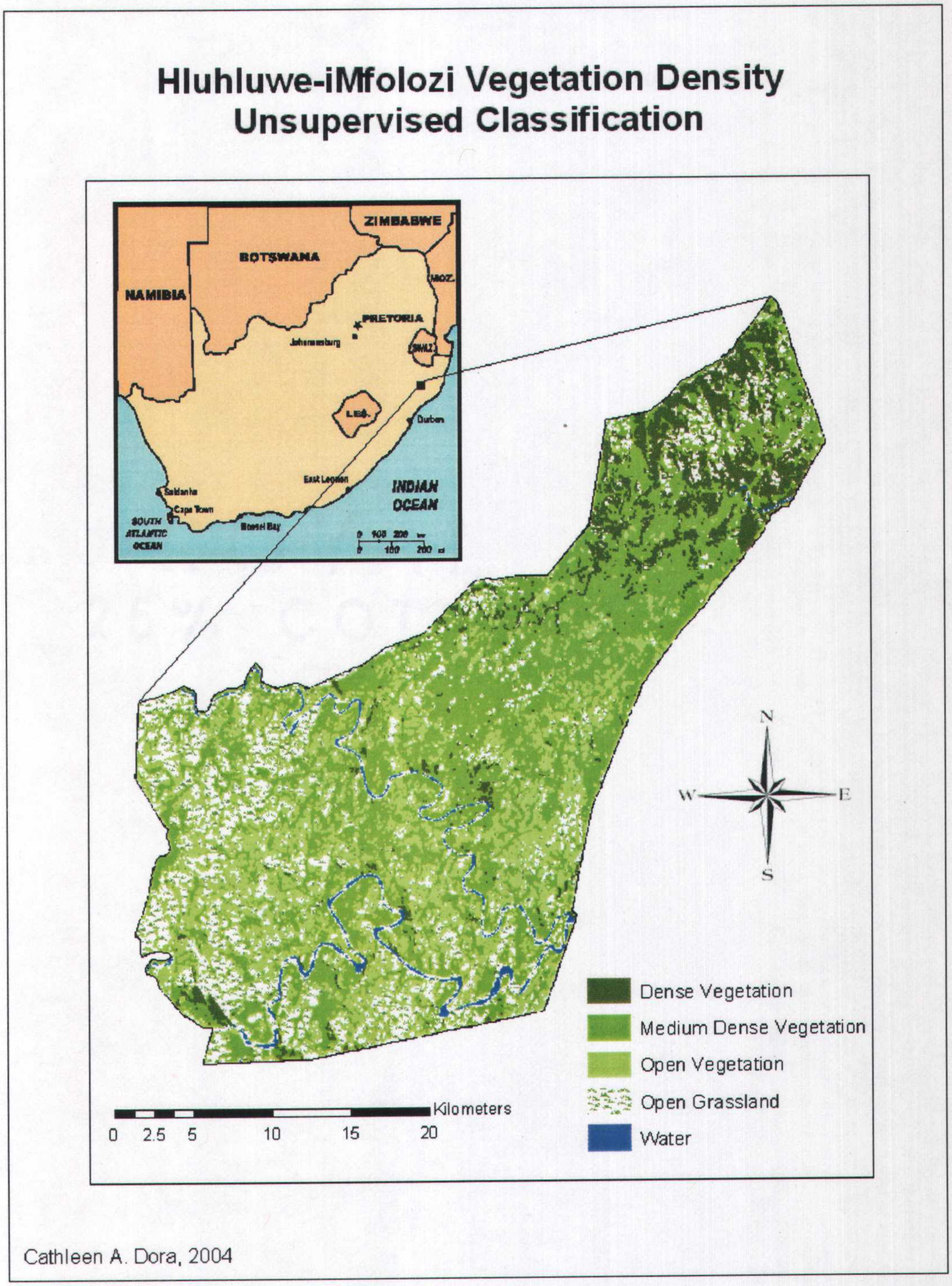

Fig. 8. Results of an unsupervised (ISODATA method) classification of a 20 March 2001 Landsat ETM image.

4.2 Supervised Vegetation Classification

The supervised classification was verified with ground-truth data and found to have an accuracy of 83% (Fig. 9 and Table 6) which is considered good (Lillesand and Kiefer 1994). However, the class definition scheme has limitations. As previously stated, the classification results of thicket vegetation were more generalized than a functional definition would be. Open woodland (10% of field points and 18% computer points) and medium dense thicket (25% of field points and 29% computer points) produced the largest discrepancies. Areas defined as open woodland in the field were misclassified by the algorithm into dense and medium dense woodland and thicket. In the cases of misclassification into thicket types this was probably due to the generalized thicket definition. Open woodland containing thicket stems under 0.5m were misclassified into dense and medium dense thicket. The other misclassifications may be due to the same problem; however, a more detailed examination of specific areas would be necessary to analyze the error properly. Three classification types had fewer than ten field collected ground-truth points. These small sample sizes occurred by chance as ground-truth locations were designed to cover the optimum area of the reserve rather than to collect an equal number of points in each classification type. There could be undetected error in three types open grassland, medium dense woodland, and water. Additional ground-truth data could help eliminate uncertainty in those classification types.

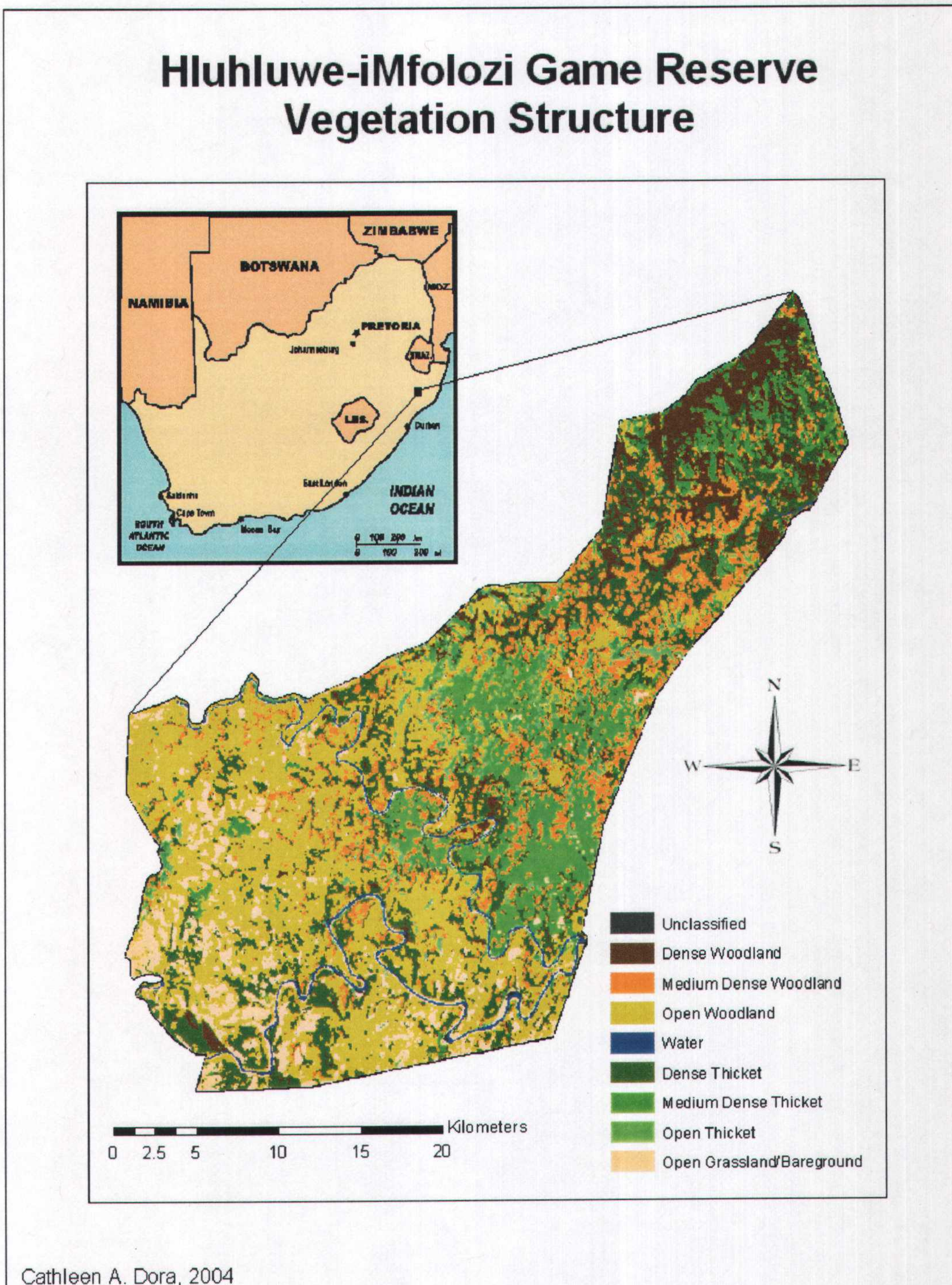

Fig. 9. Result of supervised (maximum likelihood) classification of a 20 March 2001 Landsat ETM image.

Table 6. Accuracy of Supervised Classification. Across the top are the computer generated values and down the left are field collected data from the same locations. Numbers indicate how many points are found in each. Boldface numbers indicate matching field and computer generated data.

Computer *Field*	**Dense Woodland**	**Med.Dense Woodland**	**Open Woodland**	**Dense Thicket**	**Med.Dense Thicket**	**Open Thicket**	**Open Grassland**	**Water**	**Total**	*Field*
Dense Woodland	**14**	0	2	2	1	0	0	0	19	17%
Med. Dense Woodland	0	**8**	1	0	1	0	0	0	10	9%
Open Woodland	0	0	**11**	0	0	0	0	0	11	10%
Dense Thicket	0	0	4	**14**	1	0	0	0	19	17%
Med. Dense Thicket	0	0	2	0	**26**	0	0	0	28	25%
Open Thicket	0	0	0	0	1	**11**	0	0	12	11%
Open Grassland	0	0	0	0	2	0	**2**	0	4	4%
Water	0	1	0	1	0	0	0	**6**	8	7%
Total	14	9	20	17	32	11	2	6	**111**	100%
Computer	13%	8%	18%	15%	29%	10%	2%	5%	100%	**83%**

4.3 Mapping Buffalo Herd Home Range Areas

Home range areas were incorporated into the GIS and overlaid with the supervised classification vegetation data (Appendix B). Dry season home range areas were consistently larger in total size than wet season areas, regardless of herd ID (i.e. geographic range of the herd). Home range size varied between herds, but was not significantly influenced by the total size of the herd, only season and geographic location. Herds' home range sizes did not vary significantly in size between years but did shift in location. The year to year location shift of home range areas varied vegetation composition which allowed us to consider each year independently (Appendix B).

Table 7. ANOVA results comparing total home range size between wet and dry seasons, over three years, between ten herds across the geographic range of Hluhluwe-iMfolozi reserve.

Home Range Area (m^2) =	F-Ratio	P-Value
Season	8.34	0.0064
Herd ID	2.64	0.018
Year	0.008	n.s.
Total Herd Size	1.98	n.s.

4.4 Seasonal and Geographic Differences in Buffalo Group Size and Group Size Variability

Buffalo group sizes were smaller in the dry season than the wet season and average group size varied between herds. There was less variability in the dry season because herds were constrained to a smaller average size due to forage availability (daily group size choice results). During the wet season, groups were found in a wider variety of sizes (Table 8). Total herd size influenced group size variability, where larger herds had greater group size variability than small herds, but did not influence average group size.

Table 8. Average Buffalo group sizes and group size variability compared between herds and seasons.

Average Group Size/ Variability =	Group Size f-Ratio	Group Size p Value	Variability f-Ratio	Variability p Value
Season	53.37	<0.0001	21.84	<0.0001
Herd ID	5.98	<0.0001	1.32	n.s.
Year	13.55	0.0007	3.40	n.s.
Total Herd Size	0.89	n.s.	10.52	0.0025

Herd ID had a significant influence on average group size, but not group size variability. Therefore, I inferred that some home-range-specific variables may have influenced grouping behavior. Buffalo group size and vegetation datasets all met or nearly met the assumptions of normality and equal variances required for analysis of variance.

4.5 Influences of Habitat Structure and Landscape Heterogeneity on Group Size

4.5.1 Daily Group Size Choice

Woody stem density influenced buffalo group sizes on a day to day scale throughout the year. Tree stem density (vegetation > 4m) was a significant influence in both seasons. Larger buffalo groups were found in more open habitats. During the dry season, buffalo group size was also driven by grass quality; larger groups were found in areas of homogeneously high or homogeneously low grass quality, while smaller groups were found in areas of intermediate grass quality (Fig. 10, Table 9). The interaction between tree and shrub density was also a significant influence on group size in the dry season. As my field definitions of shrub density were found to be too broad, I cannot interpret this interaction but can infer from the other results presented here that an increase in shrub density would further decrease group size. The shrub definition included too wide a range in stem size. Very small stems (under 0.5 m) were classified in the same way as much more structurally substantial stems (1 m to 4 m).

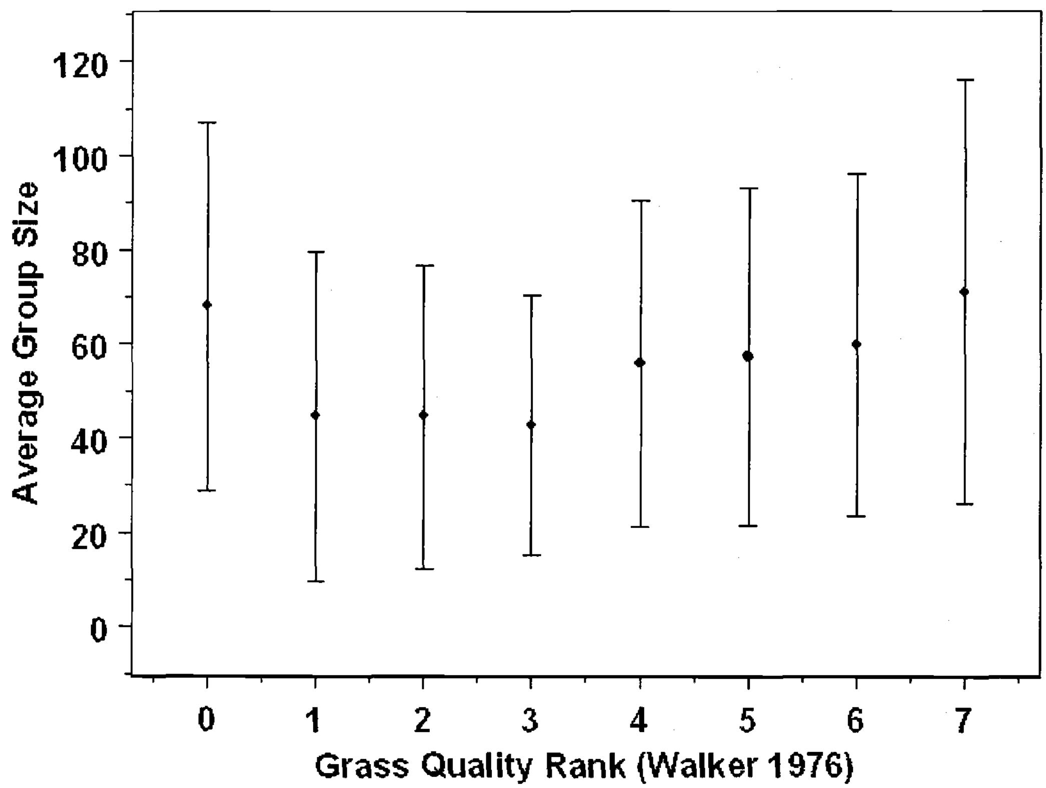

Fig. 10. Daily group size choice in the dry season according to the ranked (Walker 1976) grass quality within the habitat at each buffalo sighting. Average group size in each rank category is plotted with standard deviation. Though the trend of larger groups at very low and high quality ranks is subtle, it's influence is found to be significant in the ANOVA (p = 0.0066).

Table 9. ANOVA results for daily influences on buffalo group size for dry and wet seasons left to right respectively.

Group Size =	Description	Dry Season f-Ratio	Dry Season p Value	Wet Season f-Ratio	Wet Season p Value
Tree Density	Rank of 0-4 indicating ground cover percentage of stem density (>4m)	17.98	<0.0001	18.91	0.0159
Shrub Density	Rank of 0-4 indicating ground cover percentage of stem density (<4m)	0.36	n.s.	1.42	n.s.
Grass Quality Rank	Rank of 0-7 indicating quality in terms of relative greenness (Walker 1976)	7.45	0.0066	1.70	n.s.
Waterhole Presence	Binomial variable present or absent	0.12	n.s.	1.99	n.s.
Tree Density * Shrub Density	Interaction between stem density ranks	6.32	0.0123	0.12	n.s.

Seasonal difference in group size (smaller groups in general during the dry season) was not due to a difference in habitat choice between seasons (linear regression, d.f. = 1235, $p = 0.2398$, $R^2 = 0.0011$). Herds chose habitats with varying densities in both seasons.

4.5.2 Seasonal Influences of Home Range Variables on Group Size and Group Size Variability

Buffalo group size was influenced not only by daily habitat choice, but by the composition and organization of their home range environment. During the dry season, the average vegetation density of the home range area was a significant factor in determining group size (Table 10). Buffalo herds occupying densely vegetated environments split into smaller groups than herds occupying more open home range areas (Fig. 11). Buffalo density (number of buffalo per square meter) within the home range was not significantly influenced by vegetation density (linear regression, d.f. = 48, $p = 0.53$, $R^2 = 0.0084$). Total herd size was not a significant influence on average group size during the dry season.

Table 10. ANOVA results for home range and group size average in dry and wet seasons respectively from left to right. The response variable is average group size within season. Home range variables of water, vegetation density and edge density were calculated from GIS coverages of structural vegetation in buffalo home range areas.

Average Group Size =	Factor Description	Dry Season f-Ratio	Dry Season p value	Wet Season f-Ratio	Wet Season p value
Permanent Water (m^2)	Area of home range (m^2) covered by rivers and streams	0.84	n.s.	0.43	n.s.
Vegetation Density	Sum of the area of each vegetation type (m^2) * density rank/total home range area (m^2)	4.77	0.0452	1.31	n.s.
Edge Density (m/hectare)	(Total perimeter of all patches within home range area (m)/total home range area (m^2)) * 10,000	0.84	n.s.	6.17	0.02
Total Herd Size	An estimate, based on several herd sightings, of the total number of animals associated in each herd.	0.05	n.s.	22.81	<0.0001

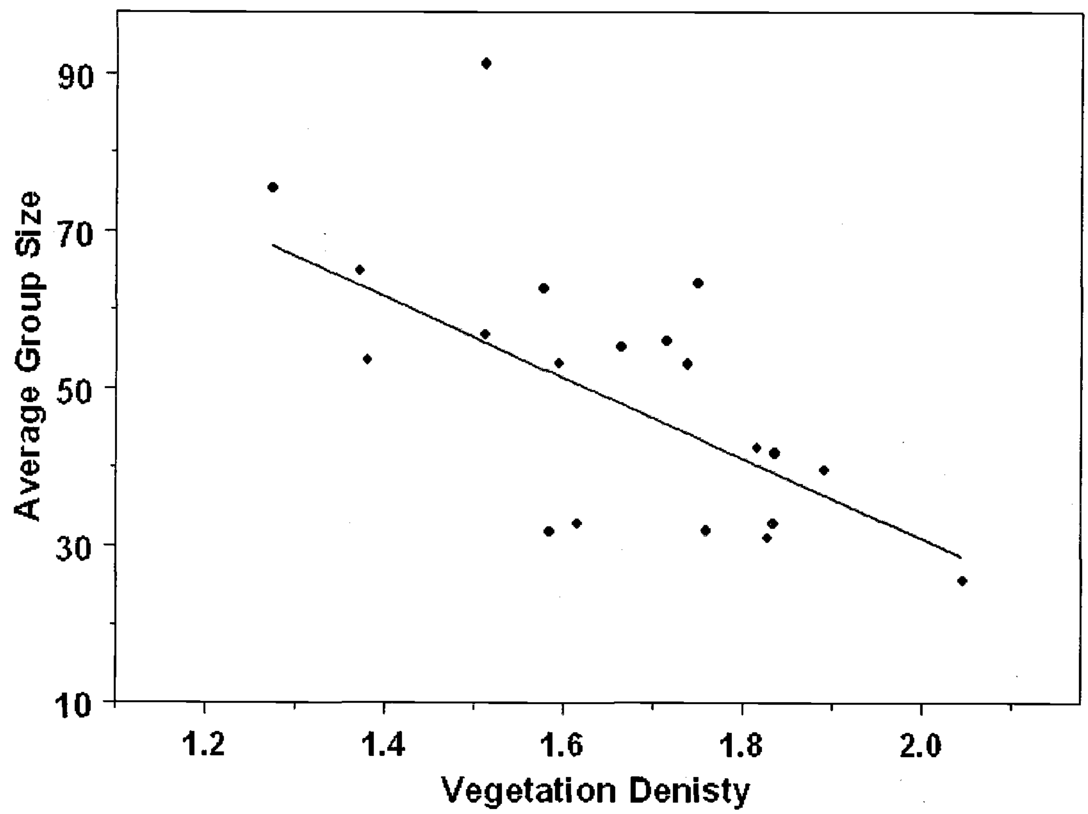

Fig. 11. Average group size in the dry season decreased with increasing vegetation density (linear regression, d.f. = 18, p = 0.0012, R^2 = 0.45).

During the wet season, edge density (heterogeneity) and the total size of the herd were significant factors driving the herd's average group size (Table 10). Herds in more homogeneous areas (with small edge density measures) split into smaller groups than did herds in more patchy environments (Fig. 12). The effect of heterogeneity on group size was not due to smaller herds occurring in more homogeneous areas as the heterogeneity of a herd's home range did not influence the total size of the herd (linear regression, d.f. = 18, p = 0.25, R^2 = 0.073).

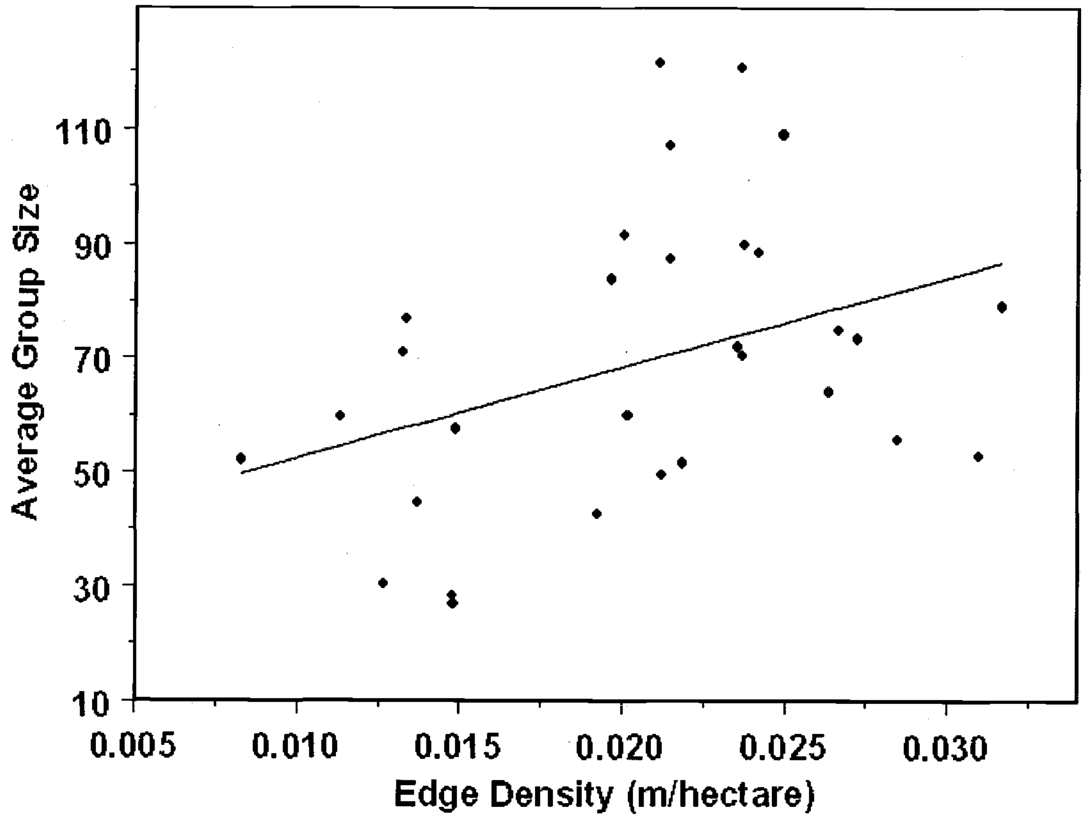

Fig. 12. Graph showing the wet season trend of average herd group size increasing with increasing home range heterogeneity (linear regression, d.f. = 28, $p = 0.04$, $R^2 = 0.14$). Edge density is plotted from coarse to fine grain (homogeneous to heterogeneous) on the x-axis.

Variability of the herds was influenced by the total size of the herd as well as the environmental factors of landscape heterogeneity and, marginally, by permanent water availability (Table 11). During the dry season, group size varied more in more heterogeneous home ranges with more permanent water (Fig. 13). Larger herds also had more group size variability than small herds.

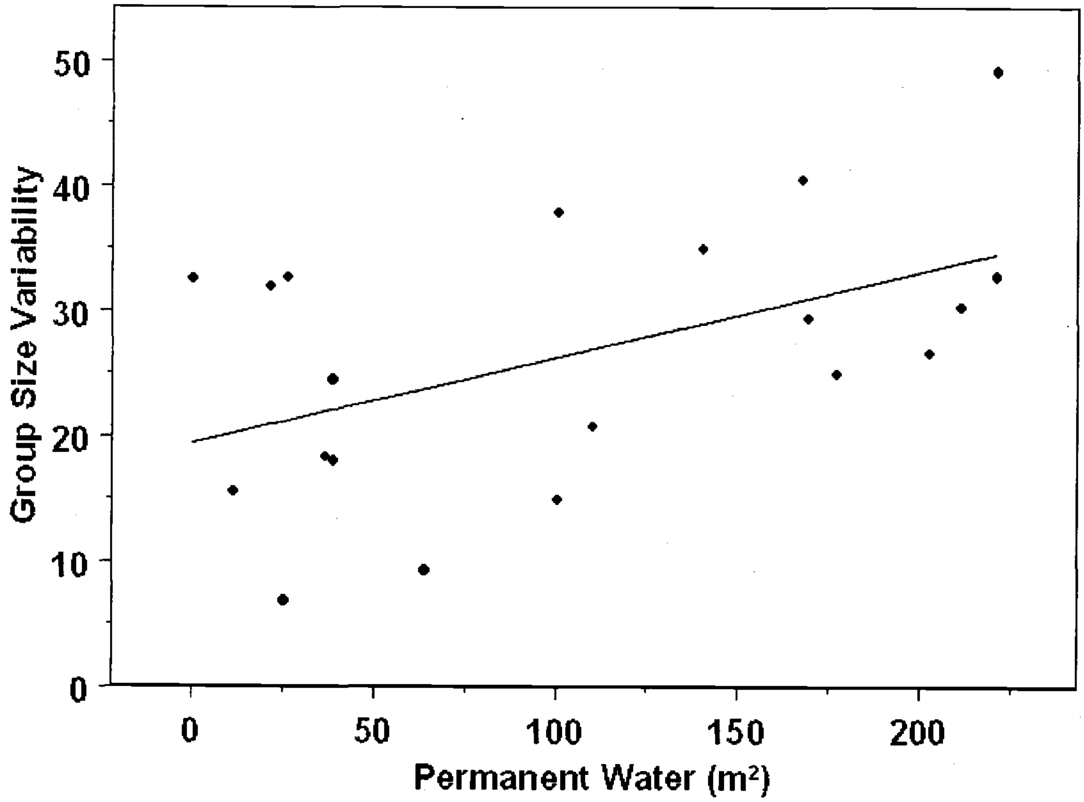

Fig. 13. Group size variability in the dry season in home range areas with varying amounts of permanent water (linear regression, d.f. = 18, p = 0.03, R^2 = 0.25).

In the wet season group size variability was not significantly influenced by home range variables, only by the herds' total size (Table 11). Larger herds had greater group size variability than small herds.

Table 11. ANOVA results for home range and group size variability in dry and wet seasons respectively from left to right. The response variable is the standard deviation of group size within season. Home range variables of water, vegetation density and edge density were calculated from GIS coverages of structural vegetation in buffalo home range areas.

Group Size Variability =	Factor Description	Dry Season f-Ratio	Dry Season p value	Wet Season f-Ratio	Wet Season p value
Permanent Water (m^2)	Area of home range (m^2) covered by rivers and streams	4.40	0.0533	0.18	n.s.
Vegetation Density	Sum of the area of each vegetation type (m^2) * density rank/total home range area (m^2)	1.70	n.s.	0.29	n.s.
Edge Density (m/hectare)	(Total perimeter of all patches within home range area (m)/total home range area (m^2)) * 10,000	8.06	0.0124	0	n.s.
Total Herd Size	An estimate, based on several herd sightings, of the total number of animals associated in each herd.	11.50	0.004	135.84	<0.0001

5. Discussion

5.1 Vegetation Classification Method

In this thesis, a method was developed to quantify vegetation structure that required a modest amount of field work to produce an accurate map product. Using a map such as this, wildlife managers will be able summarize and analyze the landscape in broad terms. The effects of animal introductions, removals or changes in the reserve burning regime could be predicted and analyzed in terms of how such changes may influence other animal populations in the reserve.

The vegetation map could be made more specific by incorporating aerial photographs post-classification. Tanser and Palmer (2000) demonstrated that spectral data alone may not be adequate for detailed mapping of vegetation types. Aerial photos would be a reasonable addition to a classification of this kind because they rely on visual interpretation and are captured at a finer resolution than satellite imagery. The addition of aerial photos would be particularly useful to more accurately define the thicket habitat as visual interpretation could define stems that are not structurally significant (under 0.5 m).

A limitation facing this method is the expense of satellite imagery. Remotely sensed datasets are increasingly available; however, they have not yet reached a widely affordable cost. A Landsat ETM half-scene image (about 17,000 km^2) costs approximately $1,100.00. Game reserves with limited budgets, especially those in developing countries, may not be able to afford purchase and processing of these data. It is my hope that projects such as this will not only outline methods for data processing and analysis but will also make data free and available to wildlife managers and game reserves dedicated to conservation.

Risser et al. (1984) described major topics of study facing landscape ecology, including the influences of heterogeneity on biotic and abiotic processes, the management of spatial heterogeneity, and driving mechanisms behind observable heterogeneity. O'Neill et al. (1988) alluded to the possibility that remotely sensed data could detect ecological change at a landscape level. Since then, many methods have been developed to map and measure various aspects of the environment. Still, Gustafson and Gardner (1996) concluded that the effects of landscape heterogeneity on organisms are poorly understood. This study demonstrates the utility of satellite imagery in displaying vegetation structure as one measurable variable in space. There has long been a call to connect landscape pattern to ecological process and we now have the tools and technology to do so. The method described here presents one way to display and quantify patterns of vegetation and to describe how such patterns may influence the behavior of organisms living there. The organization of this study presents a possible way to compare different size reserves with different plant and animal diversities. Vegetation classification using this method required only a modest amount of field work and digital processing time. Animal populations and management practices could be compared and contrasted across ecosystems which would allow a region-wide understanding of landscape effects on wildlife management.

Using vegetation classification methods, it is now possible to examine everything from the seafloor to tropical rainforests (Tanser and Palmer 2000, Ma et al. 2001, Pasqualini et al. 2001, Wang et al. 2001, Dominy and Duncan 2003, and Diuk-Wasser et al. 2004). Studies such as these and this will provide the necessary background data for ecologists and wildlife managers to examine the effects of spatial patterning on various ecosystems and detail universalized methods to quantify landscape pattern

5.2 African Buffalo Group Size – Daily Choice

During both the wet and dry seasons, habitat structure influenced buffalo group size dynamics on a daily basis: as tree density increased, group size decreased. Vegetation density could influence group dynamics for a number of reasons. Buffalo groups may have been smaller in more dense environments due to practicality. Thick vegetation simply may not allow for large cohesive groups. Visual contact could be difficult to maintain and forage patches in denser vegetation are likely small and may not allow large groups to maintain synchronous grazing or resting. Activity asynchrony has been studied mostly in terms of sexual segregation of herd animals (Conradt 1999 and Bon et al. 2001, Turner et al., in review) but could be applied to other social behavior.

A benefit of maintaining large groups is to decrease the risk of predation by increasing the number of vigilant animals in the group. Ruckstuhl and Festa-Bianchet (2001) pointed out that social animals face trade-offs between foraging efficiency and predator avoidance. Prins (1996) found that buffalo in open grassland areas were at a higher risk of predation than buffalo in woodland or thicket vegetation. In safer, densely vegetated areas then, buffalo could maintain smaller groups for efficient grazing without putting themselves in greater risk of predation.

The spatial distribution of resources constrained foraging group size in the dry season (Belisle 1998). In patches of high or low grass quality, group size tended to be larger than in patches of intermediate grass quality. In the field, grass quality was estimated for the entire habitat area occupied by the buffalo at each sighting, usually 50 m^2 to 150 m^2. Quality ratings of high or very low indicated homogenously good or poor forage quality across the entire grazed area. Heterogeneous areas with smaller patches of good and poor quality grass were recorded as intermediate quality due to the observer averaging over the entire grazed area. This suggests that group size may not have been driven by grass quality alone but by the distribution of palatable and high quality forage. In intermediate areas there were often smaller patches of high quality forage rather than homogeneous patches of intermediate quality. The effect of forage quality patch size drove buffalo group size. Large groups were maintained in areas with homogenously high or low grass quality, while herds utilized heterogeneous areas by splitting into smaller foraging groups. During the wet season group size was not influenced by grass quality because it was consistently high everywhere in the reserve.

5.3 African Buffalo Group Size – Seasonal Averages and Variability within Home Range Areas

5.3.1 Dry Season

The spatial organization of home range areas and the total size of the herd influenced average group size and group size variability within seasons. During the dry season, average group size was influenced by only one geographic variable – the average vegetation density within home range areas. Larger average groups occupied more open home ranges and proved the daily trend to be robust across both scales of this study. This trend could be attributed to activity asynchrony or avoidance of predation risk. Vegetation density may also affect foraging patch size, or the heterogeneity of quality forage patches. Grass quality may be more homogenous in more open areas. In the daily group size choice analysis heterogeneity of grass quality within buffalo habitat influenced group size.

Group size variability, however, was driven not by average vegetation density, but by water availability, home range heterogeneity, and the total size of the herd. In areas where a greater area was covered by permanent water sources, there was more variability in group size. Permanent water sources, such as rivers and streams, are larger in size than seasonal pans and waterholes. Group size varied more in the dry season around areas with more permanent water, probably because small dry season splinter groups convened at easily accessible and large water sources to drink and wallow. These permanent water sources are large enough to allow synchronized activity of larger groups than dry season foraging areas; therefore, group size probably varied with these activities.

Edge density also influenced dry season group size variability. Buffalo in more heterogeneous areas had more variation in group size than herds in more homogeneous home ranges. During the dry season distribution of forage and vegetation density drove group dynamics. Though I do not have the data necessary to examine this trend, perhaps vegetation patch size affects forage patch size with small vegetation patches maintaining only small foraging patches. Grazing of other species is also likely to contribute to the heterogeneity of forage quality. In an area where there is heterogeneous vegetation, forage quality may then be affected by two sources of variation – the physical variable of vegetation structure and the biological variable of grazing competition. Forage in areas of homogenous vegetation may have only one source of variation – grazing competition. If foraging patch size is the significant influence that these data appear to indicate and vegetation density does influence grass path size, then buffalo group size during the dry season would be more variable where forage quality is more variable.

The total size of the herd also influenced group size variability in the dry season, where larger herds had more variation than smaller herds. This trend is intuitive as herds with more total individuals can be divided into more sub-groups than small herds.

5.3.2 Wet Season

Landscape scale factors took over group size influence in the wet season when grass quality had no significant effects on group size. There was high quality forage available throughout the reserve. Groups were smaller in more homogenous environments in the wet season probably due to the difficulty of group cohesion in large homogeneous patches. Animals may have tended to drift further apart from one another and could have become asynchronous, in terms of activity, when the group was spread out over a larger area.

Total herd size was also a significant influence in the wet season when herds were no longer restricted to small foraging groups. Larger herds had larger average groups. Variability of group size was also determined by total herd size during the dry season. Larger herds had greater variability of group size.

6. Conclusions

In summary, buffalo group size varied between seasons and throughout geographic space. Seasonally, group dynamics were largely the result of forage distribution. Geographic differences in group size were mainly due to vegetation density and landscape pattern. Buffalo in Hluhluwe-iMfolozi utilized forage habitat patches in direct relation to their group size with denser and homogeneous vegetation limiting the number of animals that can remain cohesive and synchronous in their activities. Buffalo may also trade-off foraging efficiency and predation risk across the reserve and throughout the year.

Sale and trade of big game is a major source of funding for game reserves in southern Africa. Wildlife populations are controlled and managed with off-takes and introductions and several research projects monitor and record animal movement, group size, and habitat utilization. Prescribed burning is used to maintain forage quality. With the knowledge of how landscape vegetation matrices affect the social behavior of animal populations, the Hluhluwe-iMfolozi reserve could potentially use yearly burning to manage not only habitat and forage quality, but also the physical structure of the reserve. Animals could be accommodated or controlled by shaping the physical landscape to meet the needs of the wildlife in the reserve.

Management of animal populations depends on an understanding of their biological requirements as well as environmental influences that affect the social structure of their species. The work presented here outlines the effects of habitat structure, landscape heterogeneity, and forage quality on the dynamics of the buffalo population in Hluhluwe-iMfolozi. Buffalo maintain larger groups where there is open vegetation, homogenous forage quality, and heterogeneous vegetation across the landscape. Not only must we work to protect suitable habitat, but we cannot ignore the importance of vegetation structure, landscape pattern, and the influences of forage quality. We must consider temporal variation of these contributing factors and view animal populations on multi-dimensional scales, working to protect and understand the complexity of space and time.

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Appendices

Appendix A:
Contents of data CD

1. Zipped scripts that can be installed into ArcGIS:
   Area and perimeter calculator, Sawada, 2003
   Degrees, minutes, seconds to decimal degrees converter, Tchoukanski 2003

2. Script that can be installed into ArcView 3 for calculating Home Range Area using the Local Convex Hull Method, Andy Lyons 2004
For further information, please contact Wayne Getz, getz@nature.berkeley.edu

3. Hluhluwe-iMfolozi Game Reserve Infrastructure, shapefiles
   Management sections
   Park boundary
   Rivers
   Roads

4. Vegetation Classification, shapefiles
   Supervised, Maximum Likelihood 50%
      Legend
      0 = Unclassified
      1 = Open Thicket
      2 = Open Grassland
      3 = Medium Dense Thicket
      4 = Water
      5 = Medium Dense Woodland
      6 = Dense Thicket
      7 = Dense Woodland
      8 = Open Woodland
   Unsupervised, ISODATA Method
      Legend
      2 = Dense Vegetation
      3 = Water
      4 = Open Vegetation
      5 = Open Grassland
      6 = Medium Dense Vegetation

5. Wet Season Home Range Areas, 3 years, shapefiles
   Home range areas are clipped with the supervised vegetation classification layer (same legend).

6. Dry Season Home Range Areas, 2 years, shapefiles
   Home range areas are clipped with the supervised vegetation classification layer (same legend).

Appendix B:
Buffalo Home Range Maps

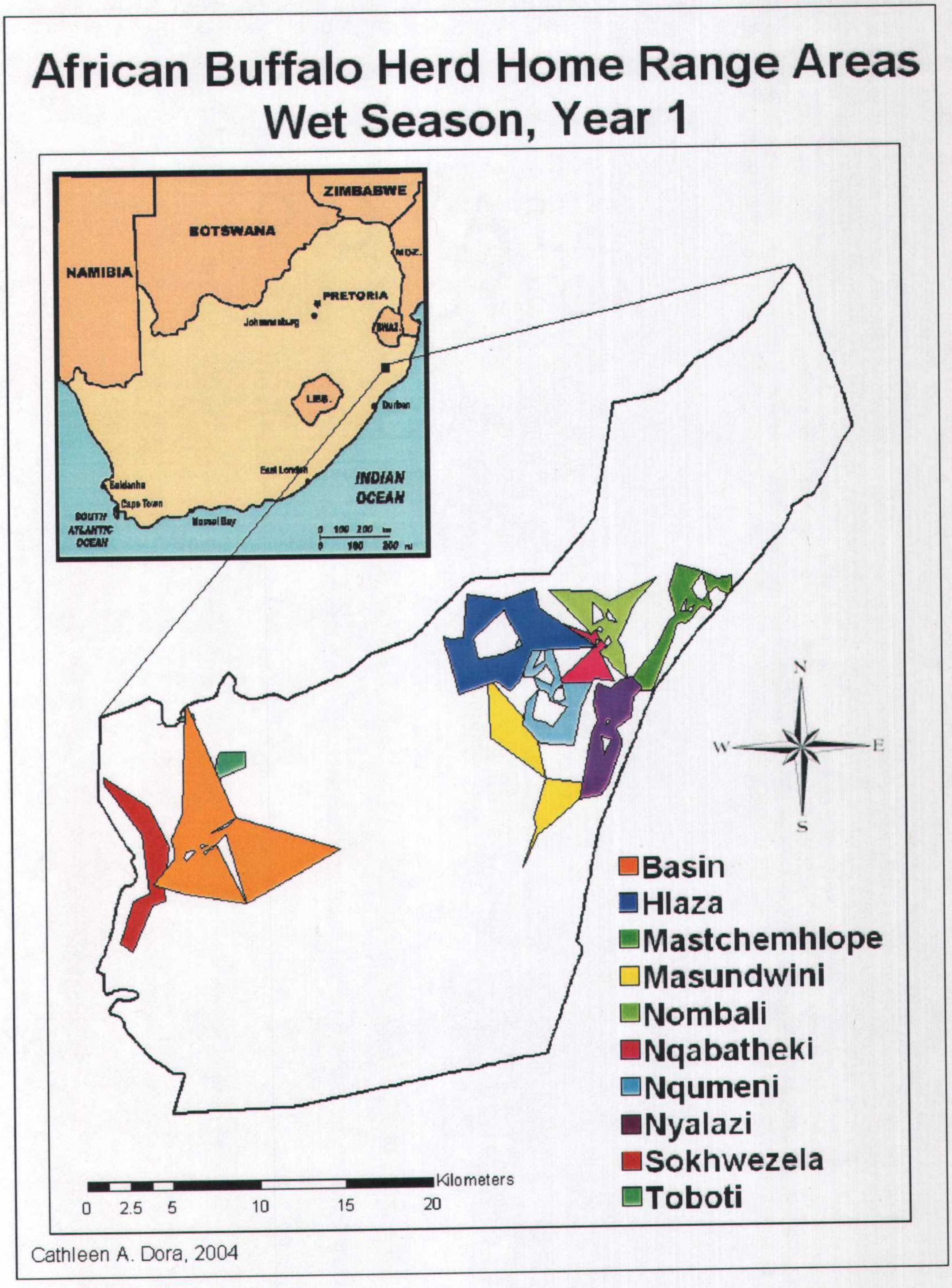

Fig. 1. Wet season home range areas of ten buffalo herds (year 1, November 2000 through April 2001).

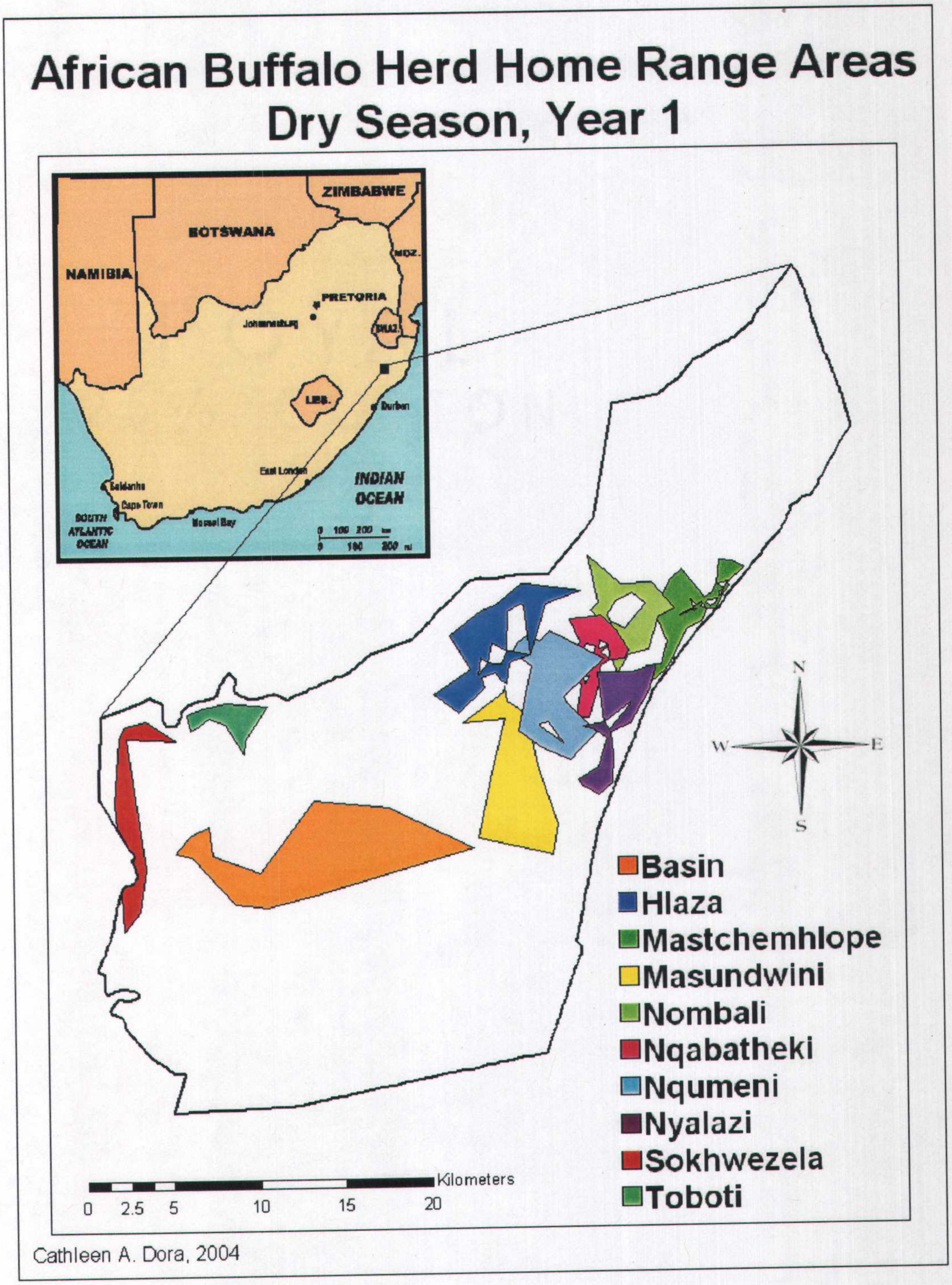

Fig. 2. Dry season home range areas of ten buffalo herds (year 1, May 2001 through October 2001).

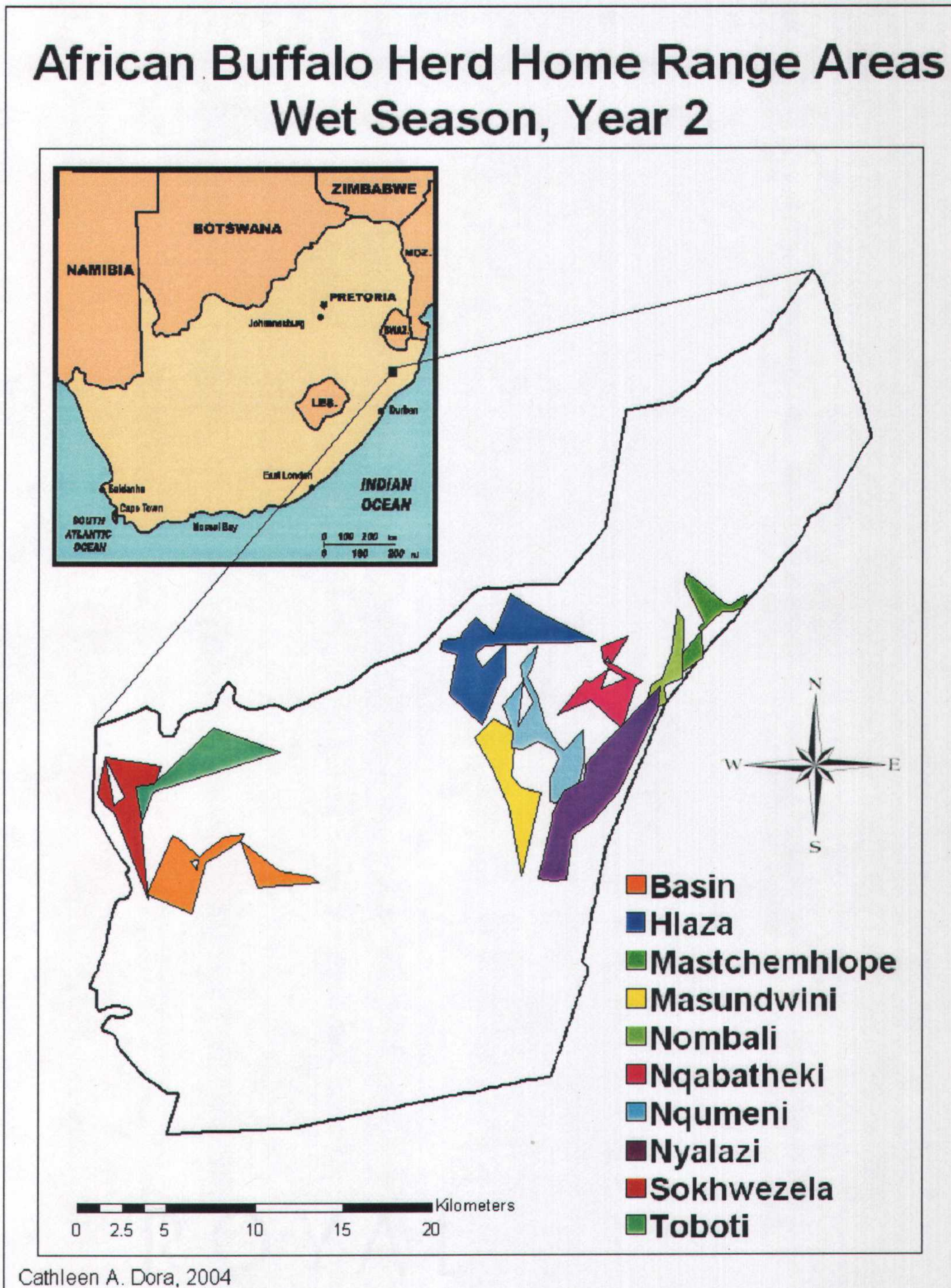

Fig. 3. Wet season home range areas of ten buffalo herds (year 2, November 2001 through April 2002).

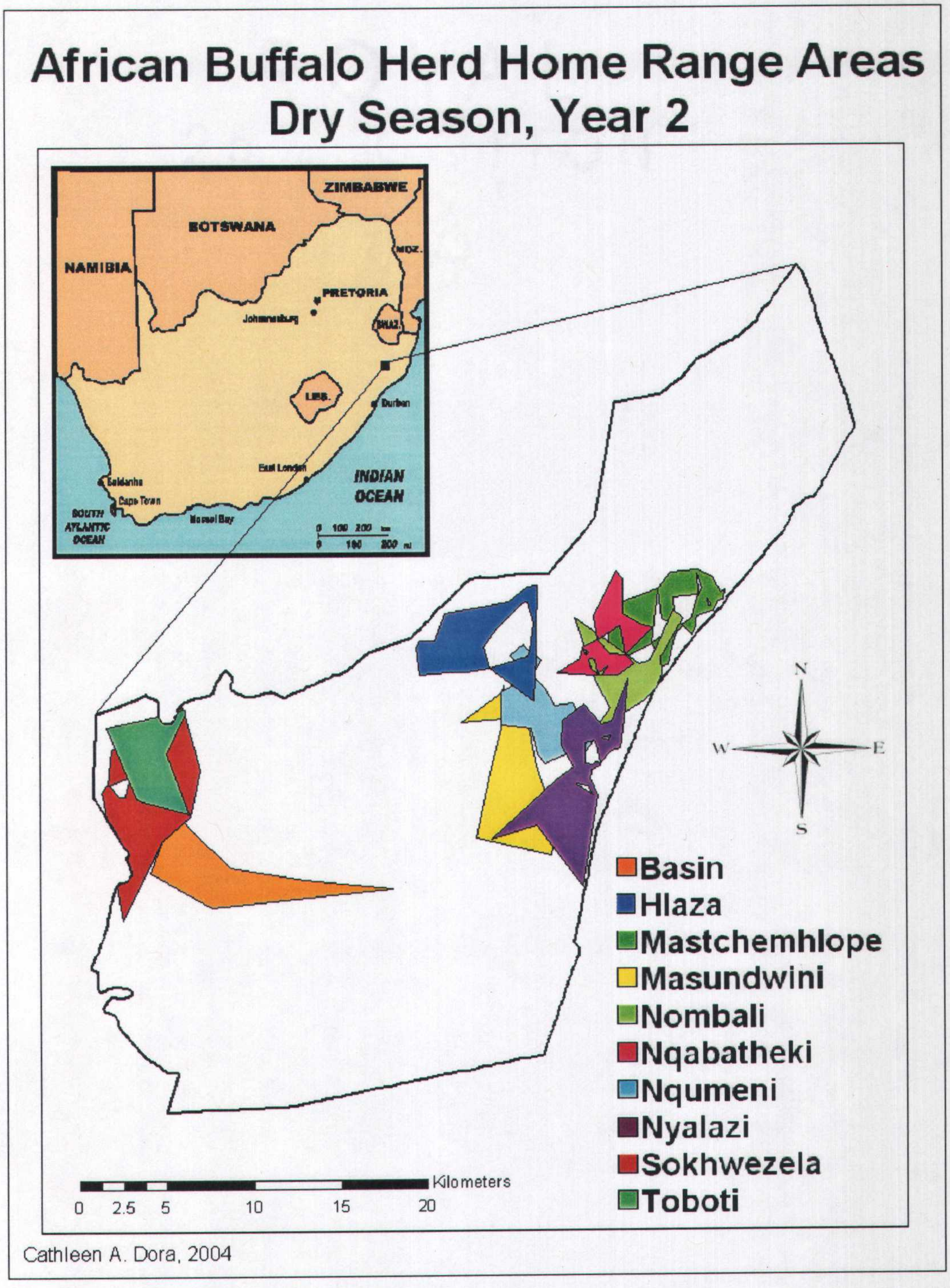

Fig. 4. Dry season home range areas of ten buffalo herds (year 2, May 2002 through October 2002).

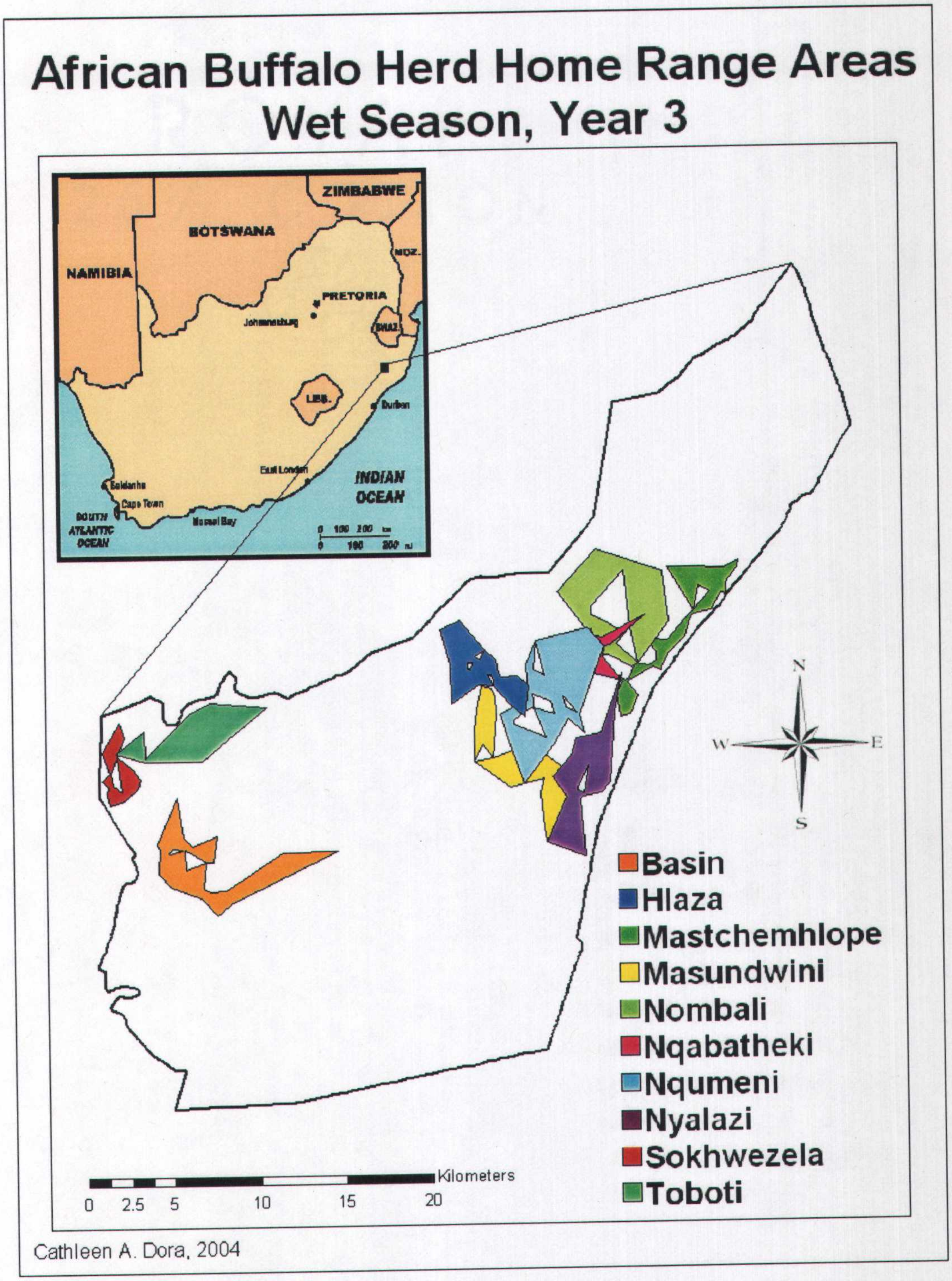

Fig. 5. Wet season home range areas of ten buffalo herds (year 3, November 2002 through April 2003).