UTILIZATION DISTRIBUTION AS A PREDICTOR IN MODELING BLACK RHINO (*DICEROS BICORNIS*) HABITAT IN AFRICA'S SOUTHERN RIFT VALLEY

By

Craig van der Heiden

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This thesis was prepared under the direction of the candidate's thesis advisor, Dr. John Volin, Department of Environmental Sciences and has been approved by the members of his supervisory committee. It was submitted to the faculty of the Charles E. Schmidt College of Science and was accepted in partial fulfillment of the requirements for the degree of Master of Science.

SUPERVISORY COMMITTEE:

John C Volin
Dr. John Volin
Chairperson, Thesis Advisor

Michael Salmon
Dr. Michael Salmon

Dale Gawlik
Dr. Dale Gawlik

John C Volin
Director,
Environmental Sciences Program

Dean, Charles E. Schmidt College of Science

Vice President for Research and Dean Graduate Studies

December 13, 2005
Date

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ABSTRACT

Author: Craig van der Heiden

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An innovative technique of evaluating resource selection for black rhino (*Diceros bicornis*) was used to assess the population utilization distribution (PUD) within a rhino sanctuary in Liwonde National Park, Malawi. The PUD enabled an evaluation of responses to habitat variables over a spatial gradient of resource selection. A Geographic Information System (GIS) was constructed using vegetation, browse availability, roads, rivers, water holes and satellite imagery. Linear models were developed to quantify habitat variables within the black rhino sanctuary and park. The sanctuary model was calibrated within a known core area (R^2=0.42, $P<0.001$), validated in a second area (R^2=0.56, $P<0.001$) within the sanctuary and, subsequently, used to predict potential black rhino habitat within the remaining sanctuary boundaries. The model for the entire Liwonde National Park predicted additional black rhino habitat (R^2 =0.25, $P<0.05$). Population utilization distribution was found to be a powerful conservation tool for determining suitable black rhino habitat.

I dedicate this work to a special woman.

Sheryl

Who gave her blessing to take our three children

to Africa for three months to track black rhino,

Who provided endless encouragement,

Who missed me like crazy while I was in the bush.

My wife

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Introduction

The highly endangered black rhino (*Diceros bicornis*) once ranged extensively over much of east, central and southern Africa (Emslie and Brooks 1999). In 1960, an estimated 100,000 black rhino existed (Emslie and Brooks 1999). By 1992, rhino populations had been reduced by 96% leaving only remnant sub-populations surviving in isolated pockets (Emslie and Brooks 1999). Today, the number of black rhino is beginning to increase, the total estimated population remaining slightly above 3,600 (Emslie 2004). Part of the success of stabilizing black rhino numbers is the result of intensive anti-poaching programs, international pressure on the trade of rhino horn (Martin 1983; Mills 1997; Emslie and Brooks 1999), and the increased use of protected areas, such as sanctuaries.

In several African countries, black rhino were translocated from high-risk areas and concentrated on government and private lands that afforded better protection (Dublin and Wilson A. 1998; Emslie and Brooks 1999). Rhino sanctuaries were established to protect depleted populations and for reintroduction purposes (Brett 1990; Bhima and Dudley 1996; Emslie and Brooks 1999; Dudley 2000; Birkett 2002; Mulama and Okita 2002; Kampamba 2003). Sanctuaries are typically small areas of natural land in which rhino are confined, in most cases by a perimeter fence, and guarded by security personnel. Providing constant surveillance and intense management of the population has become increasingly important for black rhino survival (Conway and Goodman 1989; Adcock et al. 1998; Emslie and Brook 1999; Dudley 2001). In most cases, rhino in sanctuaries are wild animals, living within their historic range and retaining their natural breeding system with little or no husbandry. However, these sanctuaries have often been chosen for their protective attributes rather than their habitat suitability.

Many studies have been conducted on black rhino feeding ecology, forage preference (Goddard 1968; Goddard 1970a; Frame 1980; Hall-Martin et al. 1982; Oloo et al. 1994; Dierenfeld et al. 1995; Bhima and Dudley 1996; Muya and Oguge 2000) and habitat usage (Frame 1980; Bhima and Dudley 1996; Tatman et al. 2000). Black rhino occur over a wide range of habitats, including open grassland in East Africa (Goddard 1968; Goddard 1970a) and desert environments in Namibia (Berger 1997). While these habitats are not ideal as inferred from their very low densities, high densities of black rhino do occur in areas with dense vegetation and permanent water (Goddard 1968; Goddard 1970a; Goddard 1970b; Tatman et al. 2000). Many of the earlier studies (Goddard 1968; Goddard 1970; Mukinya 1977) describe observations of black rhino in relatively open areas and record them feeding on a large diversity of vegetation. However, in a literature review on all rhino species, Linklater (2003) reports a low number of scientific articles on habitat use and suitability. Even less research has been conducted on habitat suitability for reintroduction. As black rhino populations increase and are reintroduced to their original ranges, it is critical to understand how these large herbivores utilize the landscape. It is also critical to understand how much favorable habitat exists in an area of proposed reintroduction and to ascertain where rhino are likely to utilize the resources. Linking science with management creates effective conservation strategies and helps to evaluate current management practices.

Satellite imagery, ecological modeling and Geographic Information Systems (GIS) are increasingly becoming important for conservation and management (Walpole 2000; Moleele et al. 2001; Walpole et al. 2001; Cromsigt et al. 2002; Macdonald and Rushton 2003; Wockner et al. 2003). Many studies employ GIS, incorporating modeling and satellite imagery, to statistically analyze relationships among data layers that represent abiotic (e.g. rainfall, topography, soil type), biotic (e.g. land cover types, animal movement paths and home ranges), and anthropogenic data (e.g. distance to roads, buildings, or political boundaries) (Johnson and Swift 2000; Walpole 2000; Cromsigt et al. 2002; Lauver et al. 2002; Dettki et al. 2003). Analyses of these spatial parameters can be combined to identify locations of suitable habitat and to determine the probability for use by an animal of interest (Johnson and Swift 2000; Walpole 2000; Lauver et al. 2002).

Numerous statistical methods are available to analyze resource selection by animals (Morrison et al. 1998; Manly et al. 2002). These include linear, logistic and log-linear regression, discriminant function analysis, compositional analysis and principal component analysis (Morrison et al. 1998; Manly et al. 2002). These methods generally only indicate presence or absence of a focal species in an environment, from which one or more predictor variables are gathered. Other methods use only the presence of a species to describe the habitat (Manly et al. 2002). However, an animal rarely utilizes its territory or home range uniformly, but rather some areas are central to its activities while others are transitional (Marzluff et al. 2004). For example, an animal may spend more time feeding in one area while only traversing another.

The relative frequency of a population's or an individual's use of resources can be described by the utilization distribution (UD) (Marzluff et al. 2004). UD is a probability density function that quantifies the relative use of space (Worton 1989; Harris et al. 1990). Most often associated with probabilistic home range estimators, UD describes areas by the frequency of use and define core areas within the home range (Worton 1989; Harris et al. 1990; Getz and Wilmers 2004). Using Steller's Jays (*Cyanocitta stelleri*), Marzluff et al. (2004), were the first to relate the probability of occurrence in the home range to the selection of resources, defining the measure of UD across a gradient.

In this study, my first objective was to evaluate habitat use by black rhino within a sanctuary in Liwonde National Park, Malawi. Habitat use was determined by the measurement of habitat variables (vegetation, browse availability, density of roads, rivers and water holes), which were incorporated within a GIS, and satellite imagery and used to determine the population utilization distribution (PUD). Using the data generated in the first objective, my second objective entailed developing a predictive model to identify underutilized or unoccupied suitable rhino habitat within the rhino sanctuary. My final objective involved forming a similar predictive model that would identify suitable rhino habitat for the entire Liwonde National Park, and could possibly be used for the eventual release of surplus rhino from the sanctuary.

No previous studies were found in the literature that applied utilization distribution to predict habitat for large mega fauna like the black rhino. It is a relatively new technique first described by Marzluff et al. (2004), and it could prove useful to conservationists and resource managers. This type of information will aid in making informed decisions about future management, in this case, of black rhino populations in Liwonde National Park, although could also be used effectively for other imperiled wildlife, such as the African elephant (*Loxodonta africana*).

Methods

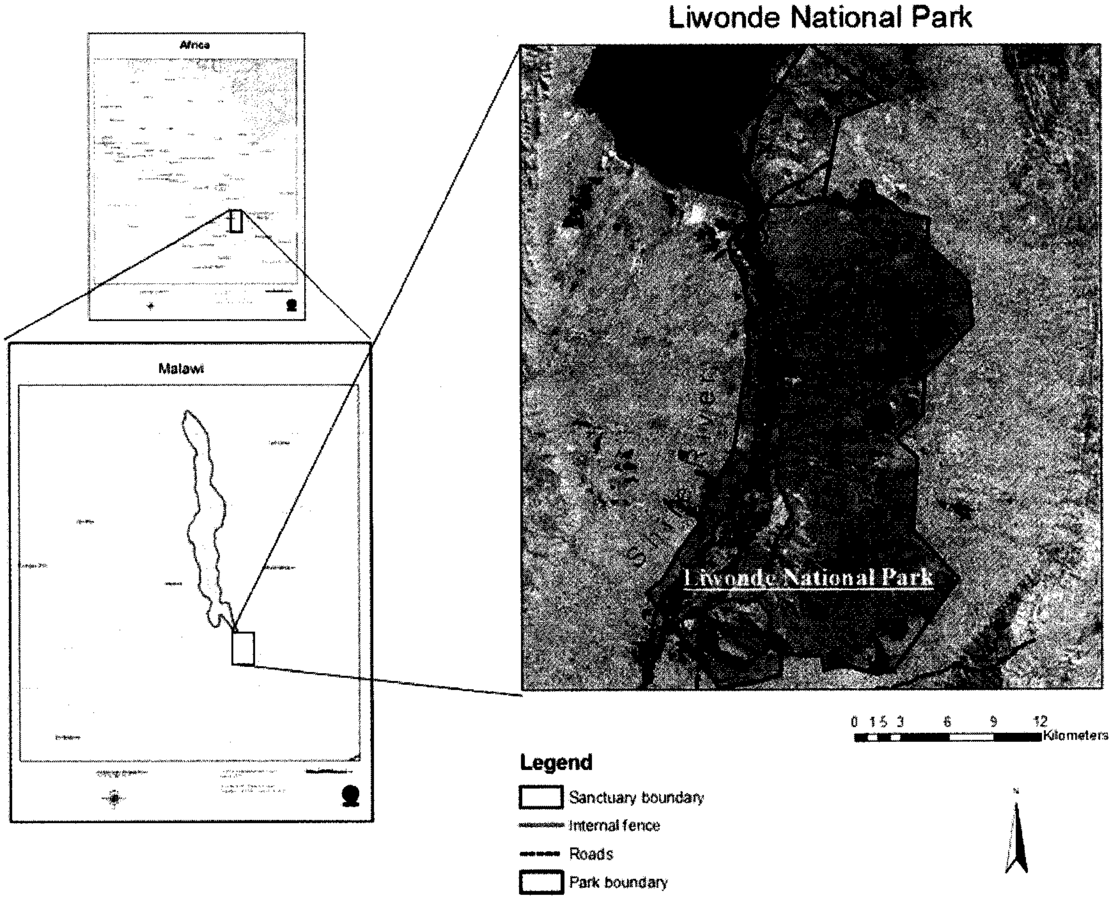
Study Area

In Malawi, a south-central African nation, black rhino were extirpated by 1992 (Emslie and Brook 1999). In response, a private group of conservationists, the Endangered Species of Malawi Group (formerly J&B Circle) introduced a breeding pair from South Africa into a sanctuary within Liwonde National Park in 1993 (Bhima and Dudley 1996).

Liwonde National Park lies south of Lake Malawi along the Shire River (14°77' - 15°02'S and 35°28' - 35°38'E) (Figure 1). The park encompasses about 528 km^2 and is Malawi's most popular for wildlife (Bhima and Dudley 1996). It experiences an annual rainfall of 700 - 1500 mm mainly during a distinct wet season from November to April. Annual temperatures range from 15° C in winter (May - August) to 40° C in summer (September - April). I conducted a preliminary aerial vegetation survey in August 2004 that showed the park to be dominated by old growth mopane (*Colophospermum mopane*) woodland, but also encompassing riverine vegetation, varying stages of successive mopane and, in the northern section of the park, both open and wooded grasslands.

Liwonde Rhino Sanctuary, a small (43 km^2) area of natural land in which rhino are confined and guarded, is situated in the center of the park (Figure 1). The western boundary of the sanctuary is less than one kilometer from the Shire River. Two major seasonal rivers, the Ntangai and the Nangondo, run through the sanctuary, carrying water only during the wet season. Three watering holes, or pans, in the sanctuary are artificial watering points, having water pumped into them from the Shire River during the dry season. Numerous seasonal pans collect water in the rains but are depleted at varying

Figure 1. Location of study site in Liwonde National Park situated in the southern African country of Malawi. The perimeter fence of the rhino sanctuary is outlined in red. The orange line indicates the internal fence which was removed in May 2004. Prior to removal, rhino were restricted to the western side of the sanctuary.



rates throughout the year.

A perimeter electric game fence, designed to keep elephant out and rhino in, surrounds the sanctuary. At the beginning of the study, the sanctuary had been divided into two parts by an internal electric fence (Figure 1). The eastern part of the sanctuary was initially fenced to increase the rhino population without intra-specific competition, mainly aggressive behavior towards newly introduced rhino. The Endangered Species of Malawi Group, which oversees the logistics of the sanctuary, removed this internal fence during the first week of the study in May 2004, thereby, increasing the area available to the rhino.

The Liwonde black rhino population serves a critical role in the recovery of this species in Malawi. Over the last decade, this population increased by reproduction and introduction of other individuals (Table 1). At the time of this study, there were seven black rhino within the sanctuary (Figure 2 A).

Determination of Utilization Distribution

The study was conducted in both a dry (May-August 2004) and wet (February-March 2005) season. To classify areas of rhino presence in the entire sanctuary, I systematically sampled all areas for rhino occurrence. During both sampling seasons, rhino occurrence was determined by direct sightings, identifying actively used middens, sleeping areas and last seen fresh spoor.

The sanctuary is dissected by many single-lane, low-intensity, unpaved roads (Figure 1). Black rhino are solitary animals. Each morning, individual fresh rhino spoor

Table 1. Rhino details from Liwonde National Park, Malawi.

Rhino names	Sex	Details	Status
Justerini	F	Translocated from KNP to LNP October 1993.	In LNP
Brooks	M	Translocated from KNP to LNP October 1993.	Died 2000
Jet	M	Born to Justerini and Brooks in 1996. Translocated to Marakele SA in 2000	In SA
Julia	F	Translocated from KNP to LNP October 1998	In LNP
Bentley	M	Translocated from KNP to LNP October 1998	In LNP
Rydon	M	Born to Justerine and Brooks. Translocated to Marakele SA in 2000	In Majete
Chimwemwe	F	Translocated from Marakele November 2000. Pregnant when moved.	Died 2001
Chimpanje	M	Translocated from Pilansberg SA to LNP in 2000	In Majete
Ntangai	Undetermined	Born to Julia in Jan/Feb 2001	In LNP
Jabesi	F	Born to Justerine October 2003	In LNP
Nangondo	Undetermined	Born June 2003	In LNP
Namagogodo	Undetermined	Born February 2004	In LNP

KNP- Kruger National Park, LNP- Liwonde National Park, SA- South Africa, F-Female, M-Male.

Figure 2A. Dominant male black rhino (Bentley) in scrub mopane (C*olophospermum mopane*) during the wet season.

Figure 2B. Rhino browse on Chinese lantern (*Dichrostachys cinerea*). The bushes pushed over varied from 2 to 5 meters in height.

were located on the roads and tracked into the bush. The locations of rhino sightings and spoor were logged on a hand-held global positioning system (GPS) at the time of measurements. To avoid bias by over-counting, I recorded one location per individual rhino per day though several individuals may have been tracked in a day. If I did not see the rhino during tracking, the coordinate of the last sighted fresh spoor was noted. Location of middens and sleeping areas were also included in the data for utilization distribution analysis.

A spatial model of rhino population utilization distribution was developed by using kernel density estimators using Environmental Systems Research Institute (ESRI) Geographic Information System (GIS) ArcView software and its Home Range Extension program (HRE) (Hooge and Eichenlaub 2000). Kernel density estimators were calculated from GPS data, gathered while tracking the seven rhino (five adults, a subadult and a calf). The data points consisted of rhino sightings, midden locations, sleeping locations, and the location of the last spoor. The HRE uses a standard bivariate normal (Gaussian) kernel density estimator to produce polygons or isopleths to predict the utilization distribution of an animal or population. The kernel estimator converts this estimate into a probability density function and joins areas with the same probability (Hooge and Eichenlaub 2000). Finally, it generates a GIS layer with gradients for the probability of high to low rhino utilization. I chose a 95% kernel density estimator because it excludes areas of habitat that are seldom utilized and, therefore, gives a more conservative estimate of the resources potentially available to the animals. Each isopleth in the PUD decreases in 10% increments from the outer 95% isolpeth. I also defined core areas, those areas having a high proportion of location records in the PUD, by the 75% isopleth. Core areas have been delineated by several studies ranging from the 50% to the75% isopleth (Harris et al. 1990; Ganey et al. 1999; Potvin et al. 2000; Tatman et al. 2000; Cimino and Lovari 2003; Barg et al. 2005).

Choosing an appropriate smoothing factor (h) is essential in kernel-based home range techniques (Silverman 1986; Warton 1989). The smoothing factor determines the spread of the kernel. If the value of h is small, the kernel is narrow and results in an extremely variable or undersmoothed utilization distribution. An h that is too large results in over smoothing, which can obscure finer details (Hooge and Eichenlaub 2000). I selected the h_{ref} in HRE, an automated method of choosing a value for h, which is recommended for home range determination with a large number of data points (Worton 1989).

Vegetation Sampling

Within the sanctuary, vegetation was sampled from May to August, 2004, along 50 random 100 m x 1 m line transects. The transects were selected by superimposing a $4km^2$ grid on 2003 satellite imagery, with three starting points at least 400m apart generated within each grid unit. In addition, twenty 100 m x 1 m vegetation line transects were undertaken from randomly selected rhino middens. Vegetation sampling from active middens assured sampling within the rhino habitat since distributions were not known *a priori*. Therefore, a total of 70 transects were sampled within the sanctuary to assess the vegetation.

Before sampling, the direction of each line transect was randomly chosen. Black rhino usually feed to a height of two meters (personal observation); however, they also push over small trees up to 5 m in height to browse the ends (Figure 2B). Therefore, I recorded all plants by species located in the woody layer vertically along the transect line from 30 cm to 5 m in height. Any unknown specimen were pressed and taken to the National Herbarium in Zomba for identification. From the transect data, relative densities for all woody plant species in the sanctuary and Simpson's Index for species diversity in each transect, using PC-ORD, were calculated (Appendix A).

Satellite Imagery

Landsat TM 7 satellite imagery with a 15 m spatial resolution was purchased from the National Aeronautics and Space Administration. The image, taken in October 2003, was georectified, but unclassified. I classified the image using ESRI ArcMap software's image analysis. I ground-truthed the image in a three step process. First, I associated the image reflectance to a particular vegetation type, based on prior knowledge of the vegetation in Liwonde. Then, I visited the initially classified area on the ground and used a GPS to verify the classification by recording and cross-referencing the area with the image. This was a continuous process of trial and error until I defined recognizable categories in ArcMap. Once certain that a classification had been correctly identified, I chose the class types randomly in the field and took a coordinate point of the vegetation type to cross reference data with the classified image in ArcMap. Lastly, I retested the image with data in the field and constructed a confusion matrix to analyze the map accuracy (Brimicombe 2003).

The vegetation in the sanctuary is very diverse, making identification of clearly distinct categories difficult. Therefore, by consolidating infrequent vegetation classes with similar types in the ground truthing of the image, my analysis identified six broad classes: water, bare ground, short grass, tall grass, and two woody vegetation layers. The first of the two woody vegetation layers identified an area that had two distinct tiers, an unclosed overstory tree canopy in association with a diverse woody understory while the second woody vegetation layer was identified as a monolayer consisting of a closed overstory tree canopy with very little to no understory woody species.

Browse Availability

Black rhino are browsers, feeding mainly on woody vegetation, but will also eat forbs and some grasses. Rhino feed with a characteristic bite that enables rhino browse to be distinguished from that of other browsing mammals. Specifically, when a rhino feeds, its upper prehensile lip pulls vegetation into the mouth, and it bites the branch at an approximate 45° angle (personal observation). The teeth cut the vegetation in a clean manner, as if a pair of side cutters had clipped the twig, leaving a far more precise browse mark than other large browsers.

While tracking the rhino, I recorded all vegetation species they ate and the number of stems eaten. If a specimen was not known, I sent a sample to the National Herbarium in Zomba for identification. Pooling data for browse collected from both field seasons, I developed a preference index of the plant species, defined as the forage ratio w_i to determine browse availability in the sanctuary, $\left(w_i = o_i / \hat{\Pi}_i\right)$ where o_i is the sample proportion of browse species (i.e. recorded as a species browsed on by rhino) in the sancutary, and $\hat{\Pi}i$ is the sample proportion of all recorded plant species in the sanctuary (Savage 1931). Hence, I obtained a forage ratio of each browse species in the sanctuary.

GIS Layers

The GIS layers were chosen for their possible influence on rhino habitat preference and potential significance to the predictive model. The layers developed for the model were browse availability, road density, river density, watering hole density, distance to permanent water, utilization distribution, and the classified satellite image. I applied the kernel density function in ArcMap to river, road and water hole densities. The program calculated the density of each output raster by adding the values of all the kernel surfaces where they overlap the raster cell center. A smooth surface was then fitted to all areas with the same value. All data layers were standardized into indices.

Browse Availability Layer

The necessity of food availability led to the generation of a layer of browse availability. I related the forage ratio of each plant species, w_i, to the random vegetation transects. The forage ratio is indicative of what the rhino ate and the proportional availability for that particular resource in the sanctuary. Therefore, the index value of each plant species was multiplied by the number of the same species (n_i) represented in each transect. The totals for all browse species in a transect were then summed to give the browse value for each transect.

$$\text{Transect Browse Value} = \sum\left((w_i = o_i / \hat{\Pi}_i) * n_i\right)$$

These point values were then interpolated into a data layer in the GIS. Interpolation is a function in ESRI ArcMap that enables point data, as in the case of the transect locations, to be generated into a density layer. In essence, it develops a contoured surface joining areas of equal value much in the same way as contours in a topographic map.

Road Density Layer

The sanctuary is traversed with small dirt roads created for game viewing. These may affect rhino's habitat preference. As the satellite image did not adequately reveal the roads in the sanctuary, I delineated them by setting a hand-held GPS to collect data every 20 m while I either walked or drove at a slow speed (2-15 km/h) along the route. The roads were constructed in ArcMap from the data points. Road locations in the greater park were outlined in the same manner as the sanctuary roads; however, two roads in the north of the park were outlined from a topographical map, as I was not able to access them. While in Liwonde, I gathered information from six safari guides, working at the Mvuu safari camp, on road use within and immediately surrounding the sanctuary. The safari guides use the roads for game drives with tourists throughout the year. Each one was asked independently to identify which roads they used and to assign an intensity road use value from 1 to 3, where 1 was seldom or never used, 2 was occasionally (weekly) used, and 3 was frequently (daily) used. The average value for the road assigned by the six guides was then used in the development of a kernel density layer.

River Density Layer

Classification of rivers in the GIS were based on their size. I ground-truthed the two large seasonal rivers running through the sanctuary by walking along their beds with a GPS point taken every 20 m. A value of 3 was assigned to these two rivers. Tributaries, leading into the two seasonal rivers were labeled with a 2, while smaller secondary tributaries flowing into the primary tributaries received a value of 1. Small drainage lines were not included in the GIS layer. I derived the locations of the rivers valued 2 and 1 from the satellite image in combination with a topographical map. All rivers outside the sanctuary were traced from the satellite image and topographical map. Kernel density layer for rivers were generated using ArcMap for both the sanctuary and the entire park.

Water Hole Density

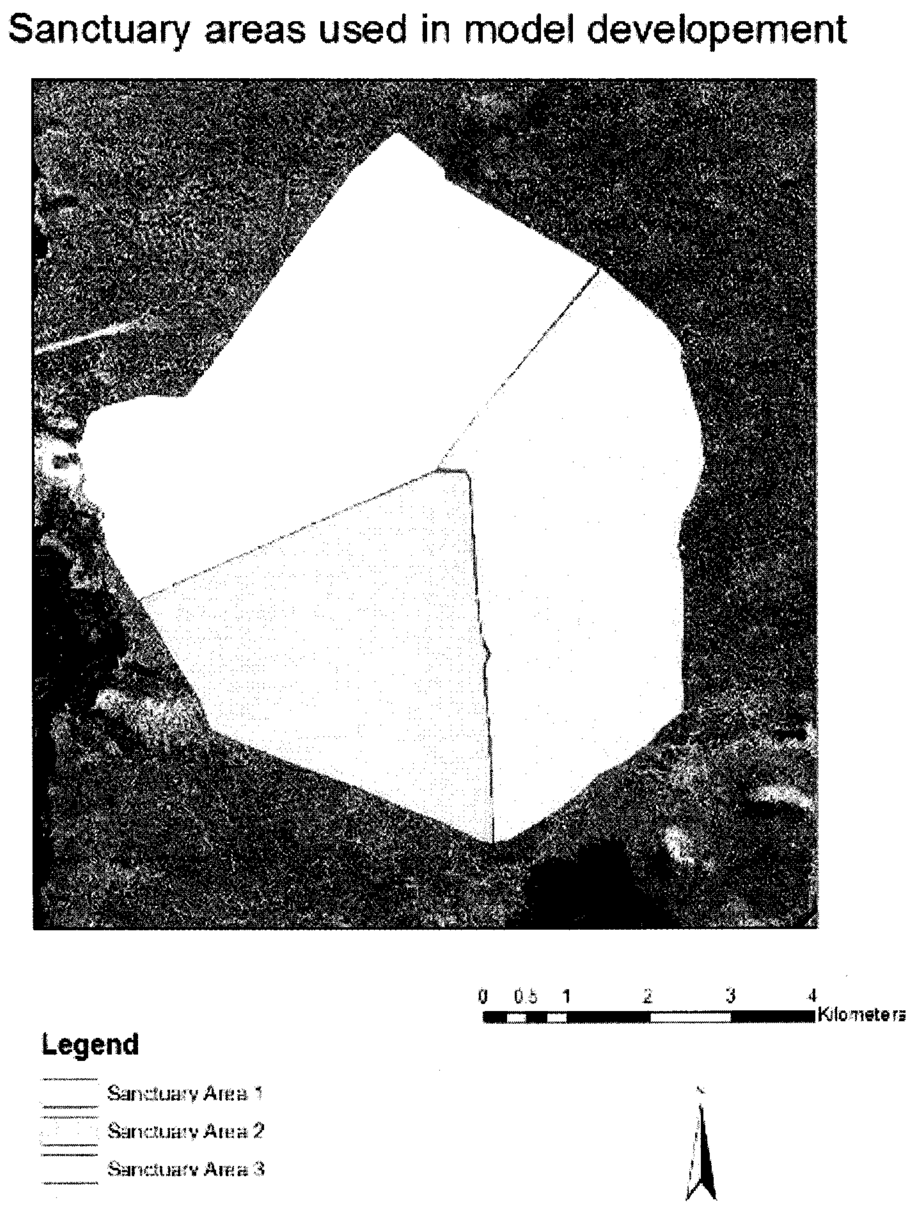
Rhino are water dependent and drink daily. Therefore, distance to water is an important factor in habitat selection, especially during the dry season. Water hole locations were recorded with a GPS while tracking or searching for rhino in the sanctuary. As before, a kernel density layer was generated from the point data using ArcMap. Consequently, another GIS layer incorporating the distance to the three permanent water holes was developed.

Habitat Suitability Model for Black Rhino Sanctuary

To develop a predictive rhino habitat suitability model within the sanctuary, I divided the sanctuary into Areas 1, 2 and 3 (Figure 3). Areas 1 and 2 each contained a distinct rhino core area as determined by the Home Range Extension program. Area 3, which had been opened to the rhino within the first week of my first field season, did not yet have any indication of rhino activity nine months later as determined by the lack of sightings, middens, browse and spoor. Area 1 was used to calibrate the model, Area 2 was used to validate the model, and Area 3 was used to apply the model to predict suitable rhino habitat.

To determine which GIS layers played a greater role in rhino habitat selection and to assess the possible contribution of each layer to the model, all GIS layers were overlaid and spatially joined to the location of the transect points. Individual values for each GIS layer at transects in Areas 1 and 2 were separated into two categories, those lying within

Figure 3. Rhino sanctuary indicating the different areas within the sanctuary used in the habitat models.



the 95% isopleth of the PUD (n=22) and those outside of it (n=10).

Analysis of variance (ANOVA) was used to compare the data sets for each GIS layer within and outside of the PUD area. In addition, I also compared Simpson's Diversity Index and the shrub layer density for transects lying within the 95% isopleths to those outside of the defined PUD.

The spatial distribution of the values identifying the utilization distribution can be viewed as a measure of the intensity of resource selection by the rhino population. To examine the relationship between resource utilization and specific landscape characteristics, a linear model was developed. To create the model, a 200 m point grid was overlaid on the entire sanctuary and spatially joined to attribute values from GIS coverage's of PUD, browse availability, road density, distance to permanent water, river density, water hole density and classified satellite imagery. The classified satellite image layer was represented in the model as a single variable by using a multiple linear regression of the dummy variables for the vegetation classes against the PUD to generate coefficients that could then be used to calculate a value for the classified image at each grid point. Within Area 1, the attribute values at each grid point were applied in a multiple linear regression analysis with the PUD as the dependant variable, yielding the linear function:

Equation 1

$$PUD=-776.8+5.7(Rd)+5.8(R)+0.688(BV)+4.9(WH)+5.1(DWH)+3.4(CI)$$

Where PUD=population utilization distribution, Rd=road density, R=river density, BV=browse value, WH= water hole density, DWH=distance to permanent water holes, CI=classified image.

To validate the model, Equation (1) was used to calculate PUD values from the value of independent GIS variables at each grid point within Area 2. The correlation between the PUD values predicted by the model and the actual values (as represented by the values generated by the ArcView HRE) was determined using linear regression. A spatial permutation test that is not biased by spatial autocorrelation (Costanza 1989) was used to evaluate the goodness-of-fit between model predictions and actual values across a range of spatial grains. This test evaluated the correlation within Area 2 by randomly regrouping the 121 grid points into blocks of 1-49.

To predict potential habitat suitability, i.e. PUD, in Area 3 of the sanctuary, which had no points for rhino sighting or sign, the regression relation given in Equation (1) was used to calculate a predicted value for PUD at each grid point in Area 3.

<u>Rhino Habitat Suitability Model for Liwonde National Park</u>

To determine potential rhino habitat in the rest of Liwonde National Park, I developed a linear model similar to the one for the sanctuary. However, satellite imagery and river densities were the only data layers available over the whole park, thus only these could be incorporated into the park model. The entire rhino PUD in the sanctuary (95% isopleth) was the basis for model development. The 200 m grid used in the sanctuary was extended over the whole park. Values were gathered as described above in the sanctuary model with a spatial join to the GIS layers at the grid intercept in the home range. A linear model was developed from these data and then projected on to the map of the whole park.

Results

Population Utilization Distribution

In this study, rhino were tracked for a total of 510 h. A typical daily routine, observed for the rhino during this period, consisted of feeding during the night and early morning hours and drinking between 3 and 5 am (as determined from spoor). The rhino continued feeding until first light when they laid down for a brief rest. Rhino chose old termitaria without canopy cover 65% of the time for these short naps, while open areas with a sandy soil and no canopy were used 35% of the time. The brief morning rest lasted approximately one hour, where upon the rhino began feeding again for a short period, defecated in a midden, and moved to a more protected area for a longer daily sleep that would often last until late afternoon. During tracking, I typically found rhino between 8 and 11 am by which time they were often asleep. Once found, I observed the rhino without threat of detection. If the rhino became alerted to my presence, I did not continue to pursue the animal. Instead, I slowly retreated downwind.

Over the course of the study, rhino were visually sighted 54 times resulting in a mean time of 9.4 hours of tracking per sighting. The rhino were found sleeping or resting 39 times and walking and feeding 15 times (Table 2). While sleeping, 46% (n=18) of the sightings occurred in riverine vegetation, with 31% (n=12) and 15% (n=6) occurring in ebony thickets and mopane scrub, respectively (Table 3). Only during the wet season were the rhino found sleeping in the relatively open mopane scrub.

I identified 71 plant browse species foraged by the rhino. Of these, seven composed the majority (52 %) of their diet (Table 3).

Black rhino PUD within Areas 1 and 2 was generated from 430 GPS data points

Table 2. Dominant vegetation types in which rhino were found sleeping. Data are from both the wet and dry season.

Vegetation type	Frequency of s
Mopane (*Colophospermum mopane)*	6
Ebony (*Dalbergia melanoxylon*)	12
Riverine vegetation	18
Tall grass	3
Total	39

Table 3. Seven woody plant species comprised the majority of the black rhinos browse during the study.

Browse species	**Total % of diet**
Acacia nigrescens	13
Dichrostachys cinerea	12
Dalbergia melanoxylon	8
Diospyros squarrosa	6
Colophospermum mopane	6
Securinega virosa	4
Ormocarpum trichocarpum	4
Total	52

(Table 4). The total area of the PUD as determined from the ArcView HRE was estimated at 18.4 km^2, which represented 43% of the total 43 km^2 sanctuary (Figure 4). Core areas, defined by the 75 % isopleths, were 6.7 km^2 (Area 1) and 2.2 km^2 (Area 2) (Figure 4), representing only 21% of the total sanctuary area.

GIS Layers

The browse availability (Figure 5) overlapped somewhat with the PUD (Figure 4), although they were not significantly correlated (P=0.33). Road density was high throughout the sanctuary with most of the intensity occurring within the current rhino ranges (Figure 6). River density (Figure 7), was high throughout the sanctuary, as well as in several other locations within Liwonde National Park. Water holes were found throughout the sanctuary with higher concentrations on the western boundary (Figure 8). The classified satellite image of the sanctuary and whole park is shown in Figure 9. The confusion matrix resulted in an overall map accuracy between producers and users of 84% (Table 5).

A comparison of variables, using analysis of variance (Table 6) from the transect points located in the 95% isopleths of the utilization distribution (n = 22) compared to those located outside (n = 10) showed river density, water hole density, road density and Simpson's Diversity Index significantly different (P<0.001, P<0.001, P=0.007 and P=0.049, respectively) between the two areas. River density had the largest percent difference, being175 % greater in the PUD compared to outside (Figure 10) followed by 110 % greater water hole density, 62 % greater road density and finally 16 % greater vegetation diversity, inside versus outside of the PUD. In contrast, there was no

Table 4. Population utilization distribution for the black rhino were generated from point data comprising the following types of data.

Type of data		Frequency
Direct sightings		54
Middens		201
Sign (Last identified spoor and sleeping areas)		175
	Total	430

Figure 4. Black rhino population utilization distribution (PUD) in the sanctuary generated using ESRI Home Range Extension. The outer contour represents the 95 % isopleth or 95 % probability of occurrence. The core area is represented by the 75% isopleths. The dashed black lines denote low intensity unpaved roads; note the large number within the sanctuary.

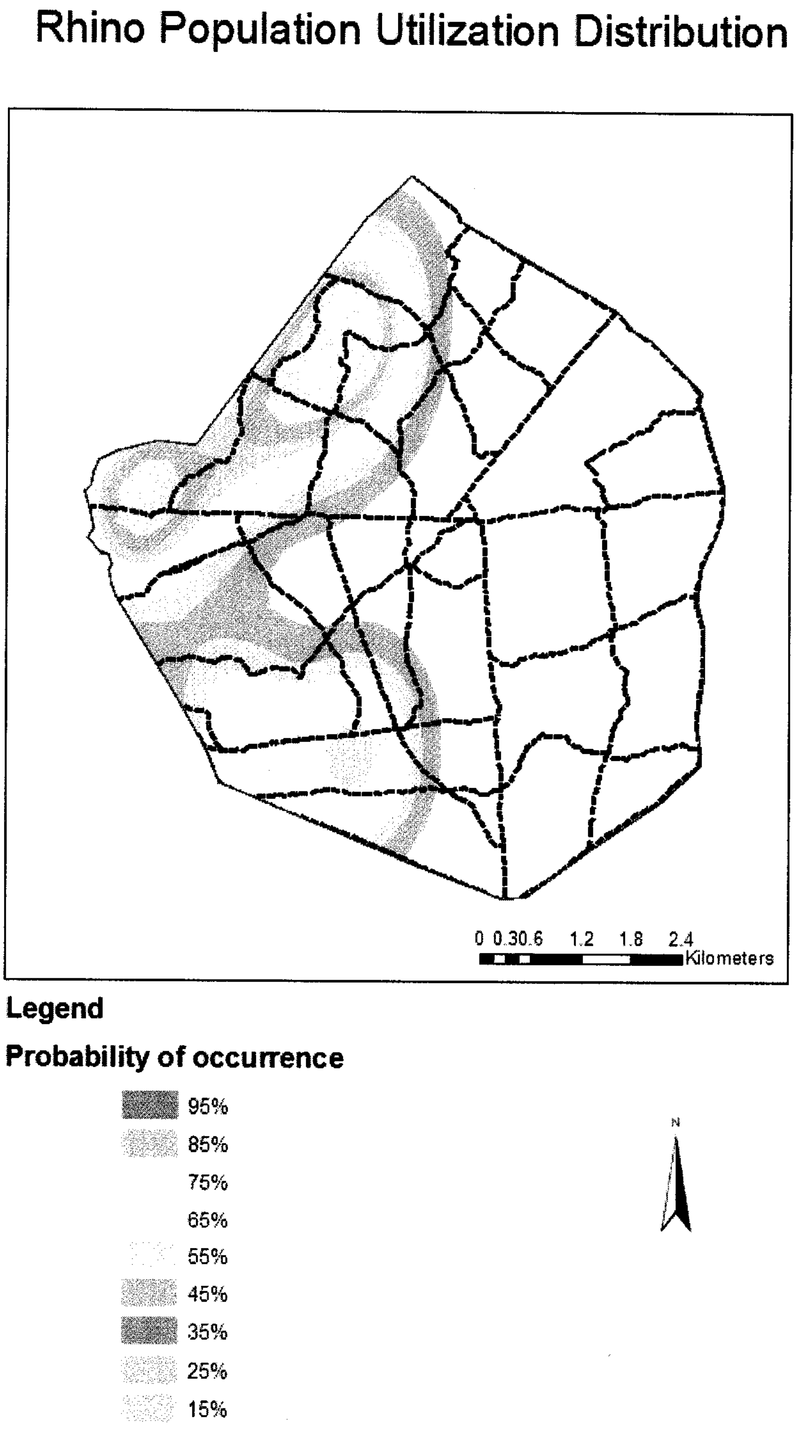


Figure 5. Contoured representation of rhino browse interpolation from the rhino browse value calculated from vegetation browse data at each transect point. The higher numbers represent a higher browse availability.

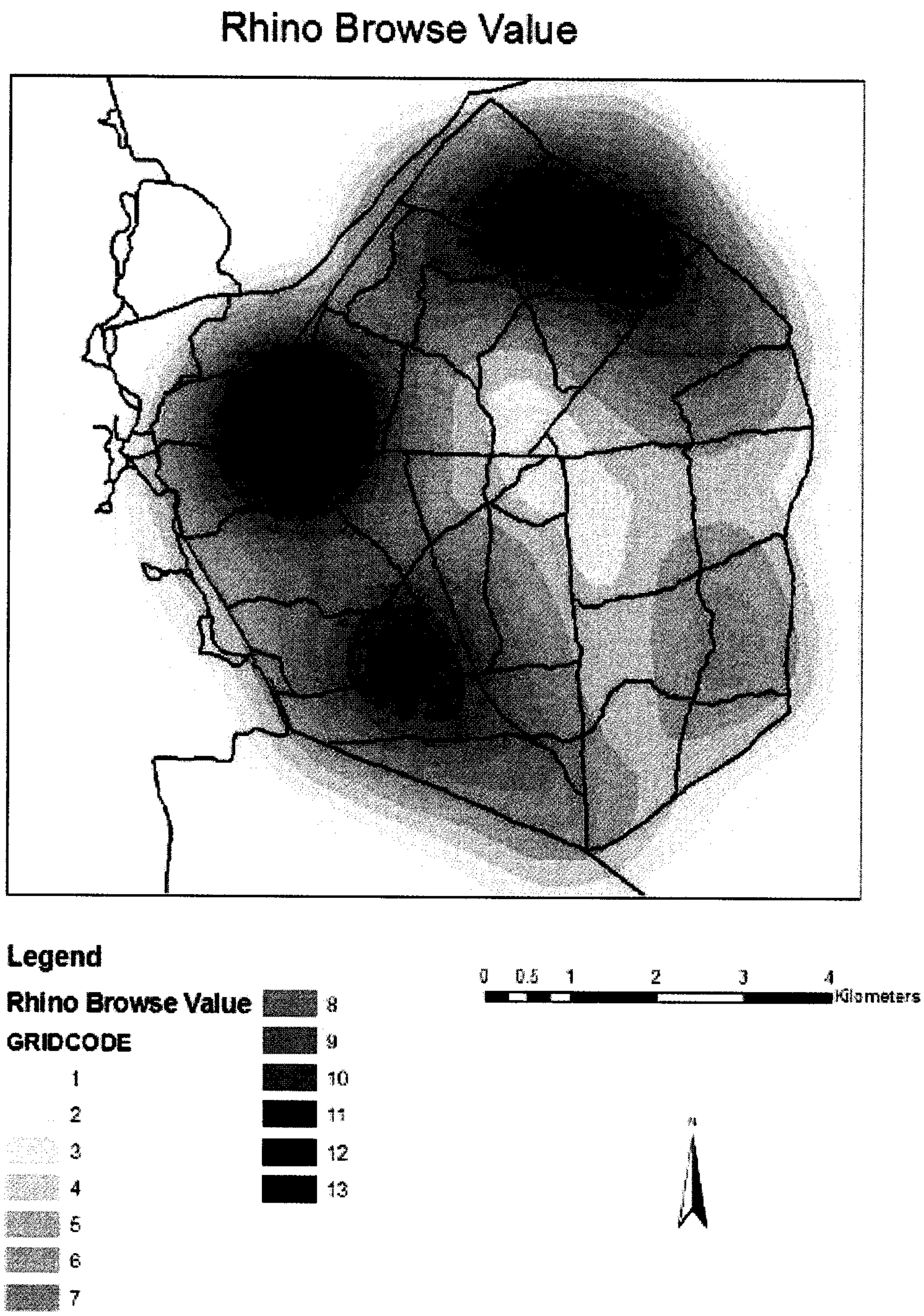


Figure 6. GIS layer of sanctuary showing kernel densities for roads in and surrounding the sanctuary. Roads were given a value of 1 (infrequent use), 2 (average use) and 3 (frequent use). Blue color values indicate greater road use.

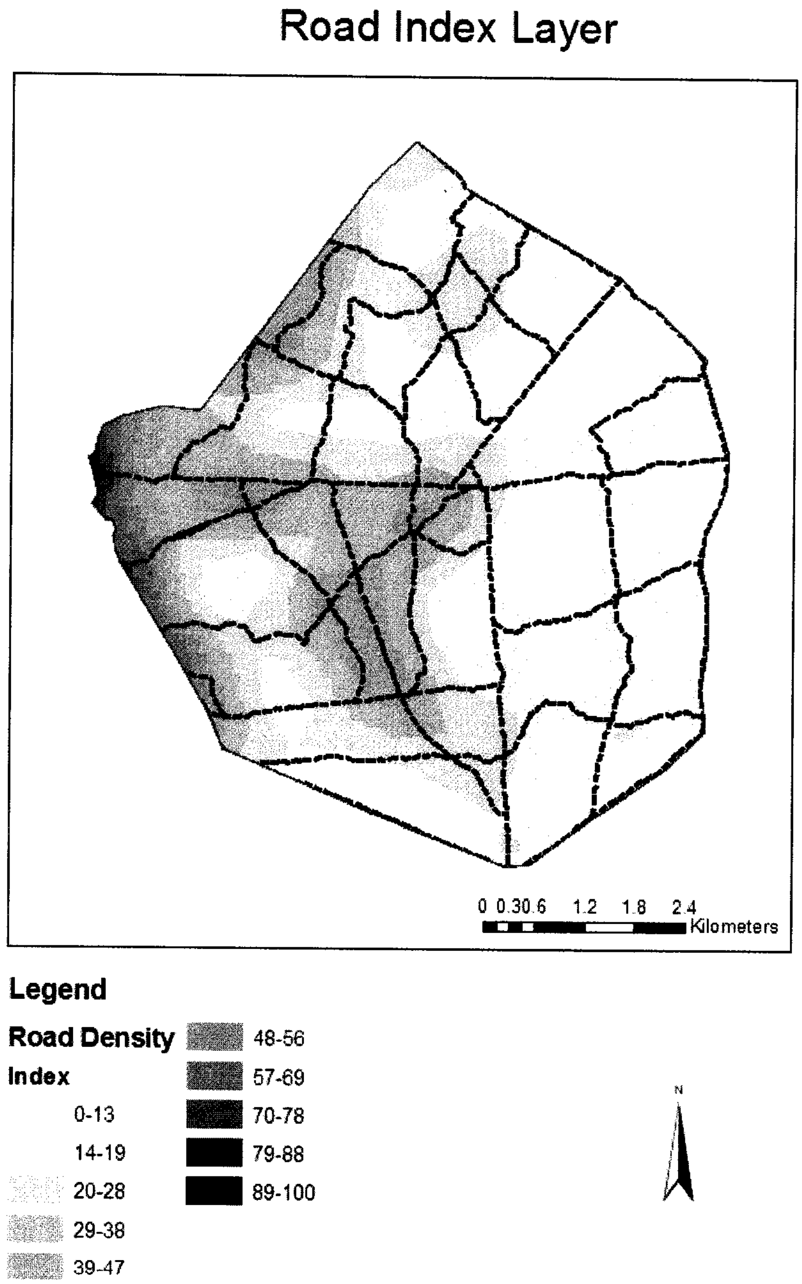


Figure 7. GIS river index layer mapping seasonal rivers in Liwonde National Park. Blue indicates a higher kernel density, while the pink and white illustrate low to no river density.

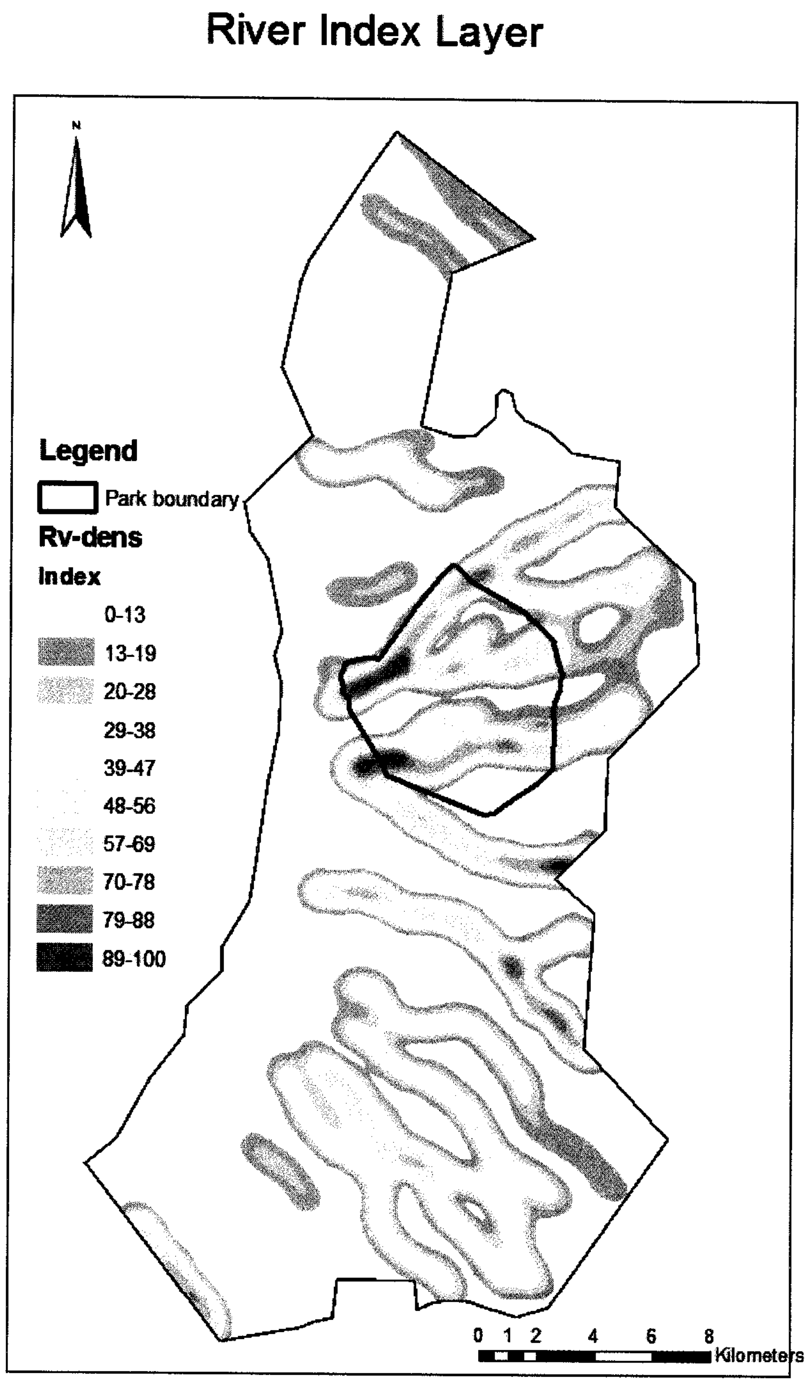


Figure 8. GIS layer showing an index of water holes in the sanctuary. The diamond shaped points are the location of water holes. The darker brown indicates areas of higher kernel density for water holes.

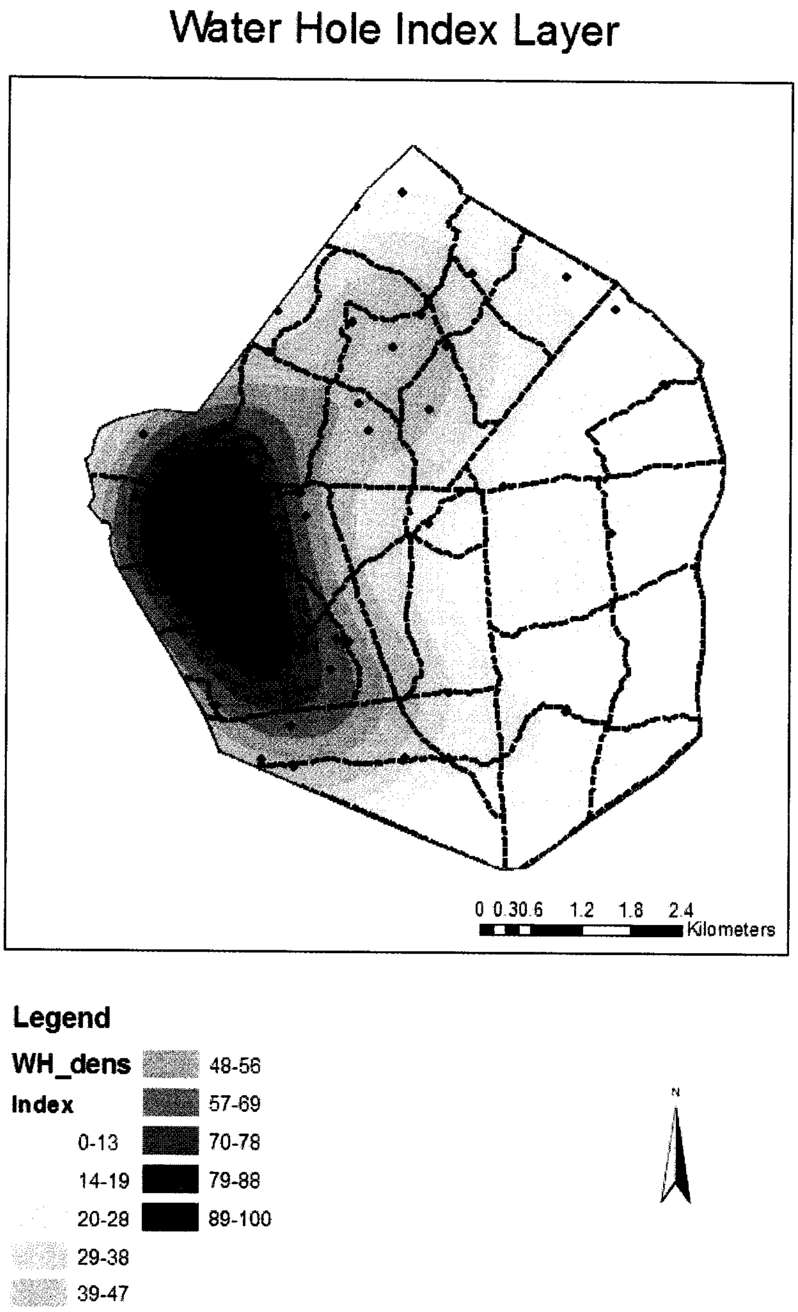


Figure 9. Classified satellite Landsat TM 7 imagery showing ground truthed vegetation classes. The satellite image recorded areas burnt by fire as closed canopy. These areas are mostly in the south eastern part of the park. The burnt areas can be seen as black areas in Figure 1.

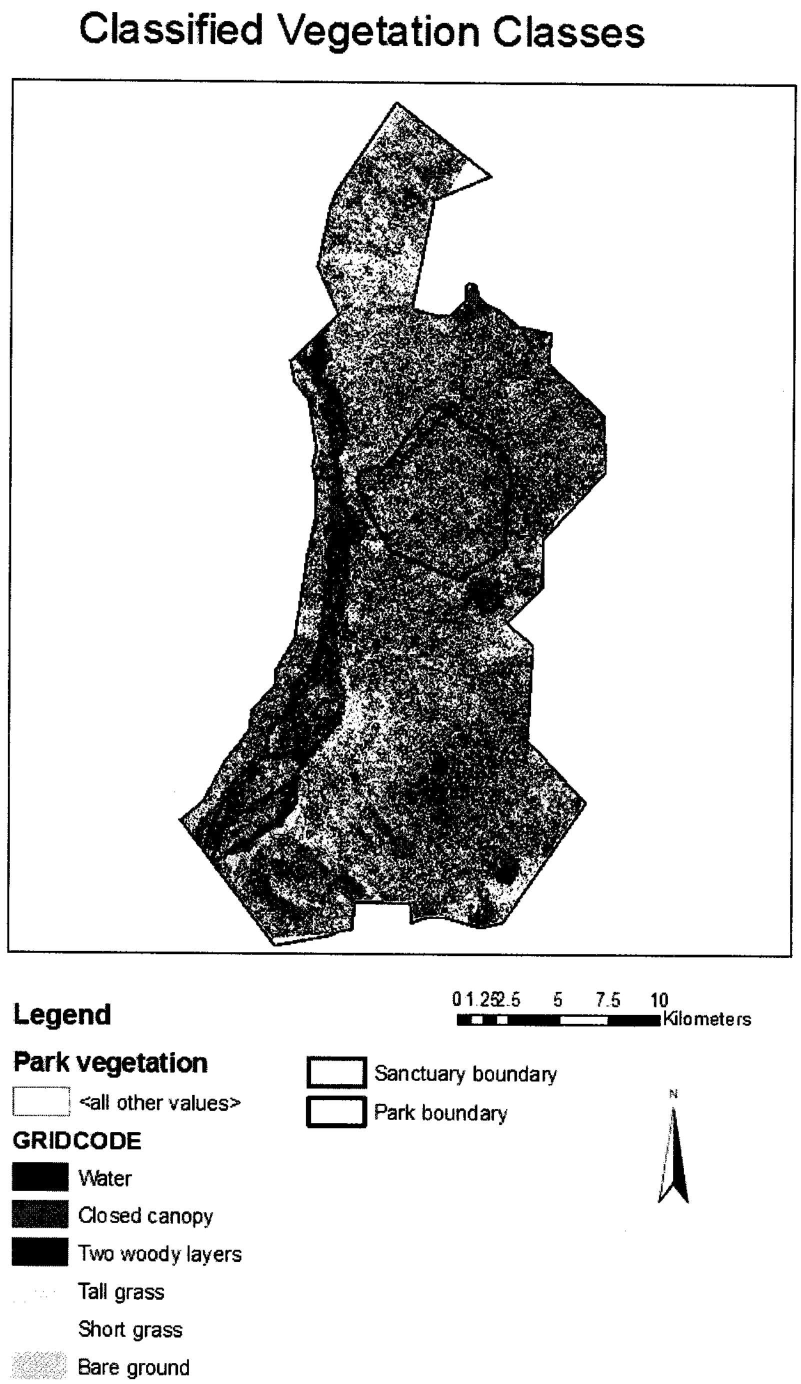


Table 5. Confusion matrix of producers and users accuracy of classified vegetation classes on satellite image. The upper table shows the number of times the vegetation was correctly identified in the field when compared to classified imagery. Overall map accuracy is 84%.

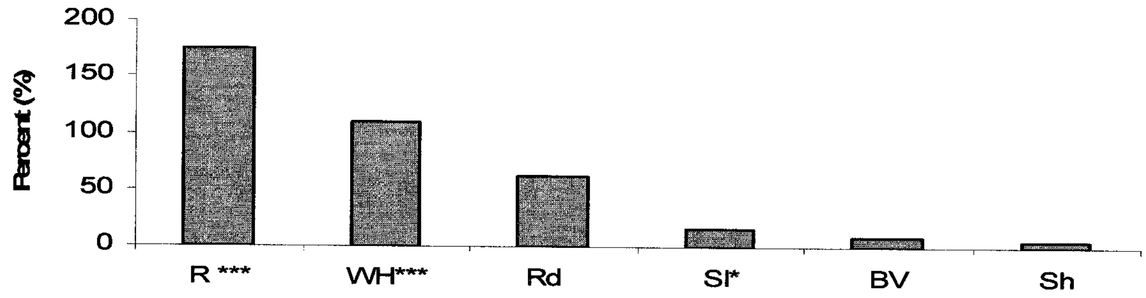
	Water	Closed canopy	Double layer	Tall Grass	Short grass	Bare ground	**Total**
Water	10	0	0	0	0	0	10
Closed canopy	0	36	4	0	0	0	40
Two woody layers	0	4	38	11	0	0	53
Tall grass	0	0	5	41	0	0	46
Short grass	0	0	0	3	30	5	38
Bare ground	0	0	0	0	4	28	32
Total	10	40	47	55	34	33	219

	Producer's accuracy	**Users accuracy**	**Overall accuracy**
Water	100%	100%	84%
Closed canopy	90%	90%	
Two woody layers	81%	72%	
Tall grass	75%	89%	
Short grass	88%	79%	
Bare ground	85%	88%	

Table 6. Analysis of variance of GIS data, in Areas 1 and 2, from transect points falling within the black rhino population utilization distribution compared with those outside.

GIS layers	Home range	Non home range	P
Rivers	53.1±0.05	19.7±5.28	<0.001
Water holes	59.6±4.22	28.1±4.97	<0.001
Roads	32.2±2.72	19.68±2.55	0.007
Simpson's Diversity Index	0.8±.002	0.7±0.05	0.049
Browse value	8.59±0.45	7.7±0.89	0.331
Shrub layer	0.02±0.001	0.02±0.004	0.969

Figure 10. Percent increase in means of habitat variables between the rhino population utilization distribution (n=22) and non-population utilization distribution (n=10). Variables include: R = River Density, WH = Water Hole Density, Rd=Road Density, SI=Simpson's Diversity Index, BV=Browse Value, Sh=Shrub Density. Data sets were collected from transect points. * denotes significant difference at P<0.05.



significant difference between either browse value or shrub density when comparing their PUD to non-PUD areas.

Habitat Suitability Model for Liwonde Rhino Sanctuary

GIS variables used to develop a predictive linear model for black rhino population utilization distribution were browse availability, road density, river density, water hole density, distance to permanent water holes, and classified satellite image. These variables were used to calculate PUD as described by equation 1. The linear regression results showed that all of the variables, except browse availability, were significant (Table 7), although all variables were used in the sanctuary prediction model. The black rhino model calibrated from data in Area 1 was validated by using the GIS variables generated on the 200 m grid in Area 2. The output of the model was highly correlated to the output of the HRE program in Area 2 (R^2 = 0.56, P=<0.001) (Figure 11). . The outer extent of the 95% isopleth, calculated by the HRE program, in Area 2 is 6.9 km^2 in area. The area of the 95% isopleth predicted by the model is 11.5 km^2 in Area 2, suggesting that an additional 4.6 km^2 could be available for rhino in Area 2. When considering core areas (75% isolpleth), the model approximates an enlargement of the core area by 4.5 km^2 or, 51% more area than rhino currently occupy as core area.

Spatial consistency between model and actual home range showed average correlations of 0.71 or better at spatial resolutions from 0.04 km^2 to 2 km^2 (i.e., 1 to 49 grid points per block) when run over a 1000 replications (Figure 12). This indicates the model is conserved across a range of spatial scales for spatially independent blocks of randomly grouped points.

Table 7. Summary results from the sanctuary linear regression model (R^2=42, P<0.001).

Predictor variable	Coefficient	Standard error	P	VIF
Road density	5.7	0.98	<0.001	1.30
River density	5.8	0.47	<0.001	1.06
Browse value	0.7	0.70	0.32	1.36
Water holes density	4.9	0.86	<0.001	2.56
Permanent water holes	5.0	0.88	<0.001	1.96
Satellite landscape composite	3.4	0.91	<0.001	1.03

Figure 11. Scatter plot showing the validation of the model ($P<0.001$) used to describe utilization distribution for Area 2 of the sanctuary.

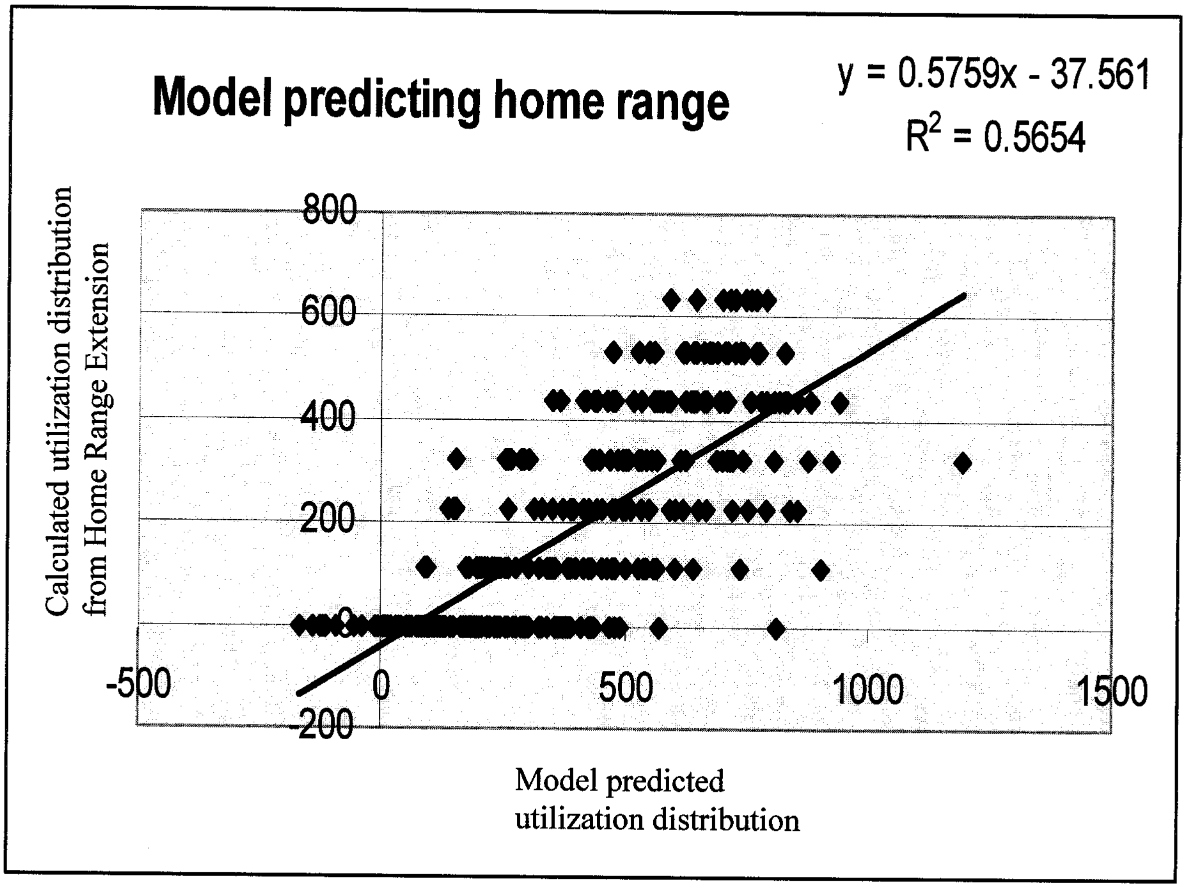
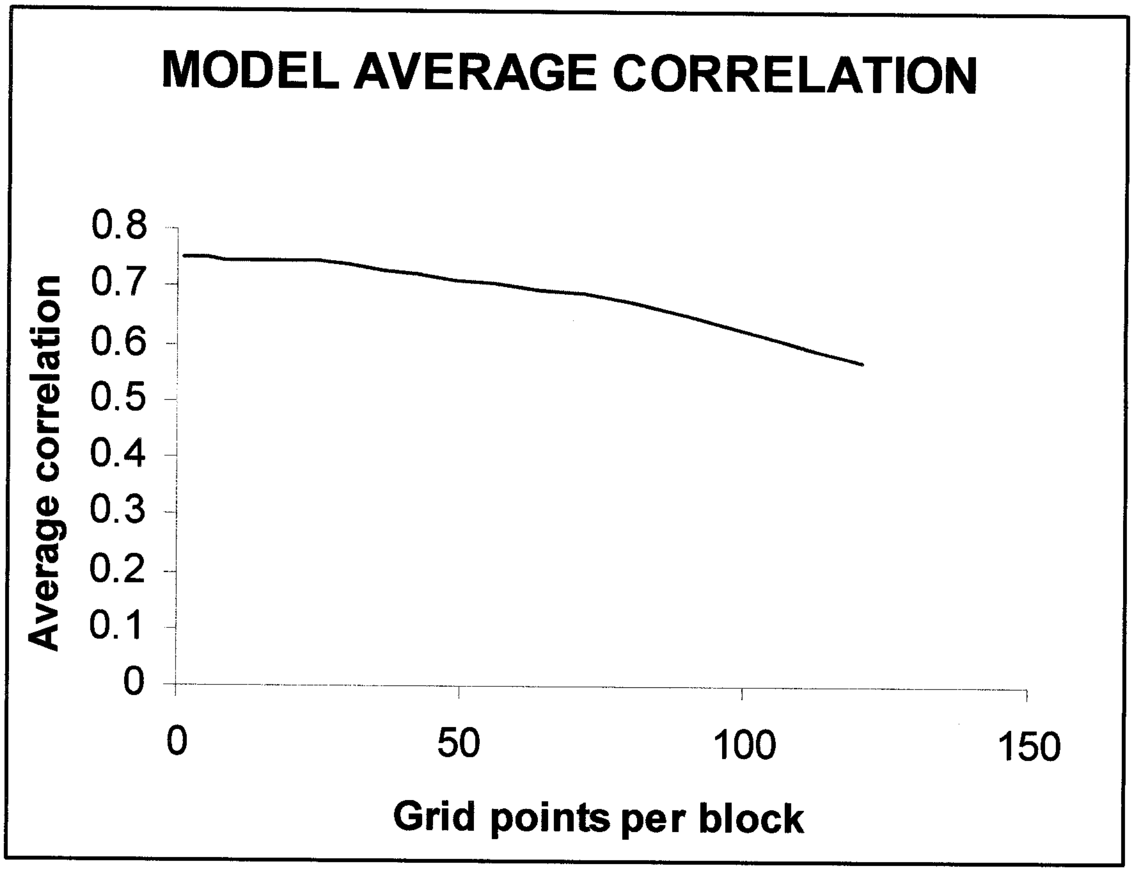


Figure 12. Average correlation between utilization distributions for model and home range for blocks of grid points numbering 1-49 with 1000 permutations. Demonstrating the model is consistent across spatial scales.



Once validated, the model was applied to Area 3 to predict potential rhino habitat (Figure 13). The model predicts an increase of 7.0 km^2 of additional rhino habitat using values from 95 % isopleth and 1.5 km^2 of core area for Area 3. Thus, over Areas 2 and 3 the available habitat as predicted from the model is 25.3 km^2, which includes 9.7 km^2 of core area, corresponding to an increase in 265 % and 373%, respectively, above current rhino usage in those areas.

Habitat Suitability Model for Liwonde National Park

The model to predict black rhino habitat in Liwonde National Park incorporated GIS data layers for river density and the satellite image. Data for additional layers were unavailable across the entire park. However, a significant predictive linear model was still developed (R^2 =0.25, $P<0.05$) (Figure 14). River density had the greatest influence in the development of the linear model, explaining 24% of the variation, while the satellite image explained only 1%. Using values for core areas (75% isopleth) the model estimated 18.6 km^2 of potential core area in the park, while the 95% isopleth predicted 206 km^2 as suitable for black rhino (Figure 14). Thus, across the entire Liwonde National Park, the model predicts 231 km^2 of potential rhino habitat, which includes 29.3 km^2 of core areas, resulting in an increase of 913% and 302%, respectively, above that currently being used by rhino.

Figure 13. The predicted habitat for Areas 2 and 3 within the sanctuary as expressed by interpolation of model grid points. The 95% and 75% isopleths follow the initial outer extent of rhino habitat and core areas generated by Home Range Extension.

Sanctuary Model Indicating Black Rhino Habitat

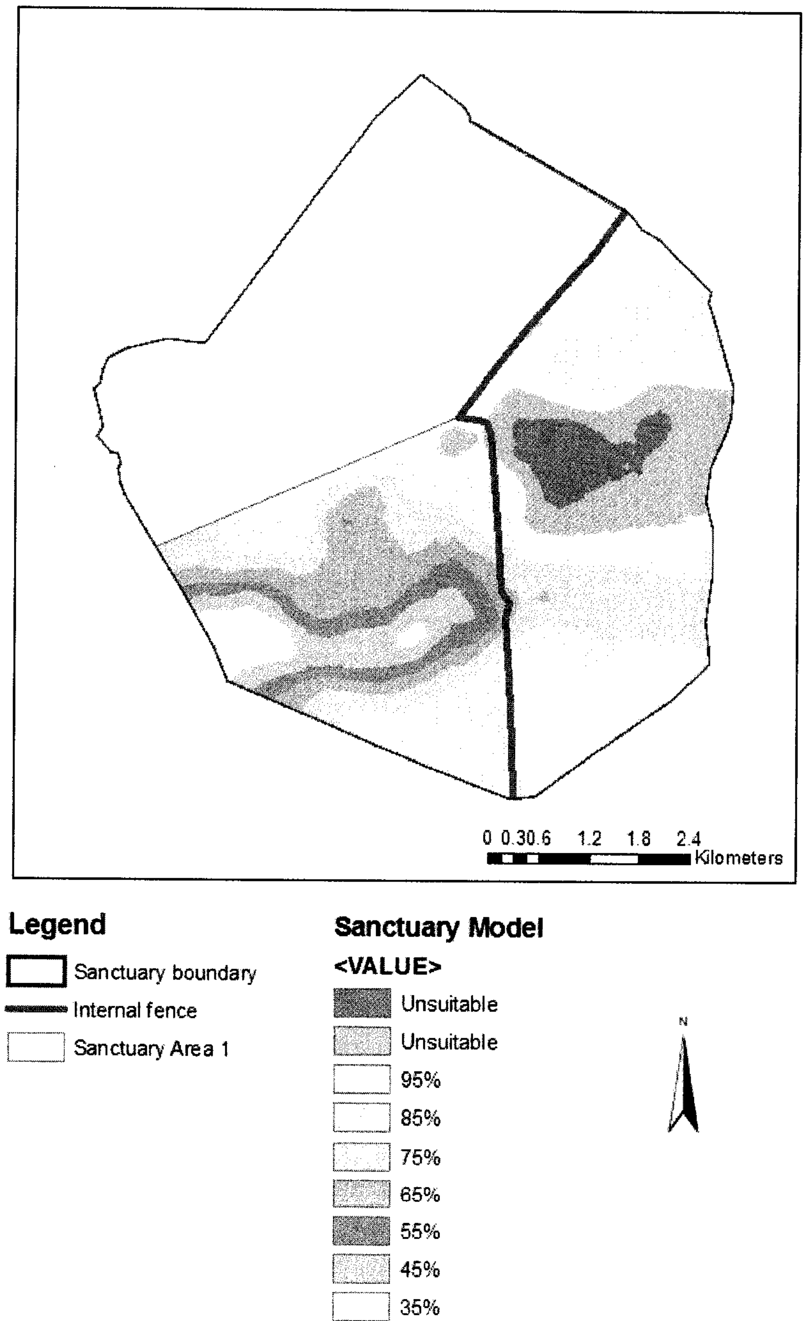
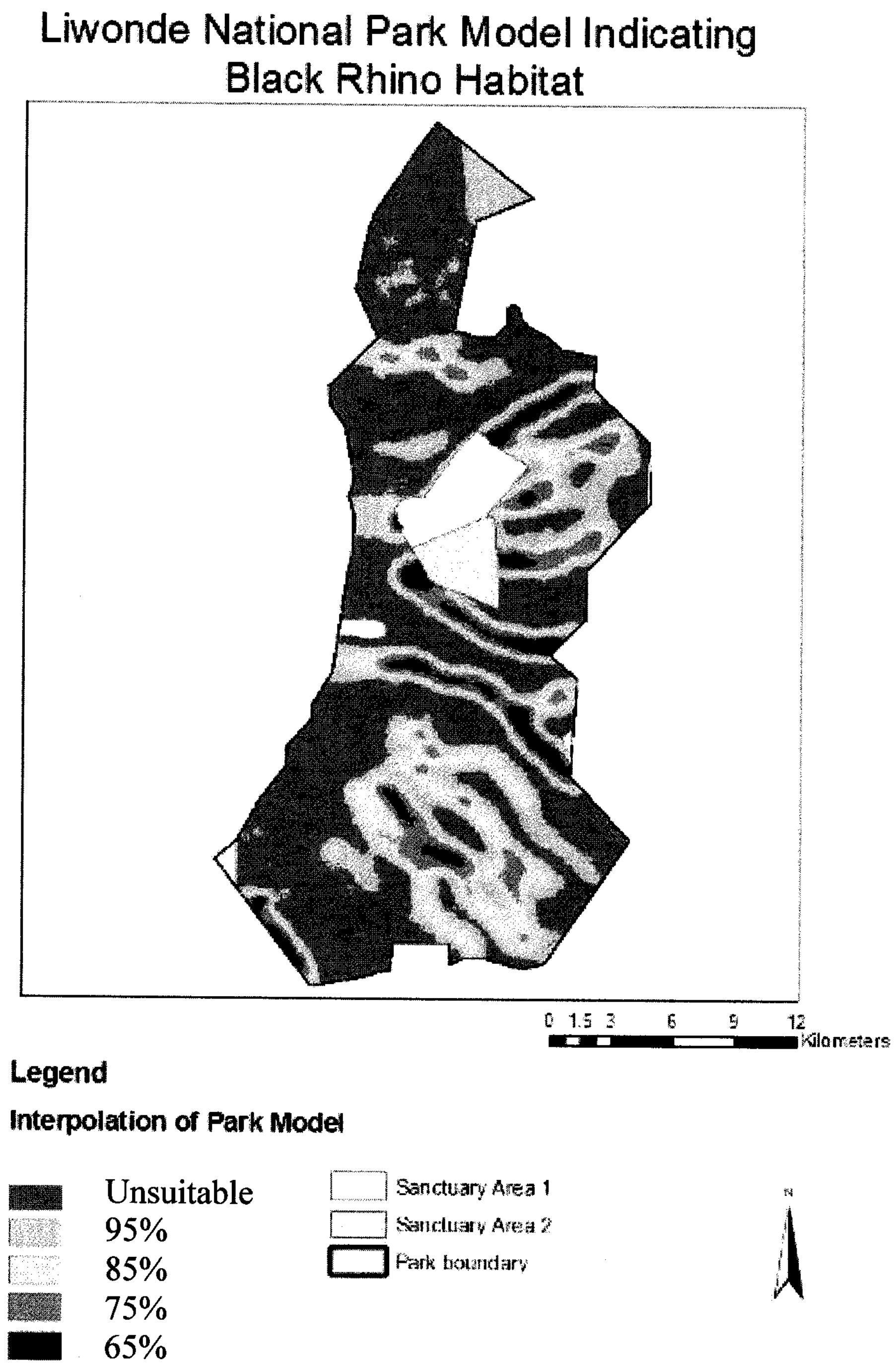


Figure 14. Liwonde National Park superimposed with the GIS interpolation of the model. Areas 1 and 2 from the sanctuary are not included as data from these areas were used to construct the model. The 95% isopleth and the core area (75% isopleth) follow the initial population utilization distribution generated by HRE.



Discussion

Population Utilization Distribution

Previous studies show rhino home range is highly variable in area and dependent on habitat quality (Goddard 1968; Conway and Goodman 1989; Tatman et al. 2000). In dry areas of the Serengeti, rhino have home ranges of 70-100 km^2 (Frame 1980). Alternatively, Conway and Goodman (1989) found seven rhino occupying an area of $4.3 km^2$, leading to the conclusion that rich habitat can support high numbers of rhino. Though this study did not look at individual home ranges, the sanctuary's seven rhino (five adults, a sub-adult and a calf) occupy a home range, with two core areas of 18.4 km^2 at a ratio of one rhino to 2.6 km^2. It is interesting to note that nine months after the internal fence in the sanctuary was removed, rhino had not moved from their established range into the new territory, which likely indicates that their habitat requirements are adequately met by their current range (Areas 1 and 2).

Many studies provide information on the optimal smoothing value h when generating the population utilization distribution (Worton 1989; Hooge and Eichenlaub 2000; Henson et al. 2005). Least squares cross validation, h_cv, is commonly accepted as generating the best value for a smoothing factor (Silverman 1986; Worton 1989; Seaman and Powell 1996). Initially h_cv was chosen as a smoothing factor; however, h_cv did not fit the data in a meaningful way (data not shown). The PUD was seriously over-smoothed, giving a labyrinth of small core areas that could not be used. On the other hand, the smoothing factor h_{ref} generated a more coherent, less fragmented PUD.

The inconsistency with other studies when choosing a smoothing factor may be explained by the black rhino's habits. Black rhino are eurytopic animals, surviving in a wide variety of habitats in a well-defined home range (Goddard 1970a; Frame 1980; Hall-Martin et al. 1982; Oloo et al. 1994; Dierenfeld et al. 1995; Bhima and Dudley 1996; Muya and Oguge 2000). Black rhino also move great distances in their daily cycles (Berger 1997; Tatman et al. 2000), thus a smoothing factor that does not incorporate sufficient area to approximate the extent of the population's functional response in a landscape may not be appropriate when generating a kernel density.

Satellite Imagery

Rhino appeared not to associate with any particular vegetation classes when considered in the context of the model. In the classified image, the polygons of classes are small and very heterogeneous, showing the complexity of the vegetation. There are few large areas of any particular classification type. After ground truthing the image and completing the confusion matrix, I found that the classifications represented a vegetation accuracy of 84%. Given this accuracy in the classification, some other factor must be considered for the inability to capture the rhino's habitat selection, pertaining to vegetation. Perhaps the classification of the satellite image was not specific enough to pick out distinct vegetation classes important for rhino. For instance, from the sighting of rhino, we could determine their preference for riverine vegetation and scrub ebony thickets, and occasionally scrub mopane in the wet season. Yet the image classes do not differentiate vegetation at such a fine scale. Classification of higher resolution satellite imagery may allow for more distinct vegetation classifications, but was unavailable for this study. The satellite imagery added some predictive value to the sanctuary model. Other studies have relied significantly upon satellite imagery for habitat modeling (Innes and Koch 1998; Osborne et al. 2001; Luoto et al. 2002(a); Luoto et al. 2002(b); Suárez-Seoane et al. 2002 Dettki et al. 2003), and as a result, satellite imagery was used even though it contributed little to the model.

Habitat Suitability Model for Black Rhino Sanctuary

Both predictive models, and in particular the sanctuary model, predicted suitable rhino habitat well, showing a 375 % increase of potential rhino core areas, as defined by the 75 % isopleth, within the sanctuary.

The most important variable, identified in the sanctuary model, is river densities (Table 7). Other studies have also shown the importance of river habitat for terrestrial animals (Woinarski et al. 2000; Robinson et al. 2002; Semlitsch and Bodie 2003). Tatman et al. (2000) found a high amount of rhino spoor and middens in riverine woodland which is consistent with this study, where I found a higher proportion of rhino sightings in riverine vegetation than in any other habitats. Besides the rather large Shire River, the seasonal rivers only contain water for short periods of time (2-3 months) during the rainy season, and then inconsistently. Water availability may only play a limited role in this habitat selection. The vegetation associated with the rivers is thick and dense with a closed canopy. Rhino most often were found sleeping or resting in dense riparian vegetation (46% of the time) or ebony thickets (30% of the time) (Table 2). During the dry season, deciduous plants loose their leaves and the only shade available, though largely leafless, is the thick riverine vegetation and dense thickets of ebony. In contrast, during the wet season when vegetation is in full leaf, rhino would sleep in relatively open areas underneath mopane trees (recorded six times). The rhino were not found sleeping in the same environment during the dry season. It appears that in the diverse riverine woodland, plant cover, whether for protection from heat, an escape habitat or both, is an important requirement for rhino habitat. Interestingly, in the early morning hours before rhino bedded down for the day they rested, without exception, for a few hours within an open area.

The ecological effects of roads on wildlife are broad and complex. Roads are favored by some animals while avoided by others (Spellerberg 1998; Trombulak and Frissel 2000). The density of roads and amount of traffic can also have an effect on animals (Trombulak and Frissel 2000; Bautista et al. 2004). Kernel density of roads appears to have a positive effect on the rhino PUD. Nevertheless, rhino were never seen on a road even when I was on foot or riding a bicycle. However, in the rainy season, when vehicles can not travel into the sanctuary, rhino were found twice within 100 m of a road. In Area 1, along the western side of the sanctuary, vehicle traffic is relatively high during the dry season with game drives from the nearby safari camp. Though spoor indicated that rhino utilized this area extensively in the dry season, it was only at night. Vehicle traffic is low during the wet season due to inaccessibility of roads in the sanctuary. The numerous roads in the sanctuary were primarily positioned for game viewing. It is likely that the positive effect on PUD is incidental, as roads traverse most of the sanctuary and cut through all habitat types.

The significance of watering holes for predicting PUD is difficult to evaluate because the water does not last into the dry season. Rhino utilize the watering holes for drinking before the water becomes muddy and are fond of wallowing in the mud, which offers protection from biting insects, like the tsetse fly (personal observation).

The importance of habitat structure for home range selection has been well documented (Ganey et al. 1999; Clevenger et al. 2002; Store and Jokimäki 2003; Wheatley et al. 2005). It was, therefore, surprising not to find a significant difference in shrub layer density and rhino browse availability in and out of the PUD, especially with Simpson's Diversity Index revealing higher plant species diversity within the PUD. In spite of this, the higher diversity may be explained by a higher river density and thus a higher variety of riparian vegetation (Robinson et al. 2002; Groom and Grubb 2002).

Knowing that browse availability is similar in Area 1 and 2 is important for management because forage availability is not a limiting factor for the population at the time of this study. This may suggest the population has not reached the carrying capacity of the sanctuary.

Habitat Suitability Model for Liwonde National Park

Although not as statistically robust as the sanctuary model, the predictive habitat model for the whole park was significant in explaining the dependent variable, the population utilization distribution. The lower explanatory power was the result of having fewer independent variables across the entire park to input in the model. But as in the sanctuary model, river density was a strong predictor of PUD. Distance to permanent water was also a strong predictive variable in the sanctuary model. It is likely that the addition of such a GIS layer would add robustness to the overall park model, but these data were unavailable in this study.

The predictive model for Liwonde National Park demonstrates that additional suitable rhino habitat also exists outside the sanctuary, and it provides an indication of where potential core areas would be, which is critical for security and anti-poaching purposes and thus ultimately for the survival of the rhino.

The application of utilization distribution in modeling provides an innovative method to pull together information on how black rhino occupy their range and use their habitat for daily activities. Collection of home range data during both the dry and wet season offered a better representation of the dispersal and dynamics of the rhino population in the landscape (data not shown). PUD enabled me to study a broad utilization of the resources. It has been found that often the spread rather than the central tendency around a point explains the most about how populations and species occur in and select their environments (Marzluff et al. 2004).

Models using predictor variables, derived from GIS layers, are mainly limited by the availability of data layers (Oborne et al. 2001). Often fine scaled habitat data are omitted from models due to unavailability or cost involved in collecting the data (Turner 2001; Gibson et al. 2004). Manel et al. (1999) suggested that model predictive success could be improved by including more detailed habitat data (for example, food availability), but these are often considered unobtainable at the landscape level (Austin 2002; Gibson et al. 2004). However, I successfully included rhino browse data in my model, featuring a detailed habitat variable. The interpolation function in ArcMap provides a novel technique in allowing models to capture fine scale data. It allows the combination of vegetation data and the browse index into a GIS layer and projects the variability at the landscape level.

The majority of ecological modeling studies agree that model evaluation should involve a comparison of two independent data sets (Manel et al. 1999; Gibson et al.

2002). Additionally, the capacity of the model to have tangible meaning for resource managers increases with the corroboration of the model with real data before employing it in a predictive role. In studies of endangered species, such independent data are often not readily available (Gibson 2004). For this study, I divided my original data set into two sets, Areas 1 and 2. Though the two sets are from the same population and may not be completely independent, they do represent two distinct core areas. From the larger core area in Area 1, the model was calibrated thus allowing the use of the smaller core area, Area 2, for validation.

Utilization distributions in modeling capture the frequency of use, but perhaps do not adequately describe why these resources are used. Marzluff et al. (2004) recommend using individual animals to analyze resource selection. Individual resource selection is not uniform and a better understanding of selection at a population level can be gained by recognizing the variation in individuality (Marzluff et al. 2004). For future research on my study population, an individual analysis should provide further insight into detailed rhino habitat selection.

Management Implications

The current study has several important management implications for black rhino:

1. For Liwonde National Park, the predictive models identified additional high-quality habitat both within and outside the existing sanctuary, which may help guide management decisions on further reintroduction and population management.

2. The abundance of browse species in the sanctuary and the consistent fecundity of the rhino indicate the sanctuary has not reached carrying capacity. This is further

supported by the rhino not moving into Area 3 even nine months after the fence was removed, indicating the rhino habitat requirements are met in the current home range.

3. Development of a predictive model that identifies the utilization distribution of black rhino could similarly be used for black rhino in other parts of their historic range in Africa, especially in the identification and development of future sanctuaries. In addition, this approach could likely be used successfully in the conservation of other imperiled animals, such as elephant.

4. The application of utilization distribution to locating and defining potential habitat for the rhino and other endangered species can prove to be a tool which expedites conservation measures. Currently, the establishment of sanctuaries and reintroduction of endangered wildlife often relies on expert knowledge in animal behavior and ecology of the wildlife biologists and managers who have gained insights through observation. To compliment expert knowledge, this technique enables managers and conservationists to evaluate potential wildlife habitat with focused field work.

Appendix A
Summary of shrub layer from seventy transects in the sanctuary

Summary of 70 Transects N = 189 Species

Transect	Mean	Stand.Dev.	Sum	Min.	Max	S	E	H	D`
1	0.512	1.672	96.818	0.000	14.000	34	0.887	3.129	0.9386
2	0.514	4.455	97.091	0.000	54.727	8	0.572	1.189	0.5989
3	0.499	5.866	94.364	0.000	80.273	8	0.302	0.628	0.2683
4	0.298	1.524	56.273	0.000	16.000	16	0.832	2.308	0.8568
5	0.412	2.068	77.909	0.000	19.000	16	0.815	2.261	0.8623
6	0.469	1.680	88.636	0.000	14.000	29	0.874	2.944	0.9271
7	0.356	1.728	67.273	0.000	13.091	13	0.868	2.226	0.8707
8	0.725	6.693	137.000	0.000	90.273	13	0.520	1.333	0.5460
9	0.395	2.137	74.636	0.000	20.000	16	0.784	2.174	0.8406
10	0.657	4.727	124.091	0.000	59.091	18	0.633	1.831	0.7219
11	0.495	3.212	93.545	0.000	39.000	17	0.699	1.982	0.7730
12	0.532	1.837	100.455	0.000	12.000	27	0.888	2.925	0.9319
13	0.306	1.623	57.909	0.000	18.000	16	0.814	2.256	0.8470
14	0.381	1.419	72.000	0.000	12.000	26	0.885	2.882	0.9217
15	0.454	3.583	85.727	0.000	48.091	19	0.620	1.826	0.6663
16	0.411	2.123	77.636	0.000	23.000	20	0.790	2.368	0.8541
17	0.407	3.229	77.000	0.000	42.000	11	0.652	1.562	0.6642
18	0.641	3.380	121.091	0.000	40.000	21	0.784	2.388	0.8482
19	0.517	4.260	97.727	0.000	51.727	8	0.611	1.271	0.6375
20	0.740	4.342	139.818	0.000	46.273	16	0.763	2.116	0.8134
21	0.551	4.550	104.091	0.000	52.818	9	0.598	1.315	0.6354
22	0.505	2.863	95.455	0.000	24.000	12	0.790	1.964	0.8256
23	0.497	2.356	93.909	0.000	20.273	19	0.807	2.377	0.8764
24	0.560	3.545	105.818	0.000	44.000	14	0.753	1.986	0.7837
25	0.548	2.874	103.636	0.000	26.818	20	0.786	2.354	0.8502
26	0.364	2.197	68.818	0.000	18.455	9	0.812	1.783	0.8032
27	0.619	3.068	117.000	0.000	33.000	23	0.782	2.452	0.8655
28	0.703	2.427	132.818	0.000	18.000	35	0.858	3.051	0.9319
29	0.468	4.217	88.364	0.000	55.000	7	0.613	1.193	0.5665
30	0.638	3.182	120.545	0.000	38.000	30	0.776	2.638	0.8637
31	0.601	4.388	113.545	0.000	54.636	14	0.647	1.707	0.7139
32	0.554	3.943	104.636	0.000	48.364	9	0.748	1.643	0.7277
33	0.480	3.708	90.636	0.000	49.636	18	0.635	1.834	0.6800
34	0.502	2.568	94.818	0.000	24.000	18	0.783	2.263	0.8568

Transect	Mean	Stand.Dev.	Sum	Min.	Max	S	E	H	D`
35	0.710	3.325	134.182	0.000	28.182	17	0.834	2.362	0.8792
36	0.979	5.076	185.091	0.000	42.364	25	0.729	2.345	0.8533
37	0.550	4.843	103.909	0.000	64.727	11	0.580	1.390	0.5863
38	0.873	4.737	165.000	0.000	47.000	22	0.739	2.284	0.8398
39	0.764	5.108	144.364	0.000	56.727	16	0.668	1.851	0.7594
40	0.722	3.821	136.455	0.000	32.000	21	0.745	2.267	0.8473
41	0.705	4.283	133.182	0.000	42.364	17	0.695	1.969	0.8003
42	0.867	3.459	163.909	0.000	34.182	32	0.826	2.862	0.9110
43	0.743	5.204	140.364	0.000	53.091	13	0.637	1.635	0.7363
44	0.628	4.545	118.636	0.000	58.182	15	0.668	1.808	0.7187
45	0.705	4.536	133.273	0.000	45.455	12	0.706	1.754	0.7770
46	0.843	4.704	159.364	0.000	43.636	18	0.741	2.143	0.8309
47	0.640	3.650	120.909	0.000	46.000	27	0.730	2.407	0.8234
48	1.005	7.311	190.000	0.000	79.364	12	0.613	1.524	0.7163
49	0.773	4.330	146.182	0.000	36.727	14	0.773	2.040	0.8298
50	1.132	8.560	214.000	0.000	109.000	18	0.600	1.735	0.6939
51	0.807	5.805	152.455	0.000	65.545	11	0.651	1.561	0.7221
52	0.626	3.548	118.364	0.000	40.000	28	0.708	2.359	0.8258
53	0.908	4.995	171.636	0.000	50.000	26	0.711	2.315	0.8355
54	0.760	4.515	143.727	0.000	48.273	23	0.697	2.186	0.8092
55	1.346	8.087	254.455	0.000	96.000	24	0.678	2.155	0.8048
56	1.009	4.144	190.636	0.000	37.000	25	0.830	2.670	0.9059
57	0.708	4.679	133.818	0.000	55.182	12	0.726	1.803	0.7649
58	0.804	6.021	151.909	0.000	73.455	11	0.648	1.555	0.6994
59	0.815	5.285	154.000	0.000	66.727	19	0.696	2.048	0.7733
60	0.873	5.159	164.909	0.000	60.000	16	0.729	2.020	0.8107
61	0.911	4.744	172.182	0.000	57.364	23	0.775	2.430	0.8520
62	1.359	5.878	256.818	0.000	61.000	38	0.781	2.841	0.8962
63	0.769	3.964	145.364	0.000	45.000	22	0.774	2.392	0.8549
64	1.551	9.104	293.091	0.000	80.000	18	0.680	1.965	0.8133
65	1.088	3.975	205.545	0.000	34.727	37	0.835	3.016	0.9244
66	1.119	5.927	211.545	0.000	57.364	29	0.712	2.397	0.8471
67	0.819	4.475	154.727	0.000	44.273	25	0.703	2.262	0.8375
68	0.974	4.358	184.091	0.000	40.000	25	0.799	2.571	0.8894
69	1.250	8.479	236.182	0.000	75.000	13	0.624	1.599	0.7524
70	0.806	5.776	152.364	0.000	64.545	14	0.641	1.693	0.7245
Averages:	0.704	4.198	132.968	0.000	45.571	18.8	0.724	2.091	0.7902

S = Richness = number of non-zero elements in row
E = Evenness = H / ln (Richness)
H = Diversity = - sum (Pi*ln(Pi)) = Shannon`s diversity index
D = Simpson`s diversity index for infinite population = 1 - sum (Pi*Pi)
where Pi = importance probability in element i (element i relativized by row total)

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