Spatial Ecology of African Buffalo and their Resources in a Savanna Ecosystem

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Abstract

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Bovine Tuberculosis *(Mycobacterium tuberculosis)* (BTB) was first identified in an African buffalo *(Syncerus caffer)* in Kruger National Park (KNP) in July 1990 on the southwestern boundary, and monitoring data have shown a continued slow spatial spread of herd prevalence, both along an East-West gradient and a North-South gradient. Management of this population of buffalo within the context of a chronic disease on a large landscape requires some fundamental understanding of the relationship between the buffalo and their landscape, through resource dependent relationships. With spatial data collected on live buffalo, we can inform management decisions and resource management strategies, and elucidate the potential patterns of epidemic spread through KNP.

In this dissertation, I focus on examining the patterns of spatial behavior and demography of African buffalo (*Syncerus caffer*), with particular attention to the resources in the landscape that affect these. Using more than ten years of data on buffalo herds in a Geographic Information System (GIS) of Klaserie Private Nature Reserve (KPNR), my collaborators and I examined ranging behavior and habitat selection at multiple temporal and geographic scales. We compared three methods of empirical home range estimation and found that buffalo travel further and range wider in the dry season than the wet and showed preference for *Acacia* shrubveld and *Combretum* dominated woodlands. We found that remotely sensed vegetation data, NDVI (Normalized Difference Vegetation Index) at 1km^2, averaged over the whole reserve were correlated with seasonal shifts in ranging behavior, but were not useful for predicting finer scale habitat preference. We found that buffalo selected areas within 1km of water sources and preferred riverine areas in both seasons, suggesting that buffalo preferentially select for areas near water, but may range further in the dry season for higher quality food.

The presence and location of water is a major driver in the dynamics of managed savanna landscapes. Studies of the role of water in Kruger National Park have led to a reversal of the former water-for-game programme to a systematic removal of water points, due to the erosion and over utilization effects of their presence. As the private reserves on the western edge of KNP having been incorporated into the KNP management area, the question of how to manage water points in a private reserve arose. This prompted my collaborators and me to develop a model of waterhole management that was suitable for individual private property management within a reserve. Using the Klaserie Private Nature Reserve (KPNR) as a case study, we compared a buffer framework, describing distances to water, a nearest neighbour framework, and a spatial location-allocation framework (SLAF) created in a geographic information system (GIS). These three frameworks were combined into one GIS to demonstrate site-specific information on water source distribution in addition to system-wide descriptions. The visually accessible quality of a GIS allows qualitative input from managers and property owners to achieve quantifiable management goals.

We then examined annual variation in the timing of conception and parturition in the African buffalo (*Syncerus caffer*) and their synchrony with resource cues using six years of monthly birth, rainfall, inferred forage protein content, and vegetation greenness data, NDVI. The monthly birth distribution has its strongest correlation with the inferred forage protein, NDVI, and rainfall levels respectively 11, 12, and 13 months in the past. Since the gestation period of buffalo has been estimated to be around 11 months, this suggests that improved protein levels, occurring approximately a month after the first green flush of the wet season, may be a trigger for conception. Alternatively, conception has evolved to be synchronous with correlated environmental cues that ensure females enter their period of peak condition around the time of conception.

We then examined more closely the potential use of NDVI data as a surrogate for habitat quality for buffalo, using fecal indicators. Specifically, we made use of several spatially explicit datasets collected to measure fecal indicators of condition in buffalo in KNP, and compared these with remotely sensed data at different scales, both spatially and temporally. We demonstrated that both fecal nitrogen (N_f) and fecal phosphorous (P_f) measures are affected by large-scale landscape differences. A division of data collected on basalt-derived (East) and granite-derived (West) soils showed that although granite is predicted to be less nutrient-rich than basalt, we see higher levels of N_f on both soil types in the North than the South. We also found seasonal effect on the levels of N_f and P_f on different landscapes. This suggests that buffalo face trade-offs in habitat selection that may change with season with respect to these limiting nutrients. We found a significant relationship between N_f and a monthly average NDVI of the prior month, and a significant relationship between NDVI and herd condition scores. We found no significant relationship between P_f and NDVI, or between P_f and herd condition.

These results suggest that NDVI data can provide a surrogate measure of habitat quality for buffalo with regards to crude protein, but may not be a good measure for the limiting mineral phosphorus. We discuss the utility of establishing measures of dietary quality that can be correlated to remotely sensed data in research and management of savanna herbivores.

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THE FOCAL HERD, KLASERIE PRIVATE NATURE RESERVE

Introduction

Bovine tuberculosis (*Mycobacterium bovis*) (BTB) was first identified in African buffalo (*Syncerus caffer)* [Sparman 1779] in Kruger National Park (KNP) in July 1990 along the southwestern boundary fence (Rodwell *et al.*, 2001). Although impossible to verify, the origin of BTB in KNP buffalo could be cattle farms along the Crocodile River (southern boundary), where there were significant outbreaks of BTB in the 1960s, and again in the early to mid 1980s (Bengis *et al.*, 1996). In 1991-1992 buffalo obtained from the annual culling program (DeVos, 1983) were examined to yield the first prevalence estimates for the north (0%), central (4.4%± 0.6%) and south (27.1% ± 1.4%) regions of KNP (Rodwell *et al.*, 2001). Skin tests of tribal cattle along the southwestern border showed negative results, despite the southwest having the highest prevalence within the park. Thus these bordering cattle were not the source of the current epidemic (Bengis *et al.*, 1996), and its origin remains unclear. Due to a severe drought, park-wide annual culling was discontinued after 1992, so prevalence estimates were unavailable until a carefully designed smaller cull in 1998 was undertaken specifically to evaluate BTB prevalence. Testing demonstrated a significant increase in prevalence in the south and central zones, but not in the north (Rodwell *et al.*, 2001), suggesting a slow spatial spread of BTB prevalence, along both an East-West gradient and a North-South gradient. To continue to monitor the overall spread of this pathogen would require periodic large-scale culling, which is no longer demographically, logistically, nor ethically plausible. However, with spatial data collected on live buffalo and spatial disease models coupled with extant demographic data, we can elucidate the potential patterns of epidemic spread through KNP.

African buffalo are large savanna herbivores in the family Bovidae, subfamily (or tribe) Bovini, which includes all cattle, in which they are the only representative native African genus (Estes, 1993). There are two extreme forms (savannah and forest types), which are commonly split into two or three subspecies or types: the large black savannah or Cape buffalo, *Syncerus caffer caffer*, the small reddish forest buffalo, *S. c. nanus*, and an intermediate form from West Africa, the Sudan buffalo *S. c. brachyceros* (Buchholtz, 1990; Kingdon, 1997). The buffalo that occur in KNP are Cape buffalo, and we refer to these as *Syncerus caffer*. Historically, buffalo occurred throughout the Northern and Southern savannas of Africa, from sea level to the limits of forest on mountains, in arid regions with sufficient forage and access to permanent water (Estes, 1993). They have been described as "supreme bulk grazers" (Owen-Smith & Cumming, 1993), as their ruminant digestion accommodates a massive body by optimizing maximum consumption of herbage, even of lower quality (Estes, 1993). They occur in herds of a few hundred to several thousand individuals, depending on the study area (Prins, 1996; Sinclair, 1977) and exhibit seasonal social ecology in which they aggregate into large mixed herds during the breeding season, splitting into mixed herds and bachelor groups for the rest of the year. In addition to a seasonal system of group organization, exchange of individuals occurs between groups throughout the year, with both males and females engaging in local and long-distance dispersal (Halley *et al.*, 2002). The membership of a 'herd' can vary considerably on multiple temporal and spatial scales, as shown in Kruger National Park, leading to a fission-fusion type of herd structure (Cross, Lloyd-Smith & Getz, 2005); although more rigid herd structure has been reported in the more temperate Hluhluwe-Imfolozi Park (Jolles, 2004).

In this dissertation, I focus on examining the patterns of spatial behavior and demography of African buffalo, with particular attention to the resources in the landscape that affect these. In Chapter 1, a collaborative paper with Dr. Christiane U. Knechtel and Professor Wayne M. Getz, published in the *Journal of Wildlife Management*, more than ten years of data on buffalo herds were used in a Geographic Information System (GIS) of Klaserie Private Nature Reserve (KPNR) to examine ranging behavior and habitat selection at multiple temporal and geographic scales. We compared three methods of empirical home range estimation: Minimum Convex Polygons (MCP), a fixed kernel method and a new local Nearest Neighbor Convex Hull construction method (LoCoH). The LoCoH method best described ranges, as it accommodated user knowledge of known physical barriers, such as fences, whereas the MCP and kernel methods overestimated ranges. Short-term ranges of the focal herd (FH), over 9 years, reveal that buffalo travel further and range wider in the dry season than the wet. Habitat selection analyses on broad vegetation categories showed preference for *Acacia* shrubveld and *Combretum* dominated woodlands. We found that buffalo selected areas within 1km of water sources and an isopleth analysis using the new LoCoH method (Getz & Wilmers, 2004) showed preference for riverine areas in both seasons. This suggests that buffalo preferentially select for areas near water, but may range further in the dry season for higher quality food.

Chapter 1 reveals that, consistent with prior studies of buffalo ranging and habitat selection (Hunter, 1996; Prins, 1996; Sinclair, 1977), the presence and location of an important resource—water—is a major driver of habitat selection and herd location. In the managed savanna landscapes we are studying, (Kruger National Park and Klaserie

Private Nature Reserve), water sources are present as both perennial river courses and managed, seasonal point sources. As the private reserves on the western edge of KNP having been incorporated into the KNP management area, the question of how to manage water points in a private reserve arose. Erosion and trampling around the water holes in KPNR had been noted (C. Rowles, *pers. comm.*) and this prompted us to develop a model of waterhole management that was suitable for individual private property management within a reserve, presented in Chapter 2 and published in the *South African Journal of Wildlife Research* (Ryan & Getz, 2005). Extant metrics used to describe the spatial distribution of water sources on the landscape often fall short of providing source-specific information making them hard to apply in small-scale management settings. Using the Klaserie Private Nature Reserve (KPNR) as a case study, we compare a buffer framework (i.e. distances to water), a nearest neighbour framework, and a spatial location-allocation framework (SLAF) created in a geographic information system (GIS). These three frameworks can be combined into one GIS to demonstrate site-specific information on water source distribution in addition to system-wide descriptions. The visually accessible quality of a GIS allows qualitative input from managers and property owners to achieve quantifiable management goals. The duality of database and visual representation provides a useful tool to assess the role of individual water sources and can easily be updated to reflect changes in their distribution.

In Chapter 3, another collaborative effort with Drs. C. U. Knechtel and W. M. Getz, we examine annual variation in the timing of conception and parturition in the African buffalo and its synchrony with resource cues using six years of monthly birth, rainfall, inferred forage protein content, and vegetation greenness data. The monthly birth distribution has its strongest correlation with the inferred forage protein, NDVI, and rainfall levels respectively 11, 12, and 13 months in the past. Since the gestation period of buffalo has been estimated to be around 11 months, this suggests that improved protein levels, occurring approximately a month after the first green flush of the wet season is either a trigger for conception or conception has evolved to be synchronous with correlated environmental cues that ensure females enter their period of peak condition around the time of conception. With a gestation period of approximately 340 days, parturition also occurs to take advantage of the period when forage has its highest protein content. Some inter-annual variation in the birth distribution suggests a degree of plasticity in time-of-conception and variation in the number of calves born each year suggest further synchrony at a time scale longer than a single year.

In Chapter 4, we examine more closely the potential use of NDVI data as a surrogate for habitat quality for buffalo. In a paper with Dr. P. C. Cross, J. Bowers and C. Hay, we use several spatially explicit datasets to measure fecal indicators of condition in buffalo in KNP, and we compare these with remotely sensed data at different spatial and temporal scales. We demonstrate that both fecal nitrogen (N_f) and fecal phosphorous (P_f) measures are affected by large-scale effects in the landscape, including soil type and season. This suggests that buffalo face trade-offs in habitat selection with respect to these limiting nutrients that may change with season. Our results also suggest that NDVI can provide a surrogate measure of habitat quality for buffalo with regards to crude protein, but may not be a good measure for the limiting mineral phosphorus. We discuss the utility of establishing measures of dietary quality that can be correlated to remotely sensed data in research and management of savanna herbivores.

Chapter 1: Seasonal and interannual variation in home range and habitat selection of African buffalo: a long-term study in the Klaserie Private Nature Reserve, South Africa

Abstract:

More than ten years of data on buffalo herds were used in a Geographic Information System (GIS) of Klaserie Private Nature Reserve (KPNR) to examine ranging behavior and habitat selection at multiple temporal and geographic scales. We compared three methods of empirical home range estimation: Minimum Convex Polygons (MCP), a fixed kernel method and a new local Nearest Neighbor Convex Hull construction method (LoCoH). For three herds over 5 years (1995-2000), the Southern Herd (SH) had the largest range, the focal study herd (FH) had the intermediate range and the Northern Herd (NH) had the smallest range. The LoCoH method best described ranges, as it accommodated user knowledge of known physical barriers, such as fences, whereas the MCP and kernel methods overestimated ranges. Short-term ranges of the FH over 9 years reveal that buffalo travel further and range wider in the dry season than the wet. Habitat selection analyses on broad vegetation categories showed preference for *Acacia* shrubveld and *Combretum* dominated woodlands. We found no significant selection of habitat at a fine geographic and temporal interval using remotely sensed vegetation data (NDVI – Normalized Difference Vegetation Index), but the index was correlated to ranging behavior at a larger geographic scale. We found that buffalo selected areas within 1km of water sources and an isopleth analysis using the new LoCoH method showed preference for riverine areas in both seasons. This suggests that buffalo preferentially select for areas near water, but may range further in the dry season for higher quality food.

INTRODUCTION

Recent studies of epidemic diseases such as Bovine Tuberculosis (Bengis, 1999; Bengis *et al.*, 1996), persistent endemic Brucellosis and Rift Valley Fever and outbreaks of diseases such as Anthrax (De Vos & Bryden, 1996), and foot and mouth disease (FMD) (Bastos *et al.*, 2000; Greyling *et al.*, 2002; Vosloo *et al.*, 1996; Vosloo *et al.*, 2001) in buffalo both in and around the Kruger Greater Management Area in South Africa have drawn attention to the need for a greater understanding of the ranging and habitat selection of these buffalo. Not only is this information vital for management of buffalo themselves, but also to address their role as a reservoir population for diseases that can spill over into other wildlife species (Bastos *et al.*, 2000) and domestic livestock (Bany & Freier, 2000).

African Buffalo *(Syncerus caffer)* are gregarious large herbivores that occur in herds of a few hundred to several thousand individuals (Prins, 1996; Sinclair, 1977). They exhibit seasonal social ecology in which they aggregate into large mixed herds during the breeding season, splitting into mixed herds and bachelor groups for the rest of the year. In addition to a seasonal system of group organization, exchange of individuals occurs between groups throughout the year, with both males and females engaging in local and long-distance dispersal (Halley *et al.*, 2002). The membership of a 'herd' can vary considerably on multiple temporal and spatial scales, as shown in Kruger National Park, leading to a fission-fusion type of herd structure (Cross *et al.*, 2005); although more rigid herd structure has been reported in the more temperate Hluhluwe-Imfolozi Park (Jolles, 2004). An ongoing capture-recapture study in the Klaserie Private Nature Reserve (KPNR), in conjunction with this analysis, shows that a core group of females has been present in the focal herd of this study for at least 8 consecutive years, with others present for at least 6 and 5 of those years. These findings are consistent with prior hypotheses of a female core at the base of herd structure in buffalo (Prins, 1996; Sinclair, 1977).

The Klaserie Private Nature Reserve (KPNR) (Figure 1) contains the range of three primary herds of buffalo. While there appear to be three foci of buffalo grouping, spatially explicit annual census data, collected outside of the breeding season from 1998-2001 (*unpubl.*) records between 3 and 5 identifiable herds and multiple small bachelor groups or single bulls at any point in time. Total counts from buffalo census data for the KPNR since 1992 show that this population is increasing (Figure 2). This is likely a combination of demography and additional growth, in the form of migration and supplementation. Stocking rates and trophy quotas for this private reserve are not available to this study, but we suspect this plays only a minor role in population trends. In 1992 a severe drought, in combination with an Anthrax outbreak (De Vos *et al.*, 1996) caused approximately a 60% decline in the buffalo population of neighboring Kruger National Park (KNP) (Mills, Biggs & Whyte, 1995). This decline appears in the KPNR also; the count dropped by 53% between 1992 and 1993. The subsequent population growth may reflect a recovery period in the dataset; the geometric mean growth over the period 1992-2000 is 1.04, which indicates an annual growth rate of 4%. The fluctuating per annum changes in population level may be due in part to migration between KPNR and KNP. It is important to note these background demographic and population trends when analyzing the range of buffalo herds, as we must be aware of the potential for increased herd size to affect the range estimate.

Locations of three primary buffalo herds in the Klaserie Private Nature Reserve were sighted in the field and recorded on hand-drawn maps over a period of five years (1995-2000). These are a “Northern Herd” (NH), a “Southern Herd” (SH), and a central Focal Herd” (FH), that is the focus of a long-term behavioral study. We first describe the ranges used by these three herds, exploring three methods of home range description. Getz and Wilmers (2004) present an explicit comparison of home range methods for a simulated dataset, including a full discussion of prior methods. Our study represents the first use of their novel method, Nearest Neighbor Convex Hull (*k*-NNCH, but referred to hereafter as LoCoH), using empirical data.

The first method we use is the Minimum Convex Polygon (MCP), which is widely used in analyses of home range (Getz *et al.*, 2004). This method provides a maximum estimate of the area of home range, by joining the outermost points of a distribution. Whereas this can be useful in the context of setting aside the maximum habitat area for a specific species, it provides an unclear picture of what geographic locations are actually used within the area, and can inflate the home range estimate dramatically with the presence of outliers.

The second method, fixed kernel home range estimator, using Least Squares Cross-validation (LCSV) to obtain the smoothing parameter, H (Seaman & Powell, 1996), gives a clearer picture of internal areas of high use (cores) and generates clearer definitions of the edges of the range. However, as Getz and Wilmers (2004) show, it has the alarming property of increasing the area estimate with the addition of data points. From the perspective of a wildlife manager, this is likely to generate spurious answers due to different frequencies of data collection between study periods, thereby masking actual trends with methodological fallacy. Moreover, as technology advances permit the use of high-frequency data, such as GPS locations as frequently as 1/hour, the apparent increase in area will become a considerable weakness in the method. This becomes problematic when trying to draw comparisons between studies, or across years.

The LoCoH (*k*-NNCH) method presented by Getz and Wilmers (2004) shows its superiority over the prior methods by being mathematically transparent, it converges to an estimate with the addition of data points, it is very useful for uncovering lacunae – areas of avoidance - and for examining high use areas using isopleth analyses.

We use this novel method to conduct a more detailed analysis of buffalo range behavior for the focal herd. Using more frequent data collected over a period of nine years (1993-2001), we look at interannual and seasonal range comparisons and conduct a temporally specific habitat selection study. We chose to use both a habitat description based on broad scale habitats in the reserve, derived from aerial photography, and a remotely sensed measure of vegetation greenness, which we take as a general signal of quality. A concurrent study in KNP reveals that this vegetation index can be used to predict the dietary quality of buffalo forage at a large landscape scale (Ryan et al., unpubl.). This provides a generalized metric for habitat quality, incorporating the roles of grass and browse species into the buffalos' dietary requirements.

The movement patterns of buffalo herds are hypothesized to shift with season as buffalo respond to available habitat. Prior studies posit conflicting theories as to the direction of this shift in response to quality of habitat, pivoting around the question of energetic requirements of forage and availability of water (Funston, 1992; Funston, Skinner & Dott, 1994; Sinclair, 1977). Previous studies have also shown that buffalo are a riverine species, preferring areas close to rivers or major lakes (Prins, 1996; Sinclair, 1977); however, these studies were conducted in larger systems with fewer sources of perennial water. In a small reserve, movements of the herd are likely restricted by fence lines in addition to expected inter- and intra-herd interactions involved in optimization of habitat choice.

STUDY AREA

The Klaserie Private Nature Reserve is located in the Limpopo Province of South Africa, bordering Kruger National Park on its western boundary (24º3-22' S, 31º2-19' E; 303-535m a.s.l.; 57,800ha) (Figure 1). The reserve comprises multiple private properties, formerly utilized as farms; it was physically separated from KNP in 1961 with the erection of fences along the western boundary to prevent spread of foot and mouth disease into domestic cattle (Witkowski, 1983). Prior to this it had provided dry season feeding and breeding grounds for many herbivores from KNP (Witkowski, 1983). KPNR now represents part of the Greater Kruger National Park Management Area, although it remains separated by fences from neighboring private reserves. Since 1990, there has been a gradual removal the western boundary fence of Kruger National Park where it borders the private reserves. The removal of the fence separating KPNR and KNP occurred around 1992, allowing immigration and emigration between the park and reserve. The current suite of herbivores in KPNR is similar to the suite in the central part of KNP.

The main geological substrate is granitic gneiss, part of the extensive granalitic system underlying most of the country (Parker & Witkowski, 1999). The seasonality of

Klaserie follows a subtropical savanna pattern: both temperatures and rainfall follow a unimodal distribution annually (Figure 3); mean annual rainfall from 1992-2000 was 486mm. We define two main seasons based on rainfall and temperature records of the reserve for the decade in which the data was collected. These seasons are a hot wet "summer" season from October to March and a cool dry "winter" season from April to September.

METHODS

Data Acquisition

Buffalo herd locations were recorded in the KPNR over a period of more than 10 years as part of a long-term behavioral study by one of us (CK) of the central, focal herd (FH). Tracking of the focal herd was conducted both by direct observation from a vehicle or by following spoor, while locations of the other herds were recorded opportunistically, often with the help of wardens and rangers in the reserve. The reserve is accessible through a network of property access routes and firebreaks, meaning that all areas of the reserve were equally accessible to the observers. Incomplete data is inevitable in a study spanning a decade and systematic re-sampling of the data is described in the methods.

Simultaneously recorded locations of three main herds in the reserve were available to this study at a frequency of approximately 1 per month over the course of 5 years (1995-2000). Locations were recorded onto paper maps, photocopied from surveyor's property maps of the reserve (*origin unknown*). These were scanned using a desktop scanner (HP ScanJet XPA), and the image files were then orthorectified and georeferenced using the Image Analysis extension for ArcView 3.x© (Figure 4). The locations were then rendered in ArcView© as point files, with attributes such as the herd's name and the date recorded into the attribute table. Locations of a focal herd were recorded onto enlarged sections of the surveyor's map, from 1993-2001, with an average of 247 (range: 180-290) days per year represented. These data are far more detailed, including tracking routes for multiple continuous days per map sheet. These data were processed in the same way as described above for the three herds.

For these analyses a single point represents a herd's location, approximately the centroid. These herds are quite small; the number of individuals in these herds varied between ~100-400 individuals, depending on season and occupies a space of less than 500m^2 (C. Knechtel, *personal observation*).

Range Calculations

Three Herds

Home ranges were calculated using a subset of the data from the three herds. As single days involved multiple tracking points, a randomly selected point from each day was chosen to ensure that each point represents an individual date event. In addition, to ensure that the comparisons are between separate primary groupings, only maps on which more than one group was recorded at the same time were used. This yielded datasets of 148 points (FH), 63 points (SH) and 48 points (NH). These data were collected opportunistically and represent observations from both seasons throughout the time span to obviate bias, but they are clearly too sparse to draw significant conclusions about annual trends. It is important to note that the northern (NH) and focal herds (FH) could have moved between KPNR and KNP as their ranges approach the fence line which was removed in 1993, and points external to KPNR may not have been recorded. In addition the NH and SH occasionally moved into neighboring reserves (C. Knechtel, *personal observation*), which may cause us to underestimate the total ranges of these herds.

For the purpose of comparison, we used three methods to calculate home ranges. The third of these (LoCoH) produced the most plausible home ranges, both in terms of size and locational coverage – avoidance of physical boundaries, defined edges on clear routes within the range - and hence was used for most of our analyses (see Getz and Wilmers, 2004). The first method used was the minimum convex polygon (MCP) method, calculated in Animal Movement Extension© (Hoodge & Eichenlaub, 1997) for ArcView©. The second method used was the fixed kernel home range estimator, using Least Squares Cross-validation (LCSV) (see Seaman and Powell, 1996) to obtain the smoothing parameter, H. This was also implemented in Animal Movement Extension© (Hoodge *et al.*, 1997), with 5% probability contours generated on a 500m grid.

The third method, for which the analysis presented here is its first application, is based on a local nearest-neighbor convex-hull construction (LoCoH) (see Getz and Wilmers, 2004, for details) that depends on a user-selected nearest number of neighbors parameter, *k*, The method then takes the union of the local polygon hulls associated with each point and its *k* nearest neighbors. Isopleths are constructed by merging these local polygons, starting with the smallest and ending with the largest. LoCoH is useful for identifying unused areas within the range, and unlike kernel methods, converges to an estimation of area with the addition of data (Getz *et al.*, 2004). This method was executed as an extension in ArcView©, which differs slightly from the method described in Getz and Wilmers (2004), such that *k*-neighbors, not *k*-1 neighbors, are used in hull construction. To examine the potential areas employed by buffalo, we ran this method for *k* values from 2 to 40 to find the plateau which gives an “stable” area value across a range of *k* values to represent the area of the home range (Figure 5). If several plateaus occur, the choice of *k* value represents a trade-off between errors of type I and type II, in that a low value of *k* will fail to represent areas that buffalo might occupy between the observation points, and a high *k* will overestimate the area of their range.

Focal Herd

To calculate annual home ranges, a randomly sampled location from each day that the herd was seen within each year from 1993-2001 was selected. For each year, the LoCoH method was run for *k*=1-40 and the optimal *k* was chosen (Table 1).

To make seasonal comparisons, these data were then re-sampled by available month to create 10 consecutive day ranges within separate months. Each sample represented 10 consecutive days internally to a calendar month and was constrained to being at least 10 days from the previous sample. This yielded 85 samples across the entire dataset. This set of 10-day ranges was reduced to 84, as closer examination of original field notes revealed one set to be the range of a small splinter group of the primary herd. These 84 10-day samples were used to calculate independent 10-day ranges, using the LoCoH method for *k*=5 neighbors. This value yielded a robust but conservative construction for each set of 10 points in terms of the Minimum Spurious Hole Covering method (MSHC), as suggested by Getz and Wilmers (2004). These 10 day samples were also used to calculate 10-day trip lengths using the Create Polyline script in Animal Movement Extension© (Hoodge *et al.*, 1997) in ArcView©, and tabulated and assigned to the wet season (October – March) and dry season (April – September) to explore seasonal differences in movement.

Broad Scale Habitat Selection

Three Herds

A habitat map created by N. Zambatis in 1984 describes 8 broad scale divisions of savanna woodland types (Figure 6). The original map delineated major habitat divisions from aerial photographs, which were then subjectively ground-truthed by qualitative assessment of dominant vegetation types (N. Zambatis, pers. comm.). This map was scanned, orthorectified and georeferenced from paper format and rendered as polygons in an ArcView © shapefile. Although this is not a current map, it delineates major divisions of savanna and woodland types within the reserve; small boundary alterations between types may have occurred during brush management, but these would be unlikely to affect these analyses.

Habitat selection was tested using the Neu Method (Neu, Byers & Peek, 1974); a χ^2 Goodness of Fit, applying Bonferroni Z statistics to establish confidence intervals for indications of preference of particular habitat types (Alldredge & Ratti, 1992; Neu *et al.*, 1974); the habitat is described in eight classes. The herd locations were tested for selection across all months, and separate analyses for locations in the dry season (April-September) and wet season (October–March)

The selection for water availability was set up as an analysis of distance of each observation from the nearest available water source. Water points and river courses were buffered with 1km bands in ArcView© yielding 5 distance classes, using the

Geoprocessing Extension (Figure 7). For the wet season, it was assumed that the two major rivers, the Olifants and the Klaserie, were flowing along their entire courses through the reserve, although this may be a generous assumption in particularly dry years; the Nsiri's partial course is described by the series of pans and dams along its course. In the dry season, only the perennial parts of the Olifants, Nsiri and Klaserie rivers were used in the analysis. A dry season buffer map was created such that only water points in which water is present in the dry season and perennial portions of river courses were used. Testing for water availability employed the Neu Method (Neu *et al.*, 1974) analysis as described above, with distance-to-water as a categorical choice.

Focal Herd

The analyses for habitat selection based on broad habitat types and for water availability for the focal herd was conducted similarly to the above methodology for the three herds, but restricted to the total range area of the focal herd.

Activity Center Identification

Using the LoCoH method to construct hulls at a k=15 neighbor resolution, isopleths were constructed as described in Getz and Wilmers (2004) to identify areas of high observation density within the overall dataset for the focal herd. The isopleths corresponding to deciles of data density are visually demonstrated for all wet season data and all dry season data (Figure 8).

Seasonal Herd Size Analysis

Spot counts of the focal herd were conducted opportunistically throughout the study period; a total of 172 counts (96 in the wet season, 76 in the dry) from 1993-2001, unevenly spaced across months and years were tested for seasonal differences in herd size. To accommodate the effect of uneven data, residuals from a regression against both year and month were used to test seasonal effect in a *t*-test. Regression analyses on these data were also used to test whether annual herd size increased with total census population size and whether either of these factors were correlated to annual range size.

Habitat Selection Using Remotely Sensed Vegetation Data

To examine habitat selection on a more local scale, both temporally and spatially, the focal herd data as described above was used in conjunction with remotely sensed vegetation data. We made the assumption that the focal herd was excluded from access to resources across the entire reserve due to behavioral mechanisms of exclusion by the other two main herds present. This is a more conservative measure of selection than including the entire reserve, obviating bias due to potential exclusion from certain areas. Thus we took the entire range generated by merging all 10-day ranges across the 9-year sample to be the potential area (292 km^2) in which the herd could make habitat selection movements, based on resource perception alone. This was converted to raster and used to clip the vegetation layer to provide the series of cells on which the choice could operate.

Post-processed NDVI (Normalized Differential Vegetation Index) data from NOAA's (National Oceanographic and Atmospheric Association) AVHRR (Advanced Very High Resolution Radiometer) sensor aboard weather satellites was made available to this project through the Agricultural Research Council, Institute for Soil, Climate and Water (ARC-ISCW) for the years 1992-1993, 1995-2001, at a resolution of 1km^2. A full description of the processing involved in this data prior to acquisition by this project can be found in Wessels et al.(2004). We use this data as a relative scale measure of the change in vegetation quality in the reserve, not as absolute values. This data was manipulated in ARC/INFO 8 (Environmental Systems Research Institute, 2000a) and ArcGIS 8.3 (Environmental Systems Research Institute, 2000b), using ArcMap for visual assessment of available images. For viable images, 0-3 images per month were used to create monthly average grids of data clipped to the KPNR.

Due to the availability of viable NDVI images for this analysis, the dataset was further reduced to 71 comparisons; 10 months in 1994 could not be used and neither could several additional months. The NDVI layers for each month available were clipped to the overall range of the focal herd for the entire study period, and for each ‘trip’ the 10-day locations were assigned to pixels, using a grid-stacking command in DIVA-GIS (Hijmans *et al.*, 2004). A logistic regression was used to test whether pixels of higher values were chosen over those not chosen. To examine larger scale quality responses, a simple regression of the 10-day range size and trip-length against a reserve-wide mean NDVI value for each month was also conducted.

Statistical Tests

The χ^2 statistics, with Bonferroni correction criteria were calculated in Excel©; all other statistical tests were performed in S-PLUS 6.0 Professional Release 2.0 (Insightful Corp., ©1998-2001) or JMP 4.04 Academic Version (SAS Institute ©1989-2001).

RESULTS

Range Calculations

Three herds

The size of the home ranges as calculated using Minimum Convex Polygons (MCPs), 95% Fixed Kernel and LoCoH (k=2-40) methods are shown for the three herds in Figure 5. The Northern Herd (NH) had an MCP of 102.76 km^2, a 95% Fixed Kernel estimate of 196.91 km^2 and a LoCoH of 83.17 km^2 at k=18. The Focal Herd (FH) had an MCP of 245.13 km^2, a 95% Fixed Kernel estimate of 282.04 km^2 and a LoCoH of 226.19 km^2 at k=16. The Southern Herd (SH) had an MCP of 266.05 km^2, a 95% Fixed Kernel estimate of 341.50 km^2 and a LoCoH of 251.41 km^2 at k=17.

Focal Herd

The annual home ranges of the focal herd are given in Table 1. The average annual home range was 240.13 ± 16.77 km^2 (mean ± S.E.). To test whether the number of points used in a year was introducing bias into the estimates, the estimated area was regressed upon the number of points used. This revealed that there was a trend of increasing area with number of points, but the trend was not significant (R^2=0.29, p=0.13). Note the year 1997, in which there are a higher than average number of points, an average k-value derived and a smaller than average home range calculated. In addition, a regression of the k yielded by the LoCoH method on the number of points used showed no trend (R^2=0.04, p=0.59), indicating that the method itself is also not subject to point number bias.

An examination of 10-day ranges of the focal herd reveal that the buffalo travel significantly further (27.81 ± 0.98 km dry; 21.91 ± 1.03 km wet; (mean ± S.E.); Welch modified one-way ANOVA: $t = 4.21$, df = 75.57, $p<0.0001$) and range wider (33.80 ± 2.30 km^2 dry; 17.61 ± 2.41 km^2 wet; (mean ± S.E.); Welch modified one-way ANOVA: $t = 5.00$, df = 65.80, $p<0.0001$) in the dry season.

Habitat Selection

Three Herds

The χ^2 analysis for habitat selection was significant for all herds in the study ($\chi^2= 107.99$, df=7, $n=283$, $p<<0.001$), and we rejected the null hypothesis that buffalo herds were using habitat in proportion to its area. Bonferroni corrected confidence intervals (95% CI) showed selection for habitat types 2 and 5 and selection against type 3. In the wet season, χ^2 analysis allowed us to reject the null hypothesis ($\chi^2=70.93$, df=7, $n=100$, $p<0.01$) and show avoidance of habitat type 3; this was also shown in the dry season ($\chi^2=52.85$, df=7, $n=183$, $p<0.01$) (Table 2). As there were no observations of any herds in habitat type 8, we can assume there was avoidance, although we cannot construct confidence intervals to demonstrate it. The χ^2 analysis for selection of distance-to-water in the wet season was significant ($\chi^2=8.51$ df=1, $n=100$, $p<0.01$). Bonferroni corrected confidence intervals demonstrated a preference for areas 0-1km from water and selection against areas greater than 1km from water. In the dry season, χ^2 analysis did not allow us to reject the null hypothesis ($\chi^2=5.74$, df=3, $0.15>p>0.10$) (Table 3).

Focal Herd

The χ^2 analysis for broad scale habitat selection was significant across all years ($\chi^2=278.44$, df=7, $n=840$, $p<0.001$) and for each season (Wet: $\chi^2=103.69$, df=7, $n=400$, $p<0.001$; Dry $\chi^2=205.84$, df=7, $n=440$, $p<0.001$) (Table 2). The focal herd showed an overall preference for habitat type 2 and selection against types 1 and 3. In the dry season, habitat types 2 and 4 were preferred and there was selection against types 1,3 and 7; in the wet season, preference for type 2 and 4 selection against types 1,3, 5 and 7 were indicated. The focal herd showed significant distance-to-water selection in both seasons (Wet: $\chi^2=27.38$, df=2, $n=400$, $p<0.0001$; Dry $\chi^2=12.74$, df=3, $n=440$, $p<0.005$). Bonferroni corrected confidence intervals (95% CI) revealed that in both the wet season and the dry season, buffalo were selecting positively for areas within 1km of water and were selecting against areas 1-2 km from water sources in the wet season (Table 3).

Overall, buffalo did not select significantly different values of NDVI than available in the environment; in 15 out of 71 logistic regression analyses, the model χ^2 was significant at $p<0.05$. However, there was no significant seasonal pattern to this; moreover, the significance was generated by lower value choice as well as higher value choice. Buffalo did not respond to prior month's NDVI value (13 of 71 significant results), nor to the relative change in NDVI value from the prior month.

A regression of the 10-day distance, d, showed a significant reduction in length with increasing mean NDVI value, v, ($R^2=0.15$, $p=0.0004$); but no significant reduction in range area estimate, a, ($R^2=0.03$, $p=0.09$). The regression equations are: $d=-0.076v+35.0$ and

$a=-0.084v+35.0$).

Activity Center Identification

The isopleth method for examining the center of activity for the focal herd demonstrated that in both seasons, the densest polygons occurred near the Klaserie River, the hypothesized center of activity for this herd. In the wet season, the activity appears to also center around two additional areas, including the Nsiri River whereas in the dry season it is more focused on the Klaserie River (Figure 8).

Seasonal variation in herd size

The effects of both year and month in the spot count data were significant ($p<0.001$); a *t*-test on the residuals revealed that the dry season herd size (183.56 ± 4.17, (mean ± S.E.)) was nonetheless significantly smaller than the wet season herd size (224.66 ± 4.17, (mean ± S.E.)) (Welch modified *t*-test: $t=2.14$, df=164.10 $p=0.034$). In addition, the average herd size, h, over a year was significantly correlated to the total census population size, n, in the reserve ($R^2=0.71$, $p=0.008$); the regression equation is $h=0.40n-68.60$. However, annual range was not significantly correlated with either average herd size or total census population size.

DISCUSSION

The analysis of the three herds' positions over the course of the study demonstrate that while buffalo herd membership may be fluid and therefore hard to define, the herd foci occupy distinct areas of the reserve. The overlap of the ranges in the analysis is small, and the points of herd location overlap were never within the same year. This is similar to findings by Sinclair (1977) and Grimsdell and Field (1976), but differs from findings by Conybeare (1980) and Whyte and Wood (1994). Hunter (1996) attributes the difference in range overlaps between studies to the presence (or absence) of perennial river courses. In this reserve, there are two major river courses with perennial portions and many permanent water points, suggesting that the herds' ranges need not overlap extensively due to water availability. While we found that the three foci are in distinctly separate areas, due to the fission-fusion nature of buffalo herds, it is possible that unrecorded subgroups of the herds created overlapping ranges. This suggests that while the herds are not necessarily territorial, they may be habitual in their resource use, preferring to use the same habitats and locations for multiple seasons. Both a previously published description (Prins, 1996) and our evidence of a consistent core group of females in the focal herd (unpubl.) suggest that this mechanism is possible. The three home range estimation methods we use demonstrate the potentially different size estimates of the area of the ranges we can obtain using the same datasets. The largest estimates of range size was given by the kernel method at the 95% kernel grid, the second largest is the Minimum Convex Polygon (MCP) method (Figure 5). Both these methods estimate a range that exceeds the boundary of the reserve and make the assumption that use occurs across the entire polygon generated. Comparisons of buffalo home ranges across studies are confounded by not just methodology, but also by water distribution regimes and other abiotic factors that we are unable to control for; not to mention possible excursions of herds into neighboring areas. In addition to the influence of perennial water sources on buffalo home ranges, Sinclair (1977) attributed the differences in home range sizes observed in different study sites to rainfall and presented a regression analysis that clearly demonstrated larger home ranges at higher annual rainfall regimes. However, re-examination of this analysis reveals that the larger home range area estimates also corresponded to larger herds, and there was no control for this factor in his analysis. The MCP values in Figure 5 (this study) and Table 4 (a comparison of other studies) suggest that an upward limit of approximately 290km^2 exists on range size, regardless of buffalo herd size in the study. In this study we were able to compare the annual home range with average annual herd size, and found that while the focal herd membership increased in number as the total census population increased, there was no additional correlation with a range increase. By virtue of long-term data, we were able to control for water supply and uncover a consistency of ranging behavior. This is interesting from a foraging standpoint, as it suggests that the three main herds will not necessarily break into smaller groups in response to increased resource pressure as the population increases.

Seasonal Range

The instability of buffalo herds between seasons implies that the home range, traditionally defined by the movements of associated individuals, differs not only in size, but also in membership between seasons. The reduction of range in the dry season seen in prior studies (Funston *et al.*, 1994) is likely to be closely tied to the availability of water sources, rather than to reduced numbers. The KPNR has a relatively high density of available water even in the dry season, so the size of the range may be more closely a function of the number of individuals in a herd, due to the metabolic needs of the group. A comparison of spot counts of the focal herd across the study period showed that the dry season herd size is significantly smaller than that of the wet season. This is consistent with prior studies (Sinclair, 1977; Prins 1996, e.g.) and with buffalo breeding ecology and seasonal behavior. Although the method of seasonal range comparison differs from that of prior studies, the mechanisms producing seasonal trends are similar, as are the results. We found that the buffalo both traveled further and had larger 10-day ranges in the dry season than the wet season. This would suggest that in the dry season, the herd was either traveling further in search of food, or simply that more time was spent walking and grazing to fulfill their metabolic needs. The regression of range length and size on mean NDVI values for the reserve suggests there is a trend toward increasing distance traveled in poorer quality conditions, although an increase in range size was not found to be significant. Studies of activity budgets of African buffalo suggest that they spend more time looking for green, palatable grasses in the dry season than wet season, because despite their reputation as “supreme bulk grazers” (Owen-Smith *et al.*, 1993), they are still limited by gut capacity and time spent ruminating in poor conditions and therefore must choose palatable graze.

Habitat Selection

The Klaserie Private Nature Reserve is a savanna ecosystem that is relatively well supplied with water: only 2.2% of the total area is greater than 4km from water in the dry season. Buffalo herds have been reported in other studies to range 5km in a day (Mloszewski, 1983; Sinclair, 1977), suggesting that water itself may not be a limiting factor for buffalo in this reserve. However, buffalo are described as riverine habitat loving animals (Prins, 1996; e.g.), and our isopleth analysis (Figure 10) showed that the highest observation densities in this data set occur at two rivers, the Klaserie and Nsiri, both in the wet season and the dry season. In the distance to water analysis for all three herds, the buffalo herds were preferentially choosing habitat within 1km of water in the wet season. From field observations, CK noted that while the buffalo were near the river in the wet season, they tended to graze at the river banks or simply cross the river as rapidly as possible, rather than spend time drinking or standing in the riverbed. Water sources used for this analysis represent both artificial and natural sources of water, whose contribution to proximate available soil moisture and thereby green vegetation may differ by source type, thus the buffalo herds could be responding to complex benefits of water availability. The focal herd showed preference for areas of the reserve within 1km of water sources of all types in both seasons. It was surprising that the analysis of all three herds did not reveal a dry season preference for nearer distance to water categories. This may be an artifact of too few data points, as it is contrary to the findings of the focal herd. However, it is consistent with a prior study by Redfern et al. (2003), in which buffalo in a dry season census were not selecting areas of Kruger National Park that were close to water on low-quality landscapes and the authors concluded that foraging further from water on poor quality soils might be an important factor in the dry season. Unfortunately that study had no wet season census to provide a contrasting seasonal analysis. We posit that in an environment wherein water is unlikely to be limiting, as in KPNR, that the driving factor for habitat selection in the dry season will be available forage.

Although buffalo are grazers and the 8 major habitat types used in the analysis are described by woody structure, the preference for habitat type 2 by all the herds and the focal herd across both seasons is likely confounded by the presence of reed beds along the Klaserie river at this point. Qualitative observation by CK suggests that when other areas of vegetation were already yellowish, greyish or brownish, the river area was still green and greenish/yellowish. The *Panicum maximum*, which grows especially densely at the riverbanks, appeared to provide palatable graze for the buffalo until the late dry season. However, the Klaserie buffalo occasionally browse on *Combretum* and other woody shrubs, which is observed more in the dry season, as has been noted in several other studies (Sinclair, 1977; Stark, 1986; Vesey-Fitzgerald, 1974). In addition, tufts of grass that grow in *Combretum* dominated areas persist into the dry season with green growth, whereas more open areas simply lignify and become unpalatable graze. Thus preferential selection for habitat types 4 and 5 by the focal herd in the wet and dry season respectively is unsurprising, despite the apparent unpalatability of shrubland. The focal herd showed a preference for short or open woodland and scrubveld, while avoiding or selecting against habitat types defined as closed woodland. Selecting against taller or denser woodland is consistent with suggestions in prior studies of avoiding dense trees as a predator avoidance strategy, in addition to the reduced likelihood of palatable grasses.

The habitat types used for the broad scale analysis were classified approximately two decades before the onset of this study, and while we assume that the broad scale landscapes have not altered significantly, fires and other clearing methods may have disturbed vegetation patterns at smaller scales. Qualitative observations suggest that burnt patches in the reserve are attractive to buffalo after sufficient re-growth occurs. The habitat types could be improved by more detailed description of the grass covers and type, at a smaller scale. This would obviate the confounded likelihood of highly palatable reed beds along the perennial river courses appearing in areas characterized by low woodland or shrubs. The presence of palatable grasses or reeds along riverbeds or near dense trees also means that NDVI values at the resolution available to the study ($1km^2$) are hard to interpret for habitat quality. The reflectance values of water and canopy cover in a pixel obscures and lowers the overall value, yielding a low greenness value where there may be sub-pixel high quality patches. Thus, a re-classification of aerial photography, or vegetation transects measured on the ground would be the best means of understanding why buffalo prefer certain areas in this reserve.

MANAGEMENT IMPLICATIONS

Removal of fences along the western border of Kruger National Park and the incorporation of Klaserie Private Nature Reserve into the Greater Kruger Management Area makes it essential to understand the utilization patterns and populations of wildlife in the reserve. The buffalo population of KNP was controlled in the past by a culling program (DeVos, 1983), and their numbers continue to be monitored via yearly censuses. As the buffalo population is able to migrate into the private reserves bordering the park, it is important to understand these reserves' role in providing both water and foraging opportunities for the buffalo. This study represents the first empirical use of the LoCoH home range method, demonstrating its application to questions regarding range and habitat use. The utility of this method depends on information available to the user regarding landscape and vegetation characteristics. We found that using remotely sensed vegetation data in predictions of buffalo habitat use was complicated at a small temporal and geographic scale. The overriding preference for riverine areas confounded interpretation of remotely sensed data in habitat selection, suggesting necessary refinement of habitat classification for this study system.

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Table and Figure Legends

Table 1: Annual Home Range Estimates of the Focal Herd Using LoCoH Method

Table 2: Broad Scale Habitat Selection

Observed Proportion occurring in habitat type
*95% Confidence Interval of area under a neutral selection hypothesis**
*Significant Preference for habitat type***
Number of Observations in habitat type
Expected Observations
χ^2

*Adjusted Alpha Level for this Analysis was 0.99, with a corresponding Z value of 2.73 for the Bonferroni corrections.

**The significant preferences and avoidances are denoted with (+) and (–) respectively.

Table 3: Distance-to-Water Selection

Observed Proportion occurring in habitat type
*95% Confidence Interval of area under a neutral selection hypothesis **
*Significant Preference for distance to water category***
Number of Observations in distance to water category
Expected Observations
χ^2

*The Wet Season adjusted Alpha value for the Bonferroni correction for the analysis of all herds is 0.99 with a corresponding *Z* value of 2.39, and the Dry Season is 0.99 with a corresponding *Z* value of 2.50. For the Focal Herd analysis, the adjusted Alpha value for the Bonferroni correction in the Wet Season is 0.99 with a corresponding *Z* value of 2.41, and in the Dry season is 0.99 with a corresponding *Z* value of 2.50.

**The significant preferences and avoidances are denoted with (+) and (–) respectively.

Table 4: Home Range Estimates for African Buffalo from Several Prior Studies

Figure 1: Buffalo Census KPNR

Figure 2: Study Site Location

Figure 3: KPNR Rainfall & Temperature, Showing Seasons

Figure 4: Scanned map, which has been orthorectified and georeferenced to KPNR showing transcription of locations of buffalo groups into an ArcView shapefile.

Figure 5: Home Range Estimates for the three herds: Northern Herd (NH), Focal Herd (FH) and Southern Herd (SH). Plots show comparisons of three methods: LoCoH (diamonds), Miniumum Convex Polygon (MCP) (dashed line) and the 95% Fixed Kernel (H_{LSCV} 500m grid) (solid line).

Figure 6: Habitat Types of the Klaserie Private Nature Reserve (*after* N. Zambatis)

Figure 7: Seasonal Distribution of Water Sources in KPNR

Figure 8: Seasonal Differences in Density Isopleths of Focal Herd Activity

Table 1

Year	Area (Km^2)	Number of Points	*k*
1993	272.46	216	17
1994	277.88	268	15
1995	247.53	290	20
1996	170.68	200	26
1997	190.90	279	20
1998	327.04	283	19
1999	243.25	258	20
2000	245.10	245	19
2001	186.30	180	18

Table 2: Broad Scale Habitat Selection

Across Seasons							Wet Season						Dry Season					
Habitat	**Proportion of Area**			**χ^2 Analysis**			**Proportion of Area**			**χ^2 Analysis**			**Proportion of Area**			**χ^2 Analysis**		
	Obs^a	*95% CI*^{b}	*sp*^{c}	*Obs*^{d}	*Exp*^{e}	χ^{2f}	*Obs*^{a}	*95% CI*^{b}	*sp*^{c}	*Obs*^{d}	*Exp*^{e}	χ^{2f}	*Obs*^{a}	*95% CI*^{b}	*sp*^{c}	*Obs*^{d}	*Exp*^{e}	χ^{2f}
Three Herds																		
1	0.04	[0.01-0.08]	ns	14	12.7	0.1	0.04	[-0.01-0.09]	ns	4	4.5	0.1	0.04	[0.01-0.10]	ns	10	8.2	0.4
2	0.01	[0.02-0.10]	+	17	3.4	55.5	0.01	[0.01-0.15]	ns	8	1.2	39.2	0.01	[0.01-0.09]	ns	9	2.2	21.5
3	0.23	[0.03-0.11]	-	20	64.4	30.6	0.23	[-0.01-0.09]	-	4	22.8	15.5	0.23	[0.03-0.14]	-	16	41.6	15.8
4	0.14	[0.14-0.27]	ns	57	39.5	7.8	0.14	[0.11-0.33]	ns	22	14.0	4.7	0.14	[0.110-0.27]	ns	35	25.5	3.5
5	0.36	[0.37-0.53]	+	127	101.4	6.5	0.36	[0.34-0.62]	ns	48	35.8	4.1	0.36	[0.33-0.53]	ns	79	65.6	2.7
6	0.09	[0.03-0.11]	ns	19	25.7	1.77	0.09	[-0.01-0.09]	ns	4	9.1	2.8	0.09	[0.03-0.14]	ns	15	16.6	0.2
7	0.08	[0.05-0.15]	ns	29	23.9	1.17	0.08	[0.02-0.18]	ns	10	8.4	0.3	0.08	[0.04-0.17]	ns	19	15.4	0.9
8	0.04	[0.00-0.00]	-	0	12.3	12.3	0.04	[0.00-0.00]	ns	0	4.3	4.3	0.04	[0.00-0.00]	ns	0	7.9	7.9
Focal Herd																		
1	0.08	[0.02-0.06]	-	33	67.2	17.4	0.08	[0.01-0.06]	-	14	32.0	10.1	0.08	[0.02-0.07]	-	19	35.2	7.5
2	0.02	[0.06-0.12]	+	77	16.8	215.7	0.02	[0.04-0.11]	+	31	8.0	66.1	0.02	[0.06-0.14]	+	46	8.8	157.3
3	0.12	[0.03-0.07]	-	44	100.8	32.0	0.12	[0.04-0.10]	-	28	48.0	8.3	0.12	[0.01-0.06]	-	16	52.8	25.7
4	0.20	[0.19-0.26]	ns	190	168	2.9	0.20	[0.21-0.33]	+	110	80.0	11.3	0.20	[0.13-0.23]	ns	80	88	0.7
5	0.47	[0.46-0.55]	ns	424	394.8	2.2	0.47	[0.38-0.51]	ns	181	188.0	0.3	0.47	[0.49-0.61]	+	243	206.8	6.3
6	0.04	[0.01-0.04]	ns	23	33.6	3.3	0.04	[0.00-0.03]	-	5	16.0	7.6	0.04	[0.02-0.06]	ns	18	17.6	0.01
7	0.08	[0.04-0.08]	ns	49	67.2	4.9	0.08	[0.04-0.11]	ns	31	32.0	0.0	0.08	[0.02-0.06]	-	18	35.2	8.4
8	0.00	[0.00-0.00]	ns	0	0.0	0.0	0.00	[0.00-0.00]	ns	0	0.01	0.0	0.00	[0.00-0.00]	ns	0	0.0	0.0

Table 3: Distance-to-water Selection

Distance-to-water (km)	Area (km^2)	Proportion of Area			χ2 Analysis		
		Obs[a]	*95% CI*[b]	*sp*[c]	*Obs*[d]	*Exp*[e]	χ^{2}[f]
All herds - Wet season							
0-1	363.5	0.63	[0.67-0.87]	+	77	62.9	3.2
1+	214.3	0.37	[0.13-0.33]	-	23	37.1	5.4
All herds - Dry season							
0-1	227.3	0.46	[0.37-0.56]	ns	85	72.0	2.4
1-2	252.8	0.42	[0.33-0.51	ns	77	80.1	0.1
2-3	76.2	0.09	[0.04-0.15]	ns	17	24.1	2.1
3+	21.5	0.02	[-0.01-0.05]	ns	4	6.8	1.2
Focal Herd – Wet season							
0-1	193.4	0.65	[0.72-0.82]	+	308	258.1	9.7
1-2	98.5	0.33	[0.16-0.26]	-	84	131.4	17.1
2+	7.9	0.03	[0.00-0.04]	ns	8	10.6	0.6
Focal Herd – Dry season							
0-1	108.6	0.36	[0.38-0.50]	+	192	159.3	6.7
1-2	139.5	0.47	[0.35-0.47	ns	182	204.6	2.5
2-3	43.8	0.15	[0.08-0.15]	ns	51	64.2	2.7
3+	8.0	0.03	[0.01-0.06]	ns	15	11.9	0.8

Table 4

Location	Method	Description of Range	# of Buffalo	# of Observations	Range (km²)
Wankie National Park, Zimbabwe[1]	MCP	Wet Season *Southern Herd*	123	*na*	170
	MCP	Wet Season *Northern Herd*	24	*na*	233
	MCP	Dry Season *Southern Herd*	123	*na*	128
	MCP	Dry Season *Northern Herd*	259	*na*	214
	MCP	Overall *Southern Herd*	*na*	*na*	207
	MCP	Overall *Northern Herd*	*na*	*na*	286
Benoue National Park, Cameroon[2]	MCP	Wet Season	50-55	*na*	46
	MCP	Dry Season	50-55	*na*	61
Sabi Sand Wildtuin, South Africa[3]	95% cluster	Annual Home Range	248	1765	120
	MCP; 95% cluster	Summer (wet)	*na*	*na*	127.76; 41.48
	MCP; 95% cluster	Winter (dry)	*na*	*na*	138.04; 120.94
	MCP; 95% cluster	Pre-summer (hot/dry)	*na*	*na*	114.93; 40.40
Sabi Sand Game Reserve, South Africa[4]	MCP	Overall	700	*na*	160
	MCP	Overall	350	*na*	90
Ruwenzori[5]	MCP		*na*	*na*	9.4-9.6

Voi Lodge, Tsavo[6]	MCP	A few weeks	350	*na*	85
Serengeti[7]	MCP	Moru (Herd 3)	900	*na*	271.4
	MCP	Nyaboro (Herd 2)	1500	*na*	296.3
	MCP	Banagi	800	*na*	143.8
	MCP	Seronera	700	*na*	178.4
	MCP	Northern (Herd 1)	1100	*na*	83.5
	MCP	Northern (Herd 4)	500	*na*	53.0
Momella Lakes[8]	MCP		200	*na*	10.9
Rwenzori[9]			130	*na*	10

[1] Conybeare (1980); [2] Stark (1986); [3] Funston (1994); [4] Kruger, J,(1996); [5] Eltringham and Woodford, (1973); [6] Leuthold (1972); [7] Sinclair, 1977; [8] Vesey-Fitzgerald, as cited by Sinclair (1977); [9] Grimsdell, 1969; in Grimsdell and Field (1976)

Figure 1

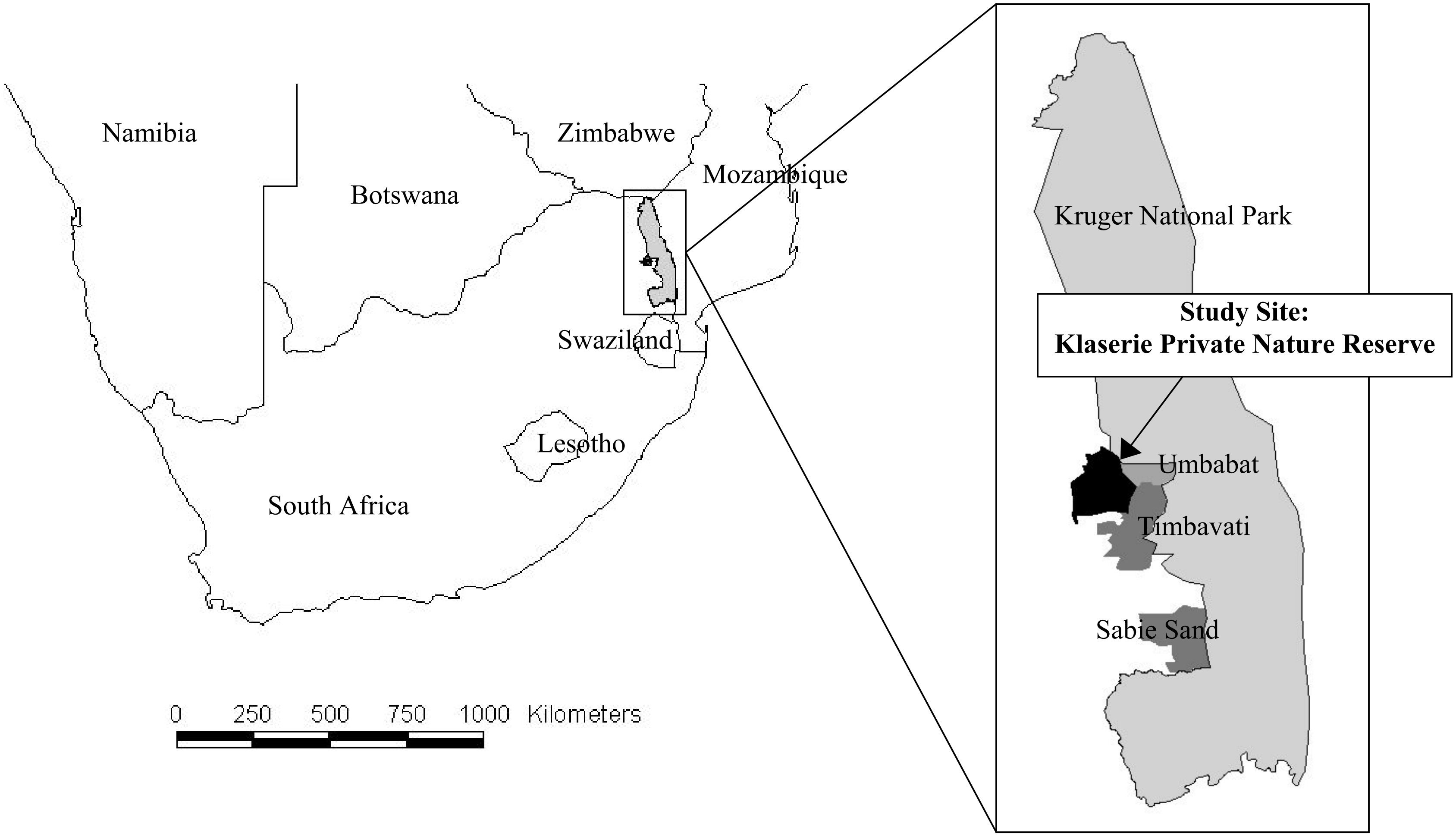

Namibia
Botswana
Zimbabwe
Mozambique
Swaziland
Lesotho
South Africa
0 250 500 750 1000 Kilometers
Kruger National Park
Study Site:
Klaserie Private Nature Reserve
Umbabat
Timbavati
Sabie Sand

Figure 2

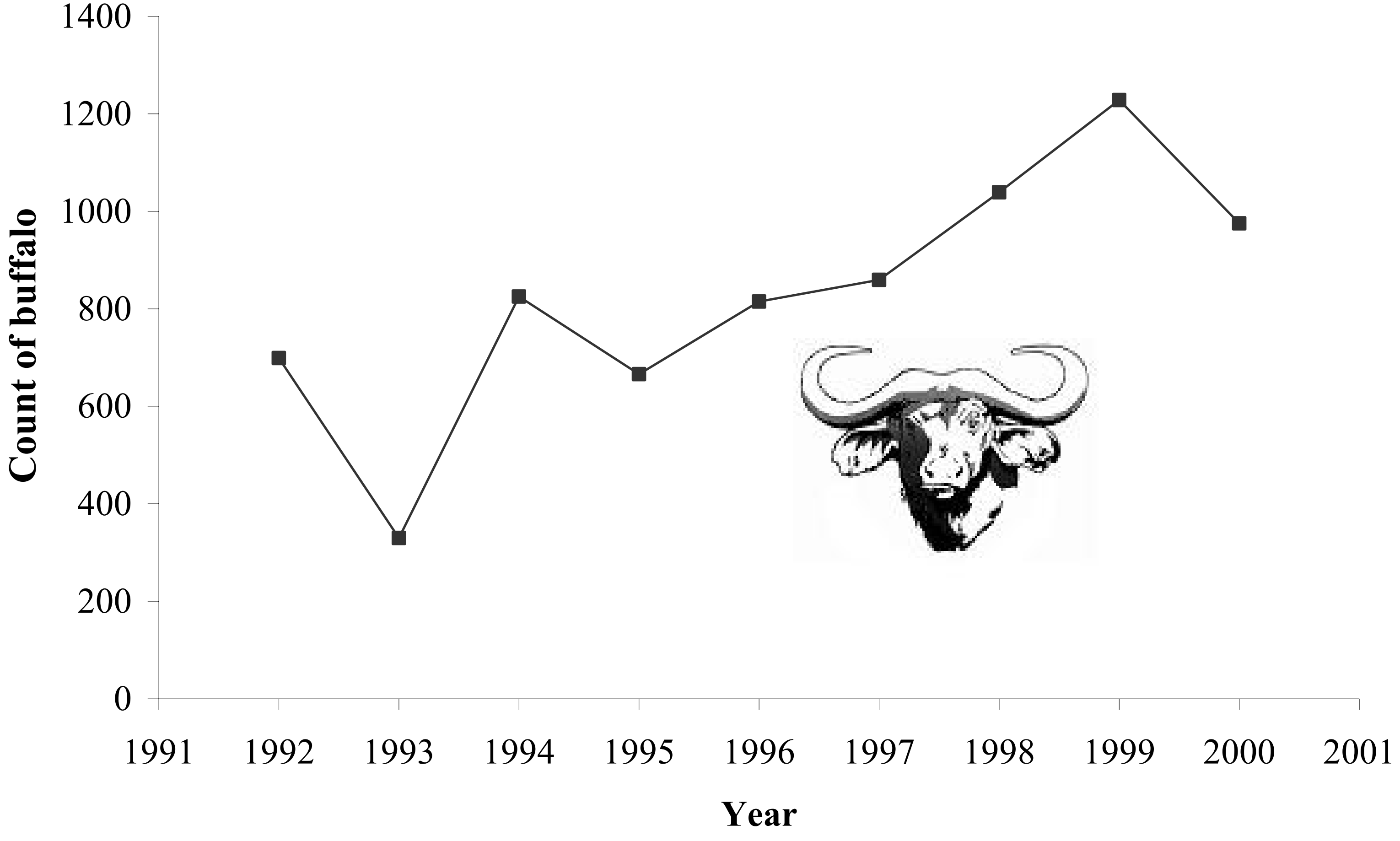
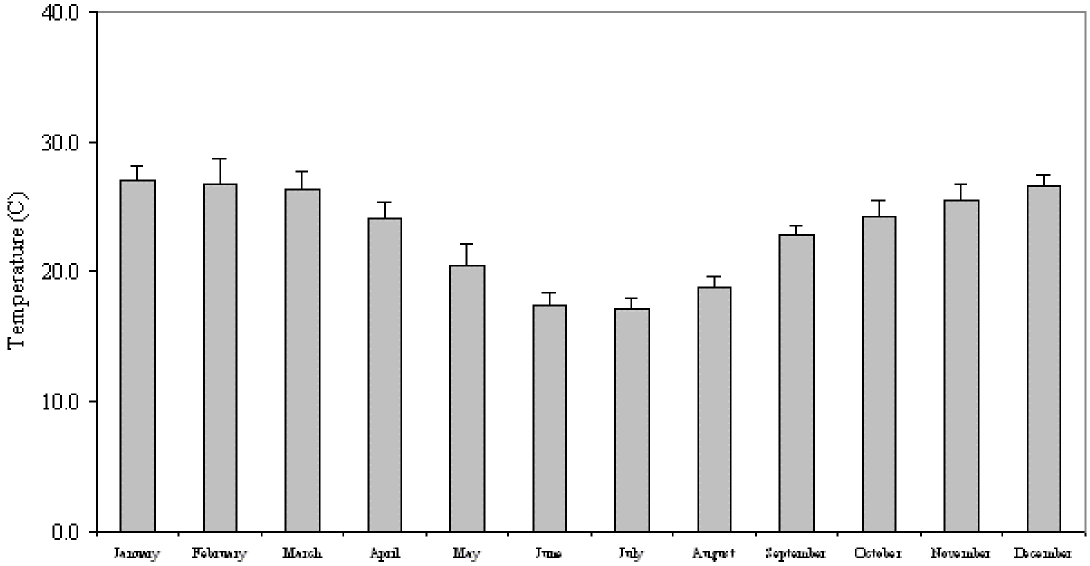

1400
1200
1000
800
600
400
200
0
Count of buffalo
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
Year

Figure 3


40.0
30.0
20.0
10.0
0.0
Temperature (C)
January
February
March
April
May
June
July
August
September
October
November
December

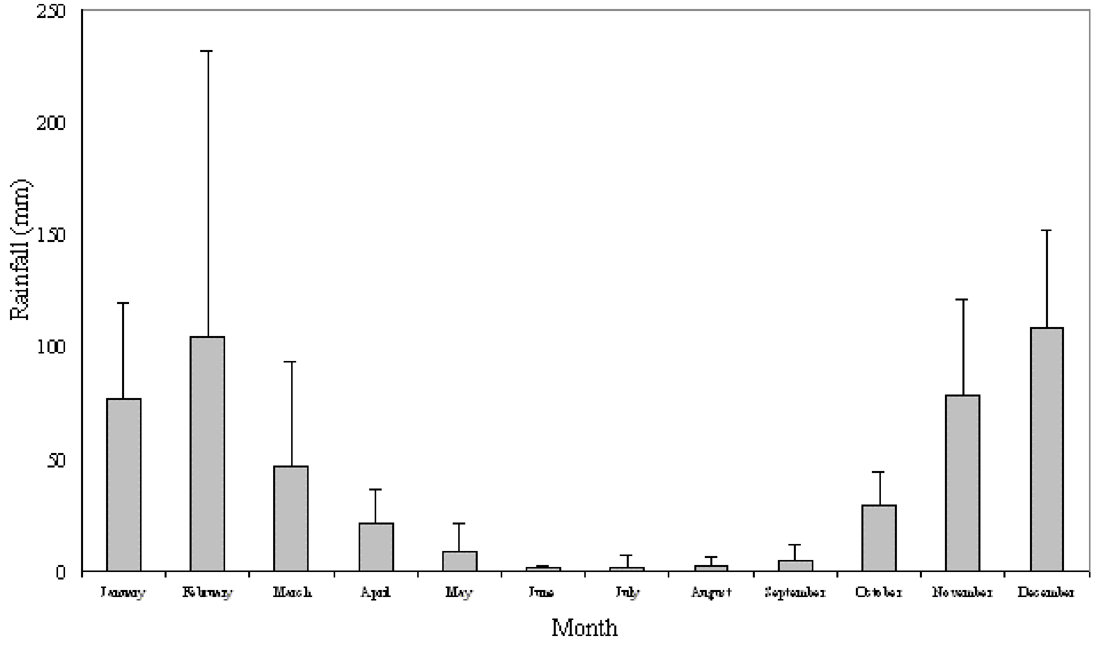

250
200
150
100
50
0
Rainfall (mm)
January
February
March
April
May
June
July
August
September
October
November
December
Month

Figure 4

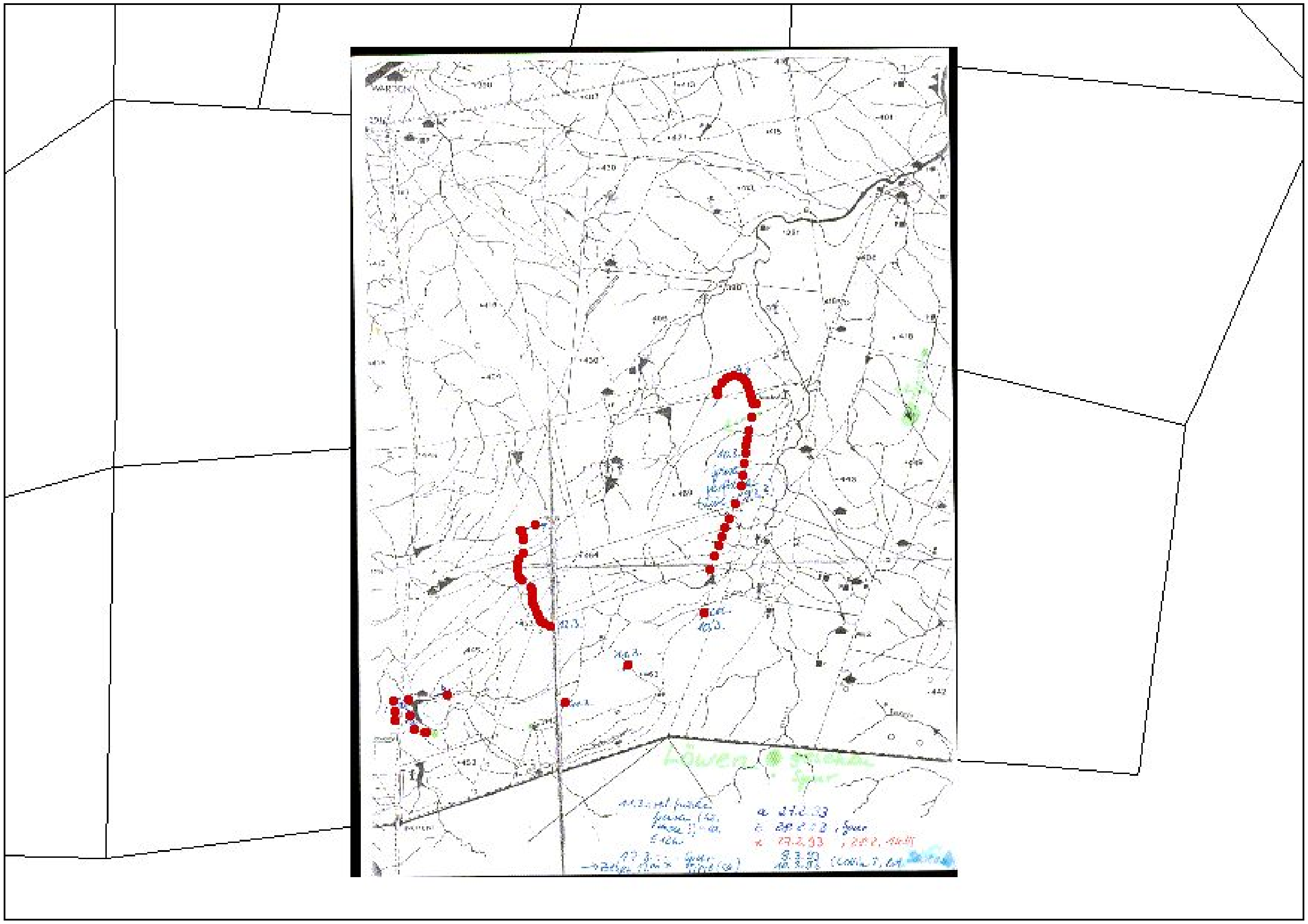


Figure 5

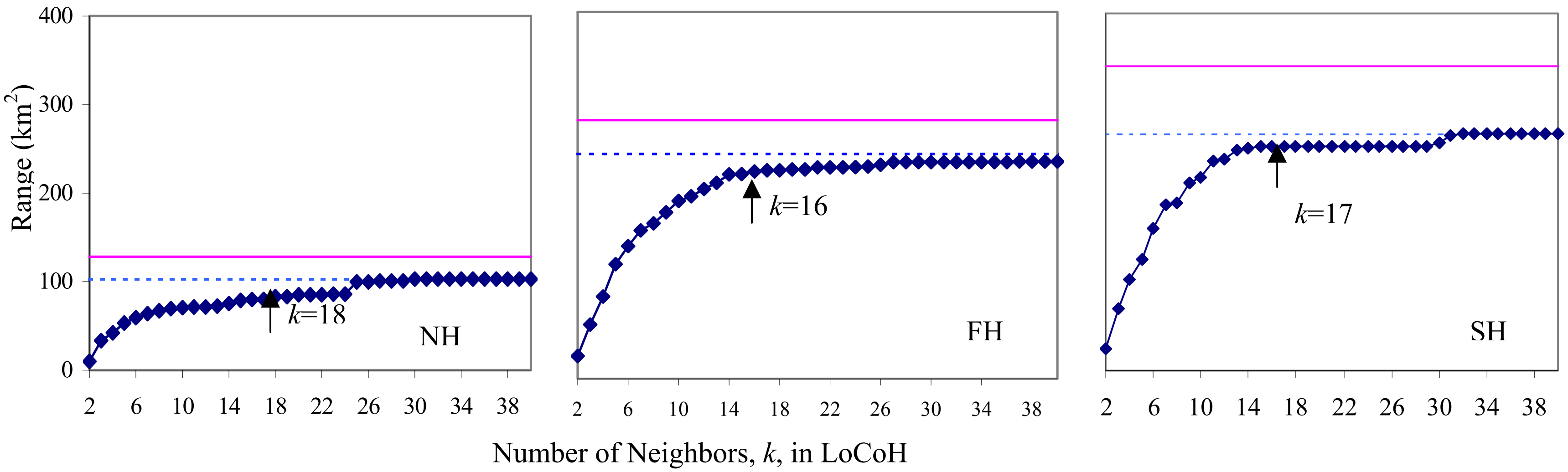
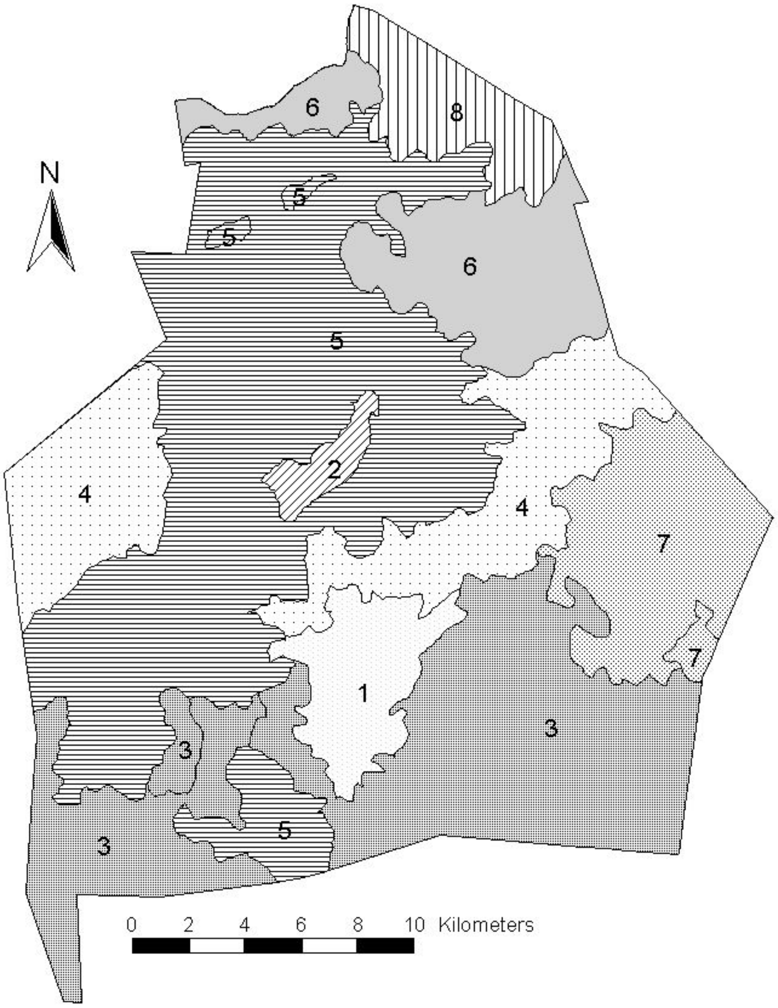

Range (km²)
400
300
200
100
0
k=18
NH
k=16
FH
k=17
SH
2
6
10
14
18
22
26
30
34
38
Number of Neighbors, k, in LoCoH

Figure 6



A. nigrescens and *Grewia sp*.: open woodland;
Mixed *Acacia sp*.: shrubveld;
Mixed woodland;
C. apiculatum, *S. birrea*: open woodland;
C. apiculatum, *S. caffra*, *Grewia sp*.: short woodland;
C. apiculatum, *C. mollis*, *Grewia sp*.: closed short woodland;
C. apiculatum, *C. mopane*: woodland;
C. mopane: woodland and shrubveld

Figure 7

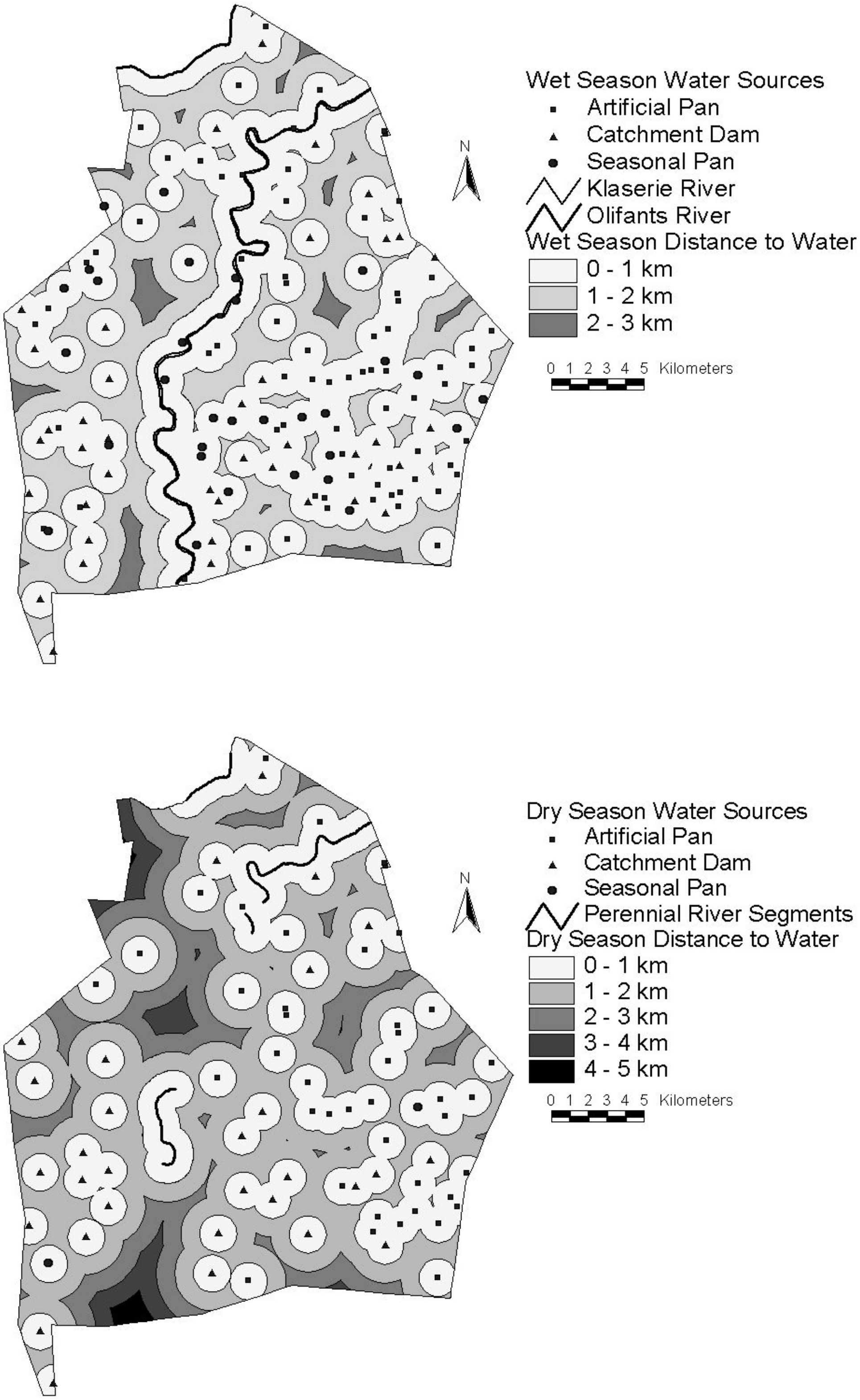
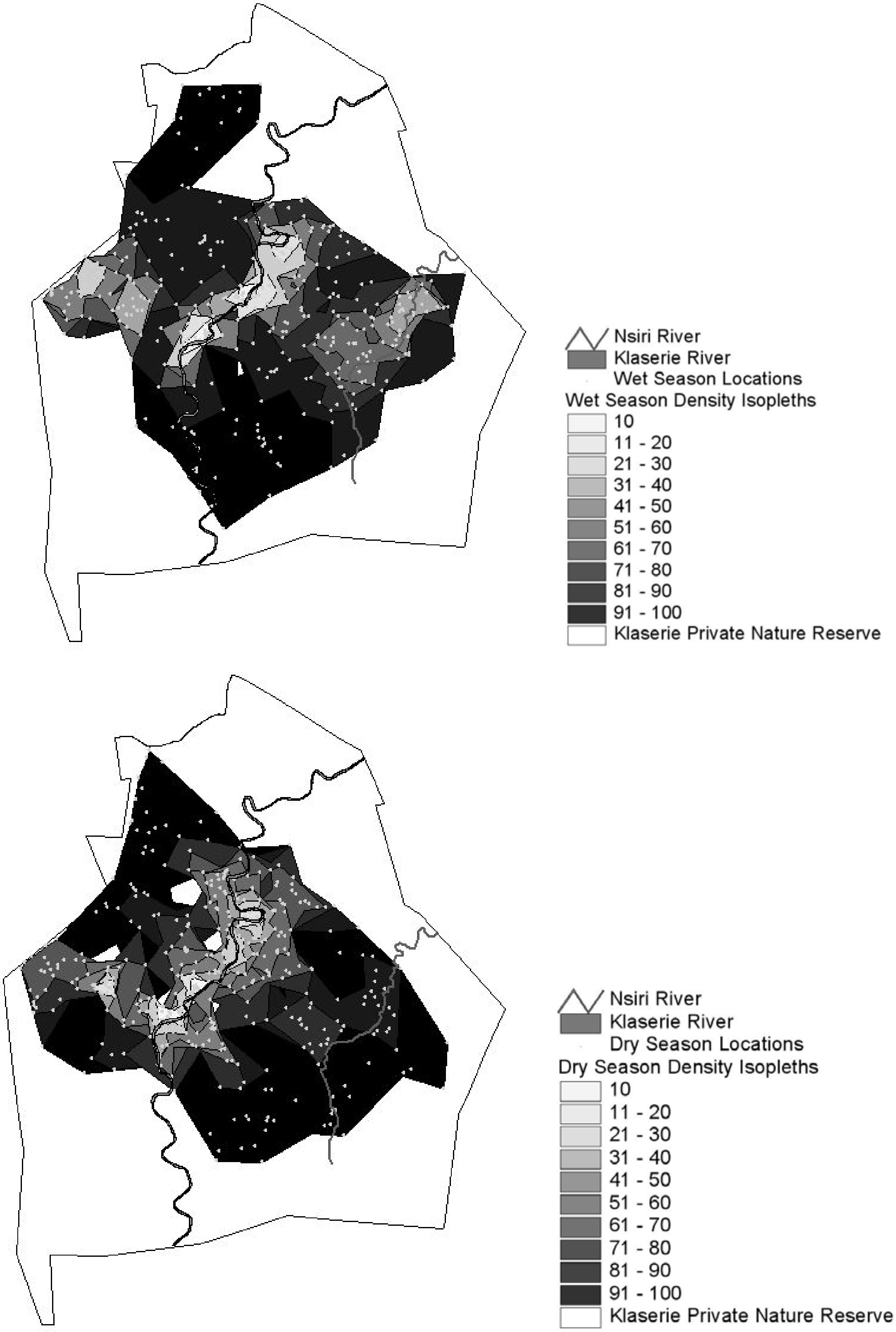

Wet Season Water Sources
Artificial Pan
Catchment Dam
Seasonal Pan
Klaserie River
Olifants River
Wet Season Distance to Water
0 - 1 km
1 - 2 km
2 - 3 km
0 1 2 3 4 5 Kilometers
N
Dry Season Water Sources
Artificial Pan
Catchment Dam
Seasonal Pan
Perennial River Segments
Dry Season Distance to Water
0 - 1 km
1 - 2 km
2 - 3 km
3 - 4 km
4 - 5 km
0 1 2 3 4 5 Kilometers
N

Figure 8


Nsiri River
Klaserie River
Wet Season Locations
Wet Season Density Isopleths
10
11 - 20
21 - 30
31 - 40
41 - 50
51 - 60
61 - 70
71 - 80
81 - 90
91 - 100
Klaserie Private Nature Reserve
Nsiri River
Klaserie River
Dry Season Locations
Dry Season Density Isopleths
10
11 - 20
21 - 30
31 - 40
41 - 50
51 - 60
61 - 70
71 - 80
81 - 90
91 - 100
Klaserie Private Nature Reserve

Chapter 2: A spatial location-allocation GIS framework for managing water sources in a savanna nature reserve.

Abstract

Associated with the establishment or removal of water sources in savanna ecosystems is the issue of the effects of such management actions on animal movement and habitat selection, longer term implications on population levels, and impacts of such change on habitat degradation and soil erosion. Extant metrics used to describe the spatial distribution of water sources on the landscape often fall short of providing source-specific information making them hard to apply in small-scale management settings. Using the Klaserie Private Nature Reserve (KPNR) as a case study, we compare a buffer framework, describing distances to water, a nearest neighbour framework, and a spatial location-allocation framework (SLAF) created in a geographic information system (GIS). These three frameworks can be combined into one GIS to demonstrate site-specific information on water source distribution in addition to system-wide descriptions. The visually accessible quality of a GIS allows qualitative input from managers and property owners to achieve quantifiable management goals. The duality of database and visual representation provides a useful tool to assess the role of individual water sources and can easily be updated to reflect changes in their distribution.

Keywords: Location-allocation models, GIS, piospheres, nearest neighbours, water sources

Introduction

A primary concern in fenced savanna nature reserves is the management of water, and the impact point sources have on the ecosystem (de Leeuw *et al.*, 2001; Gaylard, Owen-Smith & Redfern, 2003; Redfern *et al.*, 2005; Redfern *et al.*, 2003; Thrash, Theron & Bothma, 1995; Thrash, Theron & Bothma, 1993; Walker *et al.*, 1987). Considerable literature documents the concentric attenuating utilisation zones about water sources created through excessive animal use of habitat around such water points. The collection of these concentric zones was first described as the piosphere by Lange (1969) and later described by Graetz and Ludwig (1978) as a sigmoid curve of receding impact with distance. Piospheres were more formally introduced into the ecological literature by Andrew (1988) as a useful concept for the management of dry ecosystems. A review of piosphere modelling and techniques in 1999 (Thrash & Derry, 1999), describes analyses from individual piosphere measurements to system models. How best to measure attenuation with distance and define utilisation zones has been the subject of studies in arid systems in Australia, North America, Argentina and Africa (see James et al., (1999) for references). In addition, how to identify and define the sacrifice zone—the area close to a water source that is over-utilised and trampled—and the zones of decreasing use has been the subject of studies in the Kruger National Park (KNP) and neighbouring lowveld reserves (Brits, van Rooyen & van Rooyen, 2002; Thrash, 1998a; Thrash *et al.*, 1993).

Potential negative effects on biodiversity of animals and vegetation due to concentration about waterholes (Andrew, 1988; Nangula & Oba, 2004), altered distribution of prey species (James *et al.*, 1999) and erosion and degradation of surrounding habitat (Parker *et* *al.*, 1999; Thrash, 1998a, b; Walker *et al.*, 1987) arise as dry season water demand increases. These concerns in KNP led, in part, to a water-for-game programme from around 1929 to 1990, with the objective of adding water points to create a more even distribution of utilisation pressure, reduce river damage and prevent emigration into neighbouring reserves (see Brits et el., 2002 for details). In KNP and other arid and semi-arid ecosystems, attempts to create even utilisation through regular placement of boreholes or adding artificial water sources to the existing distribution have proven unsuccessful, as the whole system becomes concentrated in the sacrifice or high use zones during the dry season (Brits *et al.*, 2002; James *et al.*, 1999; Thrash, 1998a), reducing vegetation diversity across the entire water source distribution and creating sedentary over-utilisation by herbivores (Thrash, 1998). Thus current management trends have turned toward removal of artificial waterholes in KNP (Gaylard et al., 2003; Redfern et al., 2003). de Leeuw et al. (2001) point out that artificial water sources are often built to attract animals; and, in a small private reserve, this is important for wildlife viewing. In a system where water is managed by individual properties and wildlife is maintained at high densities, the impacts of dry season erosion are readily apparent (C. Rowels, pers. comm.). Removing water sources may be hard to negotiate and may also create greater erosion pressure on the remaining waterholes. Reconciling these potentially conflicting management objectives requires a framework wherein focal objectives can be combined with larger system objectives.

In the absence of piosphere data relating to specific water points in a fenced game reserve, the first step towards formulating a rational water location policy is to use an area allocation concept. What is the area associated with each water point, assuming that the burden on the piosphere is proportional to the size of the area and hence the animals in that area, representing the "utilisation burden" of that waterhole? We do not assume that this burden scales linearly with area, because animal densities drop off with distance to water (Redfern et al., 2003). A pure area approach, however, represents a first cut at framing a water source location allocation analysis that can later be augmented with specific piosphere data for the park or region of concern. The spatial location-allocation framework (SLAF) shows potential areas for increased impacts on focal water sources in a reserve during the dry season, which provides source-specific information for management. The framework reflects an economics oriented supply-demand viewpoint. If we picture the reserve as a region to which we want to provide a *service*, water, we derive a focal metric for managers to apply to individual water sources on individual properties. Location-allocation models are used in designing business networks to assess demand for point source suppliers, such as distribution hubs to franchise points. This creates a network model, whose optimal form is found by minimizing the distance between the points (see Hamilton, (1967), for further description). When demand is generalized across an area, the location-allocation model becomes a *point-polygon* location problem (Radke & Mu, 2000). A contemporary example of this is mobile phone coverage from point-sourced mast towers; each tower must produce sufficient signal for its area. In addition, a SLAF lends itself easily to the substitution model of Teitz and Bart (1968), a process wherein points are removed or added and modelled and compared to prior model outputs. This is an appropriate means for us to model management actions such as adding or removing water sources.

In this study, seasonal effects on the water source distribution are modelled first. Then two hypothetical management scenarios are modelled based on realistic management options for this reserve. For the first management scenario we map the resulting distribution when all artificially supplemented water sources are “turned on” in the dry season. For the second scenario, we augment the largest Theissen polygons above a certain size threshold generated by our SLAF, by “turning on” the nearest artificial water source. This action reduces the area associated with the original sources, while not significantly altering the average polygon area for the whole water source distribution. The results of these two strategies, a reserve-wide goal and a local goal, are compared in each of the three aforementioned frameworks.

Study Area

Klaserie Private Nature Reserve (KPNR) is located in the Limpopo Province of South Africa, bordering Kruger National Park (KNP) on its western boundary (24º3-22’ S, 31º2-19’ E; 303-535m a.s.l.; 57,800ha) (Figure 1). The reserve comprises multiple private properties, many formerly utilised as farms; it was physically separated from KNP in 1961 with the erection of fences along KNP’s western boundary to prevent spread of foot and mouth disease into domestic cattle (Witkowski, 1983). A western segment of this fence was later removed so that KPNR is now part of the Greater Kruger National Park Management Area, although it remains separated by fences from neighbouring private reserves. The species of herbivores represented in KPNR are similar to the suite of species in the central part of KNP.

The main geological substrate is granitic gneiss, part of the extensive granitic system underlying most of the country (Witkowski, 1983). The seasonality of KPNR follows a subtropical savanna pattern: both temperatures and rainfall follow a unimodal distribution annually (Figure 2); mean annual rainfall from 1992-2000 was 486mm. Two seasons are defined for this study based on the rainfall and temperature records of the reserve. These seasons are a hot wet season from October to March and a cool dry season from April to September.

Methods

Water sources in this study include seasonal pans, artificial pans and catchment dams as point sources and two major river courses, the Klaserie and the Olifants, which have perennial segments in KPNR (Figure 3). Seasonal pans are natural pans which retain water during the wet season and can remain wet into the dry season, but most dry out. Artificial pans are pans which are either natural or have been hollowed out of the ground and sometimes lined with cement, but which are supplied with water from a pump. Water supplementation is controlled by the property owner and water presence is less subject to season than in seasonal pans. Catchment dams are created by damming a drainage line, creating a three-cornered water source. Some of these dams are supplemented by water pumps in the dry season, but many dry out. What we refer to as *natural removal* of a source results from climate change in the case of seasonal pans and catchment dams, and *artificial removal* via cessation of water supplementation to artificial pans and catchment dams.

Data on the geographic locations and type of water sources in the KPNR were obtained and tabulated by KPNR management (n=145) (C. Rowels, pers. comm.). We assumed that all the water sources would be active in the wet season. These locations were censused in June 2002 by KPNR management (C. Rowels) for water presence, and this subset is the dry season dataset (n=74). The courses of the two major rivers that run through the reserve, the Klaserie and the Olifants were included as water sources; along their entire course during the wet season, and along their persistent perennial routes in the dry season. For the first hypothetical management scenario, all of the artificial pans that could be supplemented during the dry season were added back into the dry season water source data set and the three model methods were run. For the second scenario, the water sources associated with the largest polygons lying above a selected threshold value were identified based on a distribution break in a histogram of the polygon areas. Next, an additional available water source was "turned on" within each of these polygons. We then ran the three model methods once more. Relevant information was manipulated into shapefiles in ArcView 3.2 and analyses were conducted using ArcView 3.2, Thiessen ver 2.6 (Ammon, 2000), Geoprocessing Extension and Edit Tools 3.4 (Tchoukanski, 2002).

Buffer framework

For the buffer framework, the locations of all the water sources tabulated during the wet season were buffered in concentric 1km rings and clipped to the reserve boundary to assess the area of the reserve at different distances to water (Figure 4a); this process was repeated for the dry season water sources (Figure 4b) and then for the two hypothetical management scenarios and the results tabulated for comparison (Table 1).

Nearest Neighbour Framework

The locations of the wet and dry season water points were used to calculate the nearest distance to river sections and then to nearest water source. The nearest neighbour distance between two point water sources was calculated as a vector, by minimizing the results of a triangular matrix calculator for Euclidian distance in Microsoft Excel©. The lesser of the distance to nearest river or nearest neighbour was taken as the nearest neighbour distance to water.

Spatial Location-Allocation Framework (SLAF)

The simplest spatial representation of an unconstrained location-allocation model of supply points to demand regions uses the Dirichlet tessellation to generate Voronoi or Thiessen polygons (Okabe, Boots & Sugihara, 1992). A tessellation is essentially a mosaic, a tiling created in a geometric plane. This tessellation is created by the intersections of perpendicular bisectors between each point in a set, as depicted in Figure 5. It is constructed such that all the area contained within each polygon is closer to the point with which the polygon is associated than to any other point. If we have an unbounded set of points, this tessellation will generate internal polygons that are complete and boundary polygons that stretch to infinity. In this framework, the tessellation is modified to create Theissen polygons whose outer boundary edges are that of the area in question. In absence of data on the heterogeneity of the landscape with respect to water access, and the heterogeneity of species impact on these water sources, this model is the simplest and most straightforward representation of the potential pressure exerted on each water source with respect to demand. The larger a polygon associated with a water source, the greater the area it must provide water for, and the sparser the local distribution of points. Thus we expect a higher rate of herbivore utilisation impact at these sparser points because they are in higher demand.

For the location-allocation framework, the locations of all the water sources tabulated were used to create the tessellation of Theissen polygons, clipped to the reserve boundary, and the areas were spatially assigned back to the original water sources, using the Geoprocessing Extension. As this method is a point-based calculation, river lines were reduced to point sets along their courses. This generated multiple sliver polygons irrelevant to the study, and therefore we excluded all polygons whose area did not include a non-river water source (Figure 6a). Again, this was repeated for with dry season water sources (Figure 6b) and the point set generated under the two hypothetical management scenarios, and the results compared (Tables 1 & 2).

All statistical analyses were performed using SAS JMP (ver. 4.04).

Results

The dry season KPNR water source census showed that of 145 recorded water sources (74 artificially supplemented, 40 catchment dams and 31 seasonal pans), 74 still held water (42 artificially supplemented, 30 catchment dams and 2 seasonal pans). For the first hypothetical management scenario, the water sources increased to 106 (74 artificially supplemented, 30 catchment dams and 2 seasonal pans) and 81 (74 dry season sources plus 7 additional supplemented sources) under the second scenario.

Buffer Model

The buffer analysis (Table 1, Figures 5a and b) demonstrated that in the wet season no part of the reserve is more than 3km from a water source, whereas in the dry season some areas can be further than 4km from a water source. The proportion of the reserve area that is in close proximity to water sources also changes; in the wet season, 63% of the reserve is within 1km of a water source and 97% within 2km, while in the dry season, 39% is within 1km and 83% within 2km. Under the first management scenario, no part of the reserve was greater than 4km from a water source; 48% within 1km and 89% within 2km (Table 1). The second scenario changed the proportion of the reserve within 1km of water to 43% and 89% within 2km; no part of the reserve was greater than 4km from water sources (Table 1).

Nearest Neighbour Framework

The nearest neighbour distance analysis showed that the average nearest neighbour distance to water increases from the wet season to the dry season from 1.00 ± 0.05 km (μ ± SE, *n*=145) to 1.52 ± 0.09 km (μ ± SE, *n*=74). The nearest neighbour distance under the first management scenario brought this to 1.12 ± 0.07 km (μ ± SE, n=106). Under the second scenario, an *increase* in nearest neighbour distance from the dry season distribution occurs 1.64 ± 0.08 (μ ± SE, *n*=81). An ANOVA for multiple comparisons of means was significant (*F*=18.50, df = 401, *p*<0.0001). Tukey-Kramer's Honest Significant Difference (HSD) (α=0.05) showed that the wet to dry season change is significant, the first scenario is significantly different from both the dry season and the second scenario, and the second scenario is significantly different from the wet season and the first scenario, although not from the dry season.

Spatial Location-Allocation Framework (SLAF)

The SLAF showed that the area supplied by water sources increased significantly in the dry season (Figures 6a and b). The polygon area per water source increased from 3.19 ± 0.17 km^2 (μ ± SE, *n*=145*)*, in the wet season to 6.69 ± 0.47 km^2 (μ ± SE, *n*=74) in the dry season. The proportional increase in average polygon area for the dry season water sources was 110% (*n*=74). Turning on all the artificial water sources in management scenario I altered the average polygon area to 4.81 ± 0.30 km^2 (μ ± SE, *n*=106). Under the second management scenario, we identified water sources with the largest areas. We simulated manipulation of sources with polygon areas greater than 12km^2 (see Figure 7a), based on a distribution break identified in figure 7b. This yielded seven water sources; we then simulated placement of additional water sources within their polygon areas and the resulting reduction in their respective polygon areas is given in Table 2. The overall average area per water source was reduced to 6.67 ± 0.34 km^2 (μ ± SE, *n*=81). An ANOVA for multiple comparisons of mean areas among models was significant (*F*=31.57, df=401, *p*<0.0001), and post-hoc Tukey-Kramer's HSD (α=0.05) tests for differences in means showed that the wet season mean polygon area was significantly different from the dry season's; the first management scenario was significantly different from both seasons and the second scenario, and the second scenario was significantly different from the wet season and the first scenario.

Discussion

The three frameworks used to assess the change in distribution of water points in the reserve yielded generalizations, which are useful as descriptors of system change, but can be hard to translate directly into management action on specific water sources. The advantage of the SLAF over the two other frameworks is that the area of the polygon associated with each water source is visually accessible and quantified individually.

In this study, the first method used was to buffer each water source to model the areas of the reserve that lie at certain distances from water sources in the wet season and in the dry season. Clearly, the proportion of the reserve in proximity to water source changes with the dry season water source removal (both natural and managed) (Table 1, Figure 5a, b). Game species, for which in large part, water sources are placed and managed, may become concentrated into smaller areas, which may increase local degradation, concentrate prey species and alter vegetation use. This reserve represents an environment with relatively high water availability and a similar stocking rate to KNP (Thrash, 2000); the number of non-river water sources has increased from 6 in 1965, to 144 in 1980 (Parker and Wittowski, 1999), to the 145 reported in 2002. Even in the dry season, KPNR is well supplied with water, compared to the water availability of KNP, in which, under the new borehole removal program, portions of the park are greater than 8km from water, including ephemeral sources driven by dry season rainfall (Redfern et al. 2003). The buffer method yields a system-wide metric and demonstrates visually and quantifiably which areas are most subject to change of season. However, from the perspective of a property manager, who may need information on specific water sources, it is difficult to apply this metric to specific management actions. This follows because it is hard to compare the distance buffers generated under different management scenarios at a local scale.

The second method assessed the change in distance between nearest neighbour water sources under seasonal and management regimes. This is intuitively a useful metric, as it generalizes the distribution of water sources to a local "choice", and fits well intuitively with constraints on habitat selection and resource availability. The analysis showed that the distance between water sources increased in the dry season, from roughly 1 km to 1.5 km. This measure reflects the increase in the number of water points in the reserve since 1982, when the mean spacing was 2km (Zambatis, (1982); season unspecified). Although statistically significant, these seasonal and managed changes in distances may not be important for visible game species using the water sources, for which they are managed in KPNR. Large herbivores and game species such as buffalo, whose daily range is approximately 5km (Sinclair, 1977), may not be greatly affected by these alterations in distance. Moreover, the SLAF more precisely shows the midpoint between water points along an edge, representing essentially the point of trade-off between neighbouring points as it might be perceived by an herbivore.

The nearest neighbour method is hard to apply to management of focal water sources, as manipulations would require altering the spatial distribution of water sources relative to one another. An average nearest neighbour distance fails to identify which specific sources undergo the largest change or are further from others in the distribution than the average. In fact, when the second management scenario presented was run, the nearest neighbour distance analysis produce a counter-intuitive result in which the average distance *increased* under a plan directed at decreasing utilisation pressure. This occurred as the points which were added into the distribution, while closer to the seven points the plan sought to relieve from pressure, were further from the next nearest water points. The selection of these points was purely based on availability of water sources, and under the nearest neighbour model, the result could be misinterpreted as a failure to meet management objectives. However, our SLAF clearly shows a reduction in polygon area associated with the seven waterholes, and a minor reduction in the average polygon area for the whole distribution.

The SLAF demonstrated that the average area supplied by water sources in the wet season, represented by Theissen polygons, is approximately 3 km^2. A 167% increase of average polygon area to over 6.5 km^2 gives us insight into the potential for increased impacts around dry season water sources. The increased area will lead to an increased herbivore concentration around the remaining sources. This may be a positive outcome from a local or property management standpoint; given that the rarity of the water source may allow better wildlife viewing. In addition, it is suggested that isolated points positively affect diversity of vegetation (Thrash, 2000). These average area comparisons between seasons give us insight into an overall change in water supply in the reserve. We can compare this metric with the first two model metrics and draw similar inferences about dry season impact across the reserve.

Using the SLAF, each water source had associated with it a specific supply area increase in the dry season, apparent visually by the size of the polygon associated with it (Figure 6a, b). The addition of a chart showing the areas associated with each water source allows another means of visualizing the distribution. Apparent in this distribution is the upper and lower extremes of areas. Using the river segments as part of this analysis gave a more realistic quantification of the space supplied by each water source. The point representation of the curved river course created multiple sliver polygons as seen in Figure 8. The large number of polygons generated required quite high computational power, but the result approximated a curved edge on the polygon for the nearest non-river water source.

The first hypothetical management scenario sought a very quick and simple means to reduce the potential for impact on water sources present in the dry season, by reducing their average supply area significantly. All the artificially supplemented water sources were ‘turned on’ during the dry season and analyses run on the new set of data. The buffer analysis showed that this altered the reserve landscape such that less of the reserve was as far from water sources, and the nearest neighbour distance between sources was reduced by around 400m. In addition, there was a statistically significant reduction in the supply area to the dry season water sources, which could mitigate dry season impacts on those sources. Although current management strategies in nearby savanna ecosystems are now advocating removal of artificial water sources and increased heterogeneity in water source placement (Thrash, 1998; Redfern, 2002), with high stocking rates and a small total area, this may not be an immediately feasible or desired option. However, the SLAF's visually accessible information on association polygons makes planning for heterogeneity in the distribution simpler than the first two methods.

The second hypothetical management scenario is an example of using the database for a query-based management option, wherein the data on both SLAF polygon size and water source type were sorted and used to develop a management action. The charted dry season Thiessen polygon distribution showed a break in the distribution at slightly over 12km^2, which we chose to use as our cut-off for the management scenario. The seven largest polygons associated with dry season water sources were selected, and the nearest artificial water source 'turned on'. The resulting reduction in polygon area associated with the original water sources was dramatic (see Table 2), with an average reduction of 59%. This local management action had no significant impact on the distribution-wide average polygon area, and actually caused an increase in the average nearest neighbour distance.

Although a Dirichlet tessellation was used by Parker and Witkowski (1999) in the design of a piosphere study in Klaserie Private Nature Reserve (KPNR) to identify the furthest points from water sources on the attenuation gradient, the application of this tessellation framework specifically to evaluate and manage the placement of waterholes has not been seen in the literature. Aside from specific terrain considerations (e.g. obstacles to movement, and resource gradients in different directions), Thiessen polygon edges essentially represent the trade-off zone for herbivores between a local set of water sources, such that each edge will be the end of the attenuation gradient of the piosphere. Thus, a Dirichlet tessellation, in the absence of more specific habitat information, not only provides a measure of the area each water source supports, but also a visual representation of the limit of utilisation zones.

In prior studies, quantifying or describing water source distributions for management has been limited often by the models used. More specifically, inappropriate methods lead to questions being answered that do little to address the real issues at hand. Conventional spatial statistics, in which we describe a point pattern (e.g. Ripley's K, Geary's C), tend to focus on clusters of points and deviation from a 'random' distribution. This might be useful to an ecological modeller, but be far removed from applicability in a management setting. Descriptions that average over the entire distribution of water sources, such as mean nearest neighbour (Parker and Witkowski, 1999), or distance to water areas (de Leeuw *et al.*, 2001; Pringle & Landsberg, 2004; Redfern *et al.*, 2003), can be useful for examining the consequences of a management action for a distribution of wildlife or livestock. Buffer models, describing distance to water, lend themselves readily to comparison with piosphere studies. The reason is that the zone of attenuating use is radial, and therefore circular distance bands can be surrogates for utilisation zones However, when buffer maps are used in an ad-hoc manner to decide what management actions to implement, they may underestimate potential impacts on specific water sources. The quantitative result of re-modelling a new water source distribution will only yield a distribution-wide descriptive map. Creating appropriate measures for demonstrating change on a local scale, or re-applying the results to a management scenario is often left to guesswork.

The spatially explicit nature of the SLAF output in a GIS interface such as ArcView©, in conjunction with the ancillary attribute database, allow us to see *where* in the reserve the impacts may increase, and one can query these specific locations with regards to property and water source type. Data regarding the proximity to water of the land (i.e. the buffer model) within the polygon can be overlaid visually. The distance to the nearest water source can be recorded for each point and other information, such as water source type, the ability to manipulate supplementation, or other management options can be assigned to each water source point and queried by the user (Figure 9). Perhaps most important is the ease with which these models can be implemented. Although Excel© was used to calculate nearest neighbour distances, all the model functions described can be executed within ArcView© software (ESRI) using included extensions or freely downloadable extensions from the ESRI hosted website (www.esri.com). Using the three frameworks in one system, a database of focal information can be created for each source in addition to providing summary metrics of the reserve-wide water distribution. Demonstrating that the management scenario modelled will create statistically different average metrics is useful, though perhaps not always terribly meaningful. Providing this information in conjunction with a user-friendly database, however, creates a management tool in which management goals can be demonstrated and manipulated.

As the impacts of global warming in combination with effects of the El Nino Southern Oscillation become more apparent in this savanna ecosystem (see Ogutu and Owen-Smith (2003) for details), both the tools to manage, and the tools to understand the effects of management of water sources become essential. The potential for this to be used as a management tool for water sources in a small reserve is apparent. Property owners can be involved in informed decisions about placement of sources, supplementation of water and availability of resources, while managers can quickly and quantitatively assess the potential overall impacts. Combining metrics such as the proportion of reserve area at certain proximity to water and the nearest neighbour distance of water sources with the SLAF can assist management of water sources in a framework that is easy to implement.

Future Goals

This basic GIS tool can also be used in more complex assessment scenarios. Adaptive management models(Riley *et al.*, 2003; Seely *et al.*, 2003) can be linked to decision theory tools (Conroy & Noon, 1996; Westphal *et al.*, 2003) and optimization procedures can be used to attain specific management goals. If the goal is even coverage, or even supply areas for water sources, an equity generation model using optimization procedures such as proposed in Radke and Mu (2000) could be used. Alternately, if water source manipulations are subject to other decision processes, such as creating service heterogeneity, the Teitz and Bart (1967) substitution model can demonstrate potential impact changes and an adaptive management strategy adopted. Finally, our SLAF approach is the prelude to a more sophisticated management approach in which each polygon can receive weightings that reflect both the value of resources within specific polygons or degradation ratings that come for a pisosphere analysis of each water point.

Acknowledgements

Thank you to Colin Rowels, warden of Klaserie Private Nature Reserve for information and data regarding water sources. Thanks also to J.V. Redfern, M.I. Westphal, S.E. Reed and two anonymous reviewers for edits and comments. NSF grant DEB-0090323 to WMG and EPA STAR FP-916382 to SJR supported this research.

Figure 1. Location of KNPR (Klaserie Private Nature Reserve)

Figure 2. Unimodal distribution of temperature and rainfall in KNPR. Temperature data represents the average of daily minimum and maximum temperatures recorded at the Warden's office (1991-2000) by month; error bars represent +1 standard deviation. Rainfall data represents the average of monthly data (1992-2000) recorded at the Warden's office; error bars represent +1 standard deviation. Note the designated seasons according to the distribution shape.

Figure 3. Water source locations and types in the KPNR. Note that water presence in the dry season is represented by filled symbols.

Figure 4a. Buffer model showing distribution of distance to water classes during the KPNR wet season.

Figure 4b. Buffer model showing distribution of distance to water classes during the KPNR dry season.

Figure 5. Voronoi tessellation (Thiessen polygons) generated from a point set.

Figure 6a KPNR wet season Thiessen polygon location-allocation framework illustrated in an ArcView© Screen Shot and a Distribution Chart.

Figure 6b. KPNR dry season Thiessen polygon location-allocation framework illustrated in an ArcView© Screen Shot and a Distribution Chart.

Figure 7a. Thiessen Polygons of KPNR waterholes showing the 7 waterholes identified as having Thiessen Polygons of area greater than 12 km^2

Figure 7b. Distribution of Thiessen polygon areas associated with KPNR dry season water sources. Note the distribution break above 12 km^2 that identifies the water sources used in management scenario II.

Figure 8. Accommodating river curvature in a location-allocation model. Note the sliver polygons that are excluded from the analysis, but approximate the curved response on polygon edges.

Figure 9. User Interface for the GIS Model. Hypothetical query result for a water source shows the user the type of water source, the supply area and property owner.

Table 1. Summary of area and proportions calculated using a buffer framework for dry season, wet season, management scenario I (all artificial water sources are turned on in the dry season), and management scenario II (the three largest Theissen polygons generated in a SLAF are reduced by turning on the nearest artificial water source). The

distance to water is in 1km bands, the area is given in km^2, and the proportion shown is the proportion of the total area in the distance category.

Table 2. Thiessen polygon areas before and after the seven water sources are manipulated in management scenario II.

Figure 1

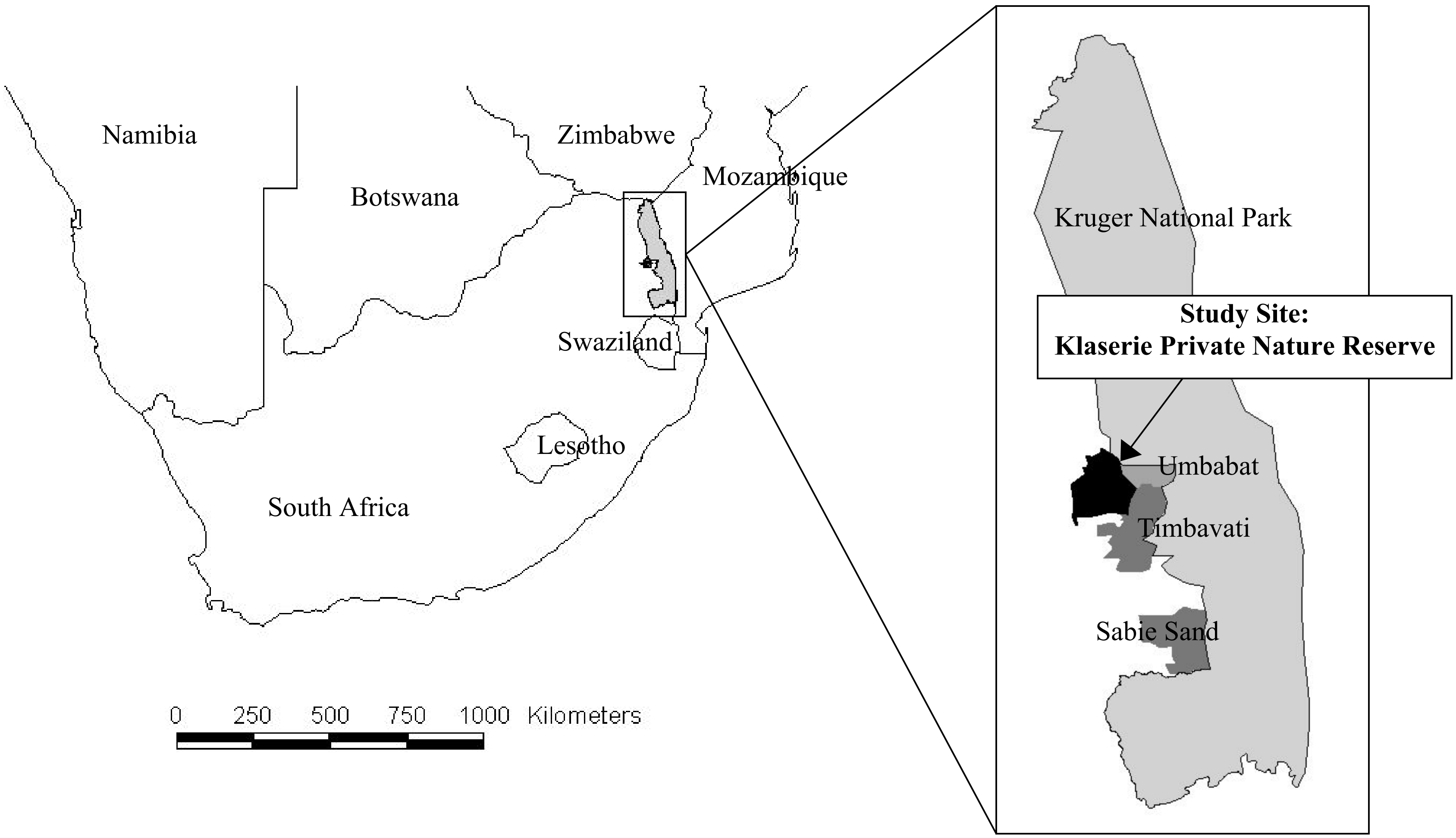
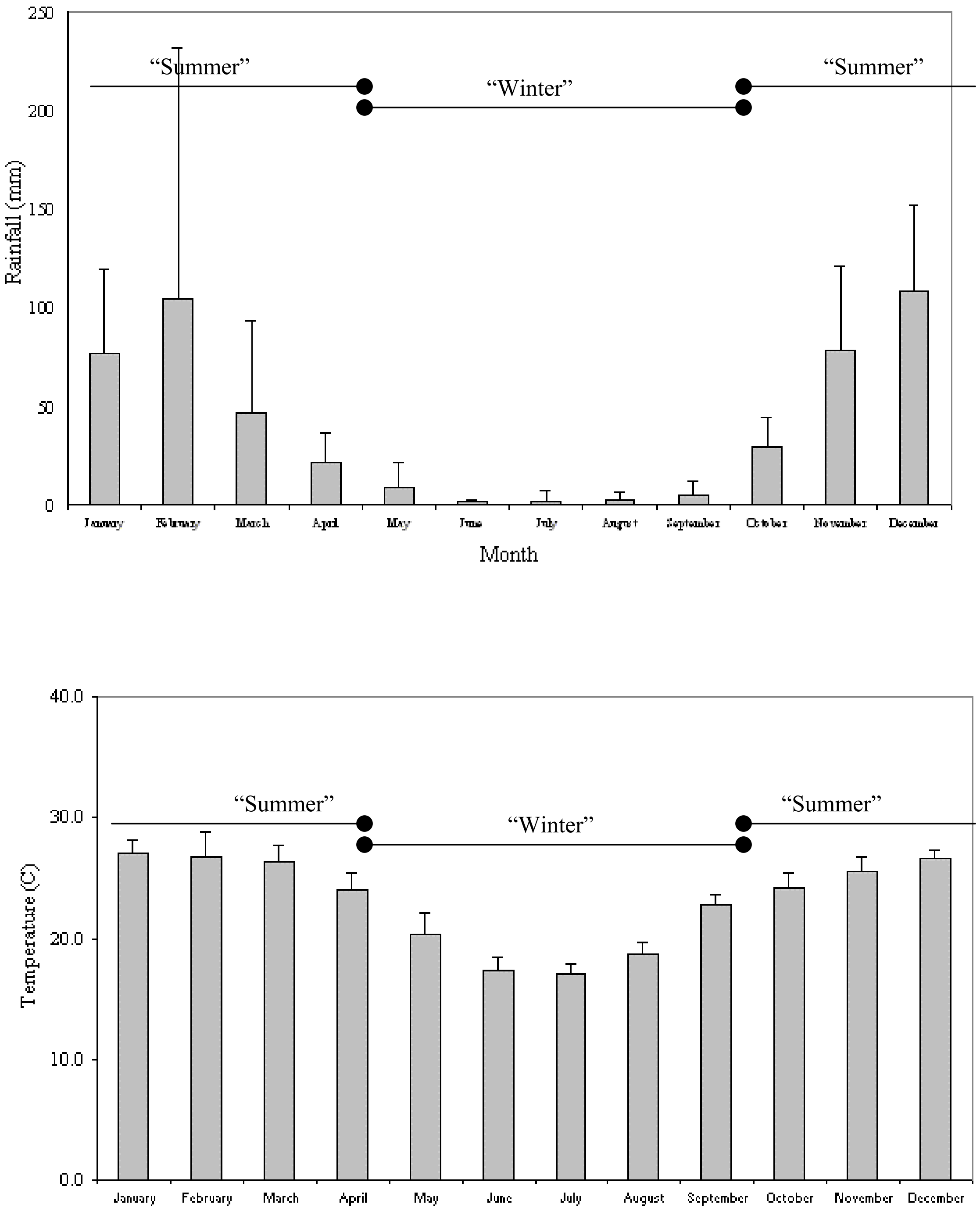

Namibia
Botswana
Zimbabwe
Mozambique
Swaziland
Lesotho
South Africa
0 250 500 750 1000 Kilometers
Kruger National Park
Study Site:
Klaserie Private Nature Reserve
Umbabat
Timbavati
Sabie Sand

Figure 2



250
200
150
100
50
0
Rainfall (mm)
"Summer"
"Winter"
"Summer"
January
February
March
April
May
June
July
August
September
October
November
December
Month
40.0
30.0
20.0
10.0
0.0
Temperature (C)
"Summer"
"Winter"
"Summer"
January
February
March
April
May
June
July
August
September
October
November
December

Figure 3

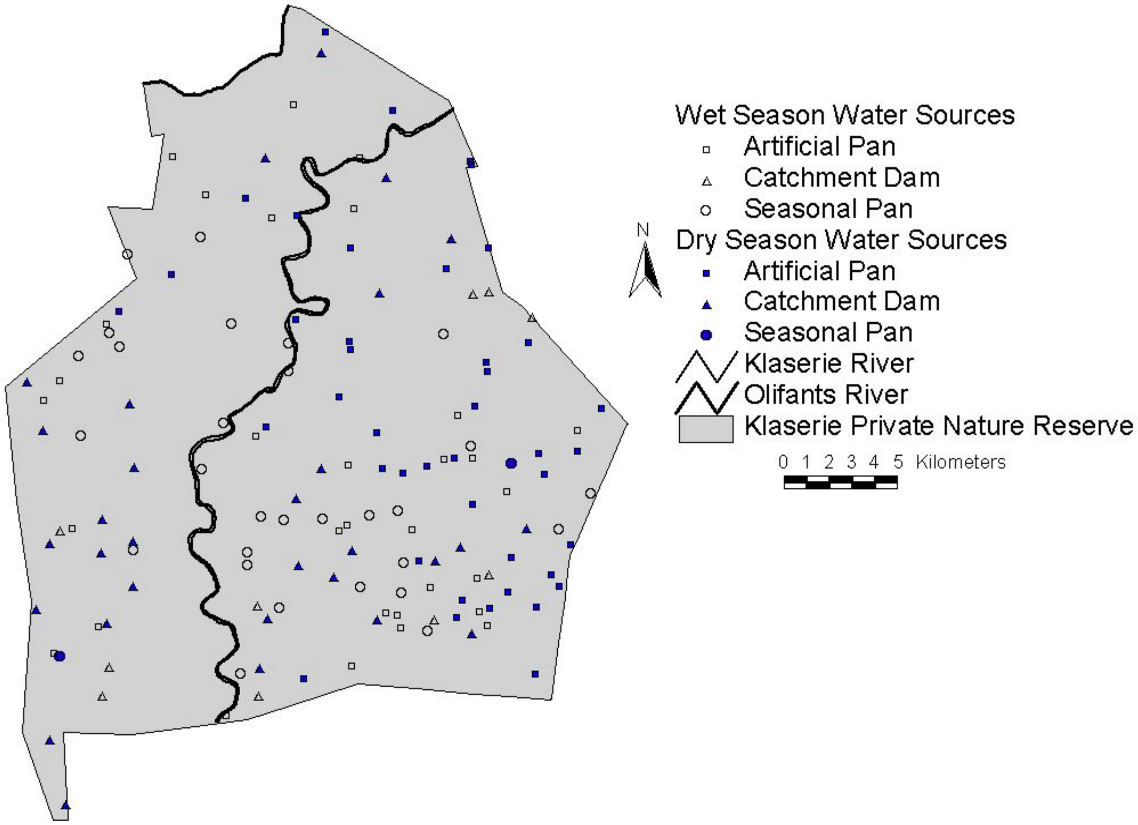

Wet Season Water Sources
Artificial Pan
Catchment Dam
Seasonal Pan
Dry Season Water Sources
Artificial Pan
Catchment Dam
Seasonal Pan
Klaserie River
Olifants River
Klaserie Private Nature Reserve
N
0 1 2 3 4 5 Kilometers

Figure 4a

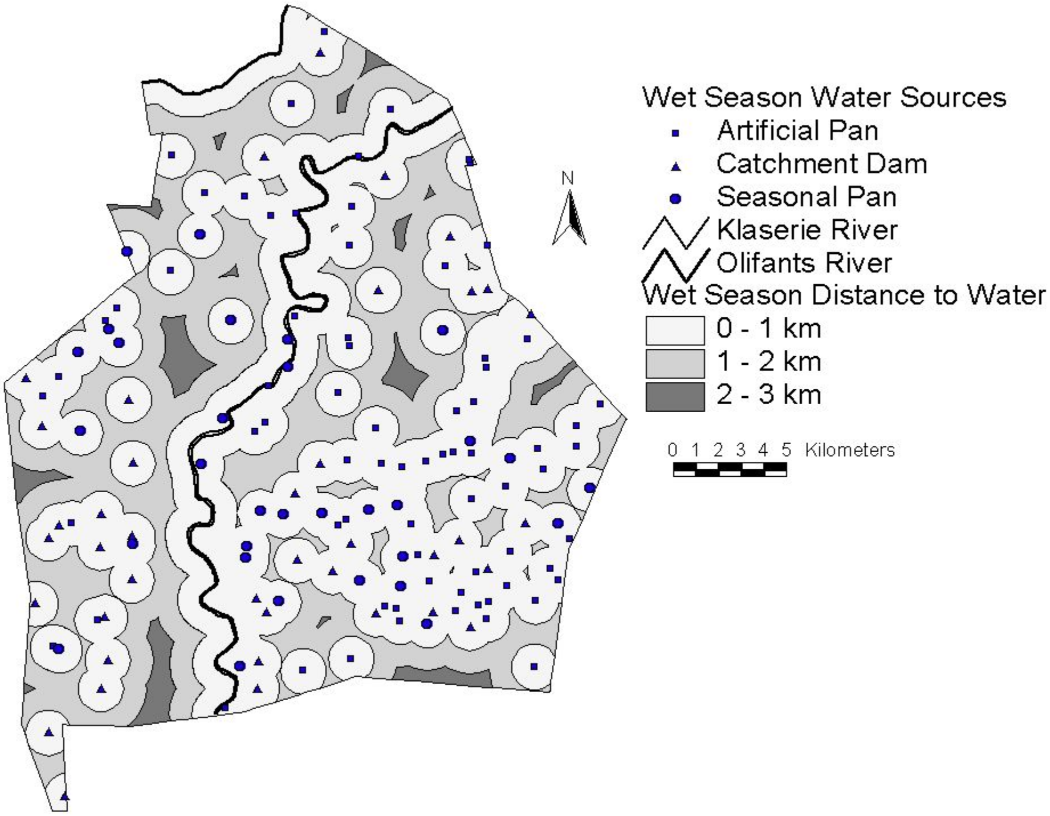

Wet Season Water Sources
Artificial Pan
Catchment Dam
Seasonal Pan
Klaserie River
Olifants River
Wet Season Distance to Water
0 - 1 km
1 - 2 km
2 - 3 km
0 1 2 3 4 5 Kilometers
N

Figure 4b

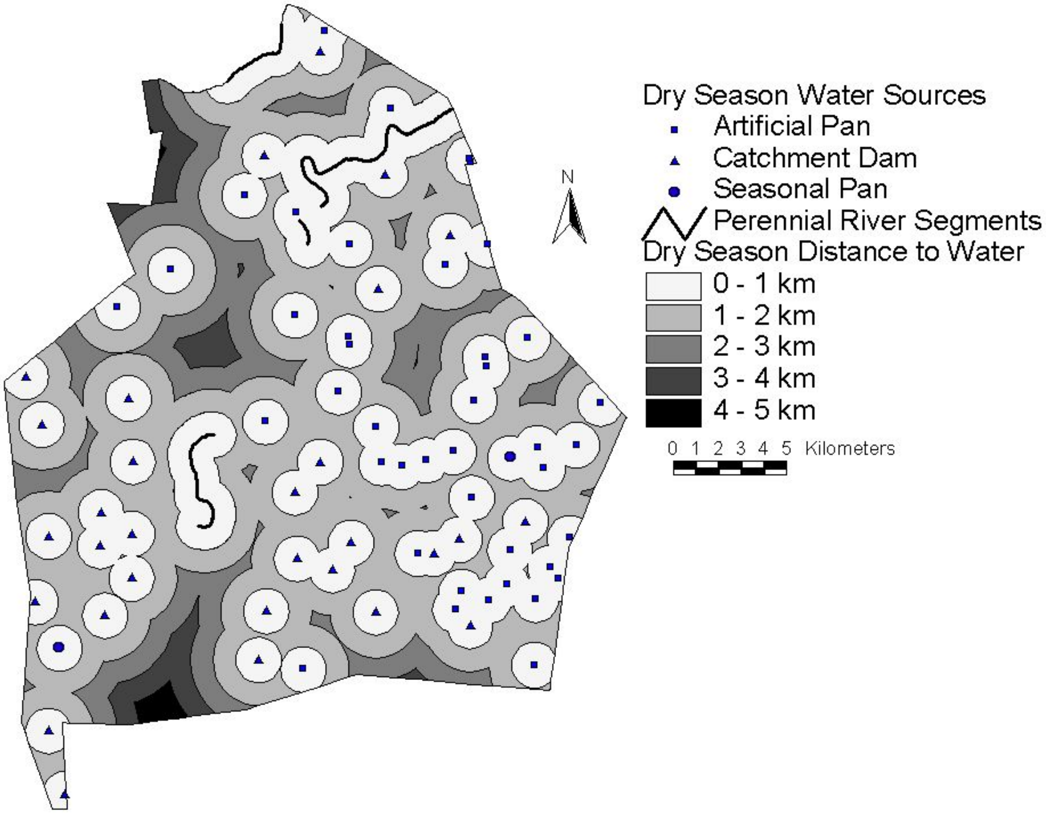

Dry Season Water Sources
Artificial Pan
Catchment Dam
Seasonal Pan
Perennial River Segments
Dry Season Distance to Water
0 - 1 km
1 - 2 km
2 - 3 km
3 - 4 km
4 - 5 km
N
0 1 2 3 4 5 Kilometers

Figure 5

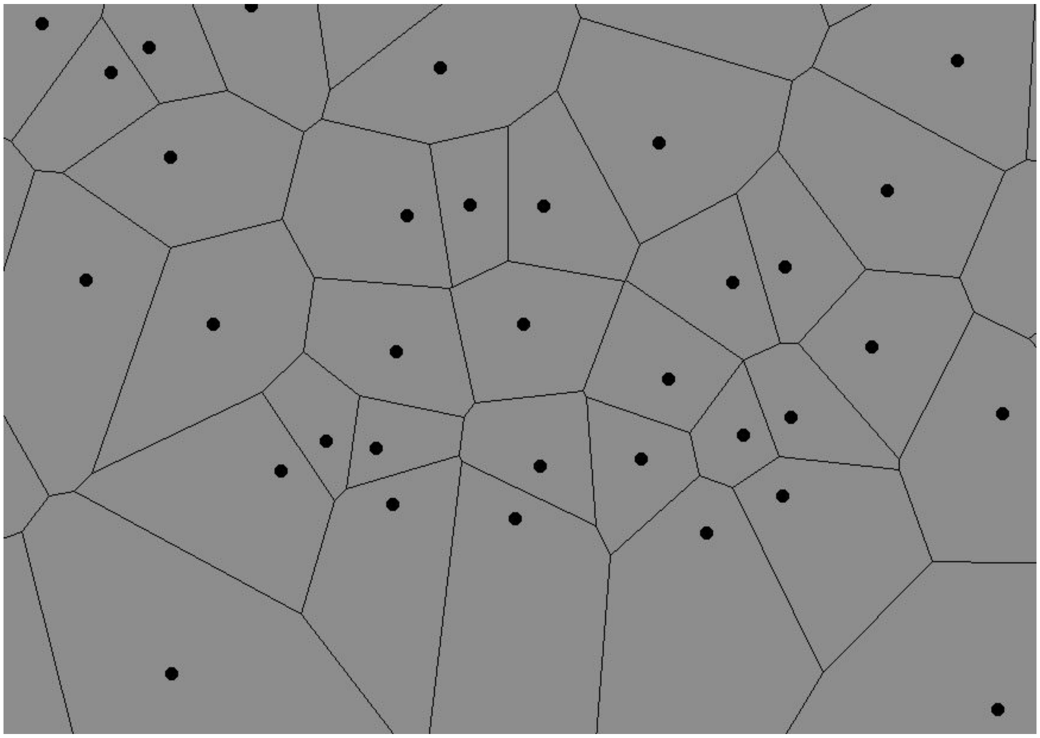
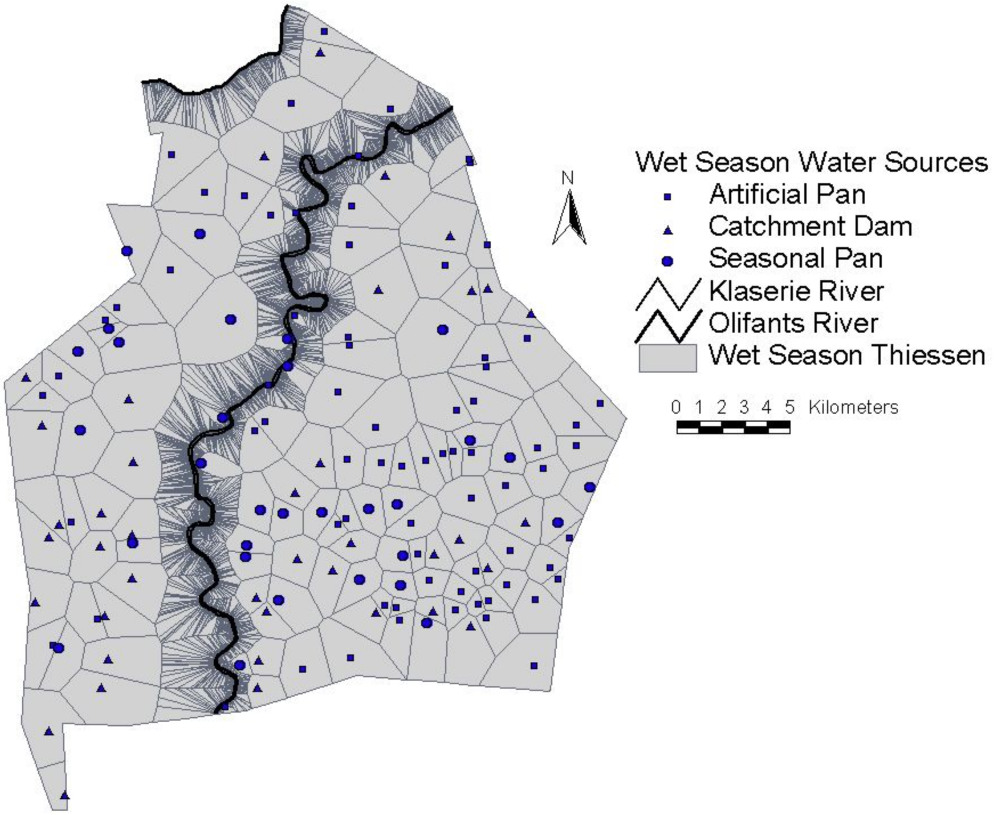


Figure 6a


Wet Season Water Sources
Artificial Pan
Catchment Dam
Seasonal Pan
Klaserie River
Olifants River
Wet Season Thiessen
N
0 1 2 3 4 5 Kilometers

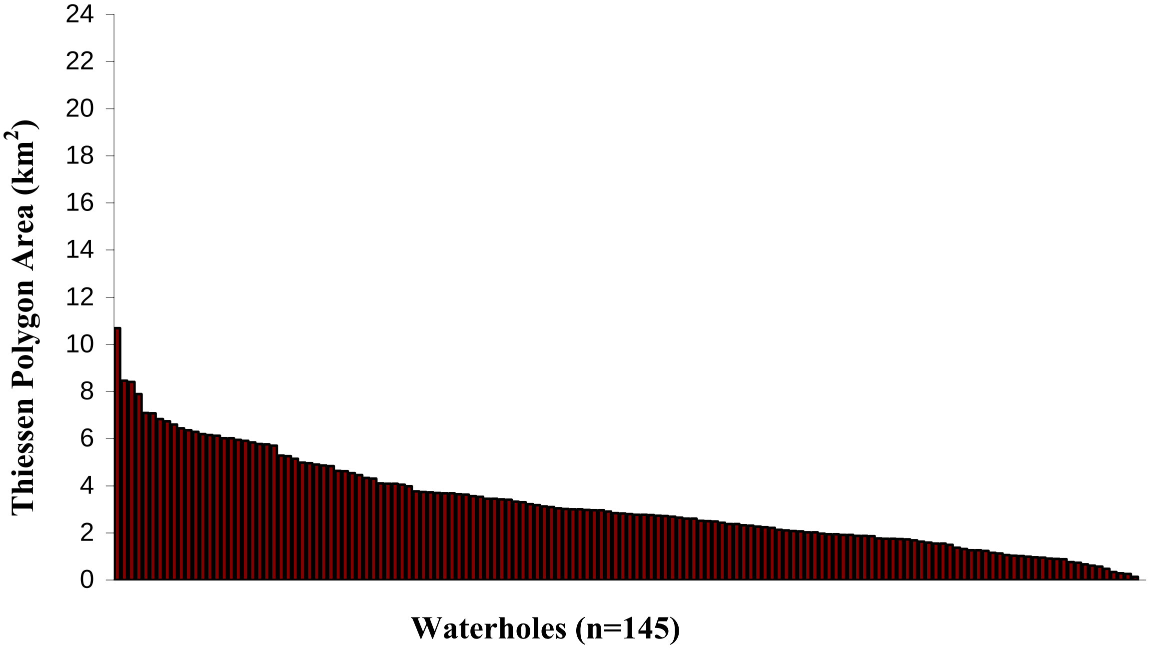
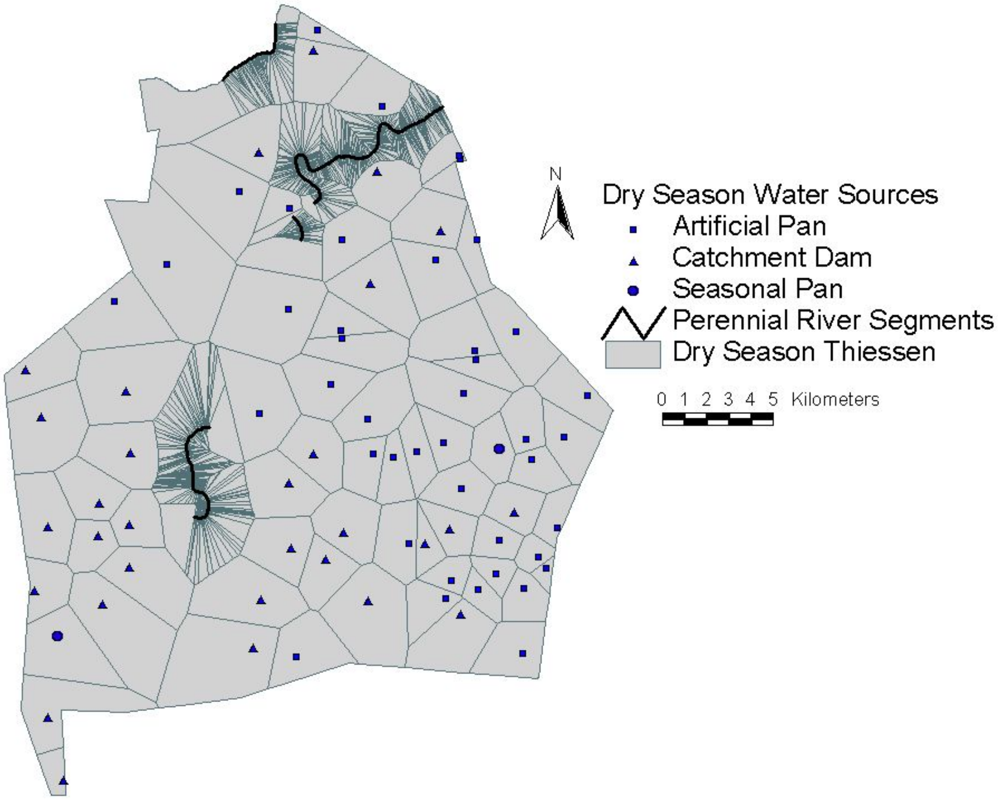

24
22
20
18
16
14
12
10
8
6
4
2
0
Thiessen Polygon Area (km^2)
Waterholes (n=145)

Figure 6b


N
Dry Season Water Sources
Artificial Pan
Catchment Dam
Seasonal Pan
Perennial River Segments
Dry Season Thiessen
0 1 2 3 4 5 Kilometers

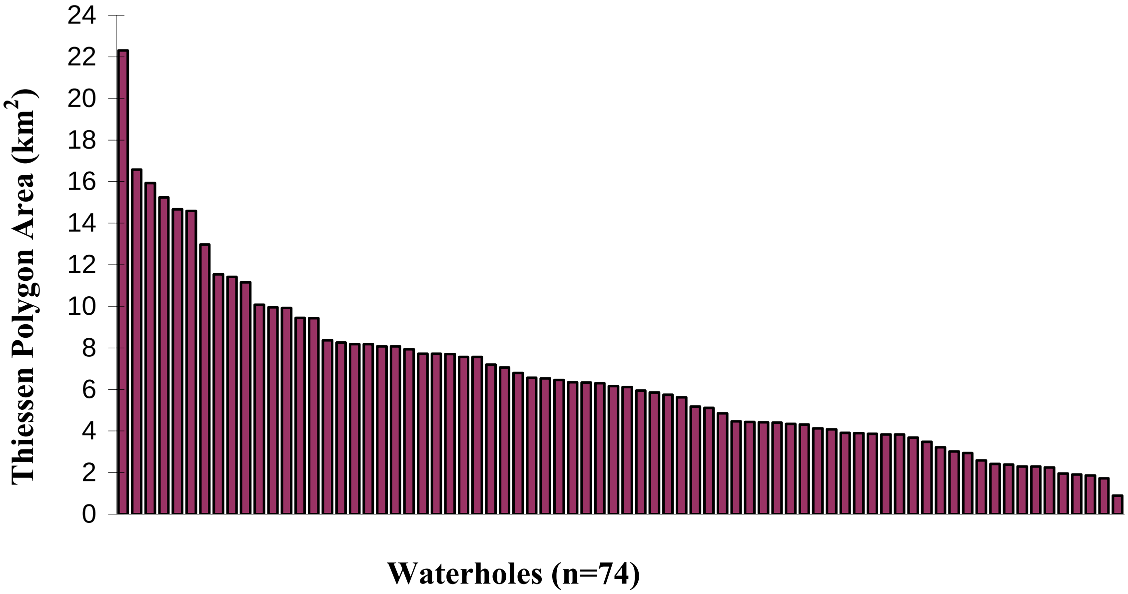
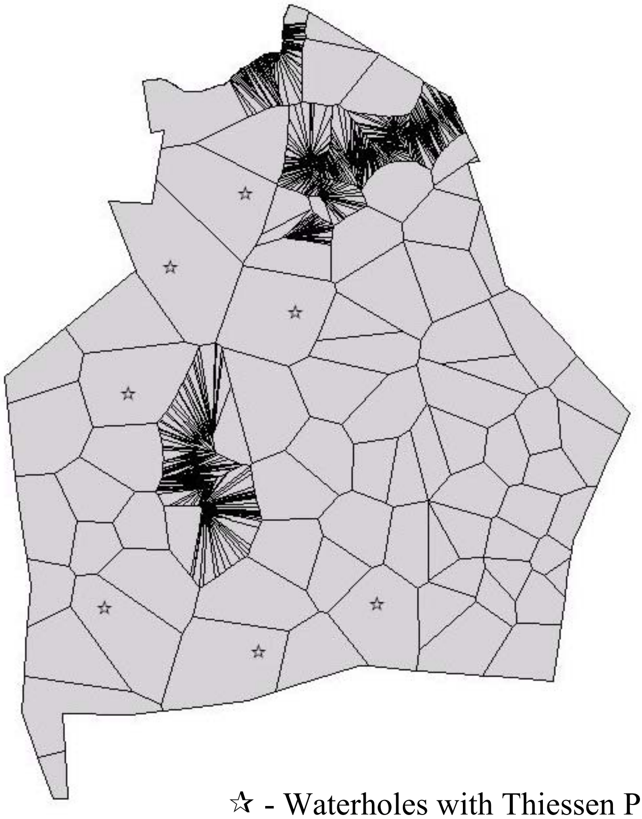

Thiessen Polygon Area (km^2)
24
22
20
18
16
14
12
10
8
6
4
2
0
Waterholes (n=74)

Figure 7a



☆ - Waterholes with Thiessen Polygon areas >12km^2

Figure 7b

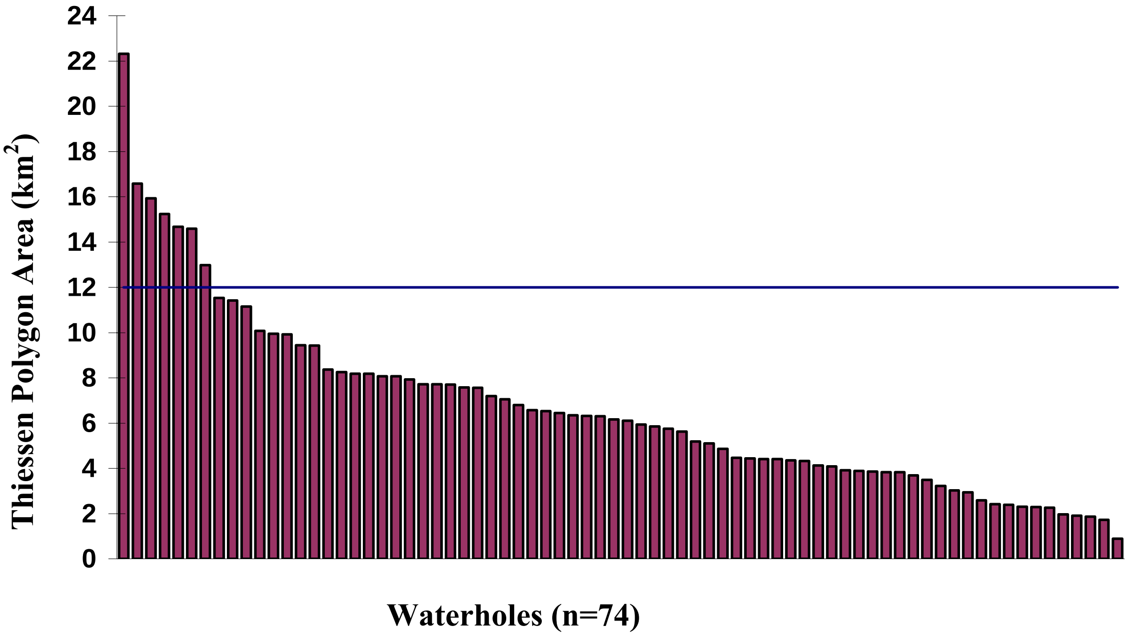


Figure 8

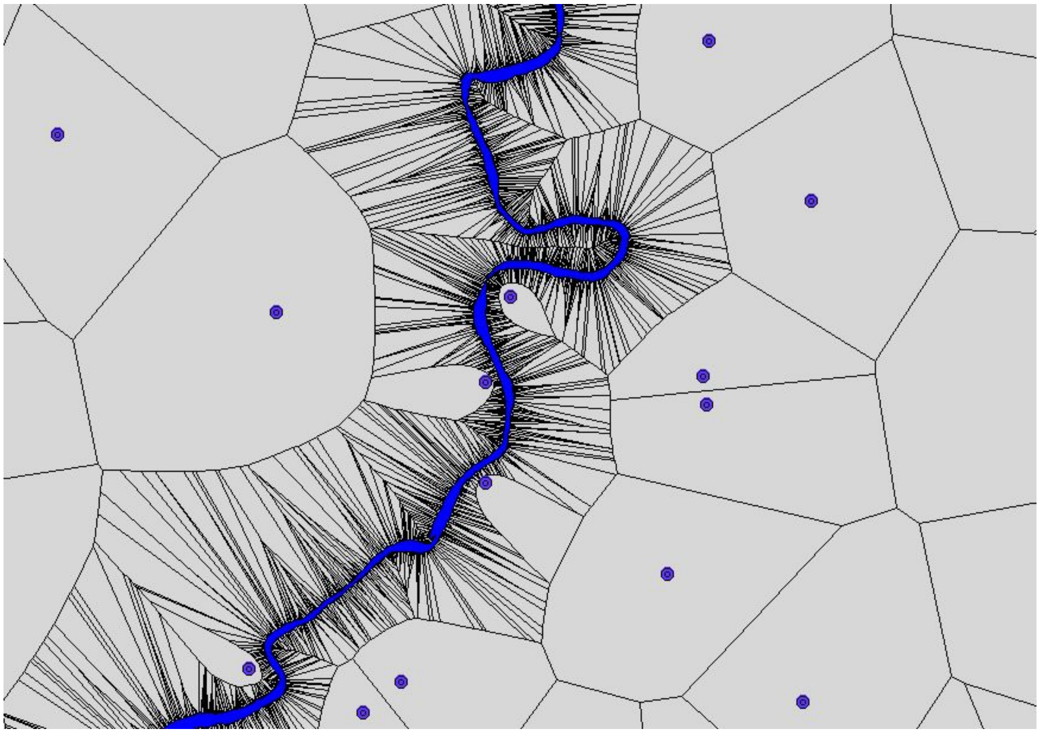
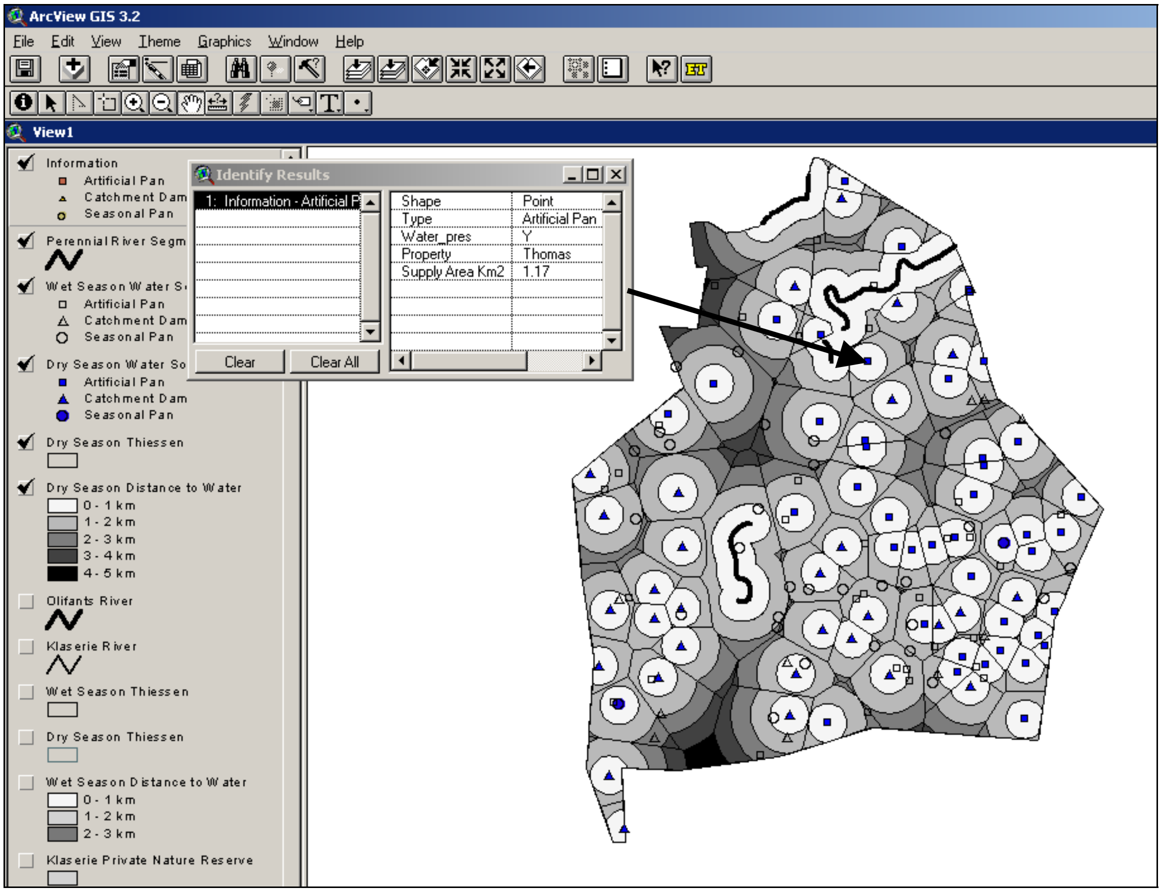


Figure 9



Shape	Point
Type	Artificial Pan
Water_pres	Y
Property	Thomas
Supply Area Km2	1.17

Table 1.

	Dry Season		**Wet Season**		**Management Scenario I**		**Management Scenario II**	
Distance to Water	Area	Proportion	Area	Proportion	Area	Proportion	Area	Proportion
0 - 1	227.27	0.39	363.53	0.63	274.50	0.48	245.47	0.43
1 - 2	252.83	0.44	194.71	0.34	236.83	0.41	266.61	0.46
2 - 3	76.18	0.13	19.59	0.03	56.71	0.10	60.80	0.11
3 - 4	19.00	0.03	na	na	9.79	<0.02	4.99	<<0.01
4 - 5	2.54	<0.01	na	na	na	na	na	na

Table 2

Thiessen Polygon Area[1]		
Before	**After**	**% Change**
22.31	9.81	44
16.58	10.17	61
15.94	11.10	70
15.23	8.55	56
14.67	7.60	52
14.59	12.43	85
12.97	6.25	48

[1] Areas given in km^2

Chapter 3: Ecological determinants of birth timing in African Buffalo (*Syncerus caffer*) in the Klaserie Private Nature Reserve, South Africa.

Abstract

1. In this study, we examine annual variation in the timing of conception and parturition in the African buffalo (*Syncerus caffer*) and its synchrony with resource cues using six years of monthly birth, rainfall, inferred forage protein content, and vegetation greenness data.
2. The monthly birth distribution has its strongest correlation with the inferred forage protein, NDVI, and rainfall levels respectively 11, 12, and 13 months in the past.
3. Since the gestation period of buffalo has been estimated to be around 11 months, the above result suggests that improved protein levels, occurring approximately a month after the first green flush of the wet season is either a trigger for conception or conception has evolved to be synchronous with correlated environmental cues that ensure females enter their period of peak condition around the time of conception.
4. With a gestation period of approximately 340 days, parturition also occurs to take advantage of the period when forage has its highest protein content.
5. Some inter-annual variation in the birth distribution suggests a degree of plasticity in time-of-conception and variation in the number of calves born each year suggest further synchrony at a time scale longer than a single year.

Keywords: Phenology, Global Warming, Breeding Ecology, Birth Synchrony, NDVI

Introduction

In ungulate systems multiple hypotheses are offered as explanations for birth synchrony: (i.) predator swamping through dilution or group protection of young (Estes, 1976; Estes & Estes, 1979; Keech *et al.*, 2000; Sekulic, 1978; Testa, 2002); (ii.) optimization of social development as a cohort within a group (Brown, 1985; Pfeifer, 1985); or (iii.) timing births to coincide with periods of optimal environmental conditions (Rutberg, 1987). These hypotheses are not necessarily mutually exclusive and may act in concert. Here we focus on the third hypothesis, which points to the role of resource availability as driving the timing of parturition in African buffalo (*Syncerus caffer*). Ungulates may time parturition to coincide with the availability of high quality vegetation to support the energetic costs of lactation (Gaillard, Delorme & Jullien, 1993a), to maximize the growth rate of neonates to assist predator avoidance (Clutton-Brock, Guinness & Albon, 1982) and to replenish maternal reserves for future reproduction while conditions are optimal (Gaillard *et al.*, 1993b; Keech *et al.*, 2000). However, we hypothesize that buffalo are rather *conceiving* while conditions are optimal, and due to an almost year-long gestation period, additionally benefit from good conditions at parturition. African buffalo exhibit similar seasonal social ecology to many other ungulates, in which males form groups in the non-breeding season to forage and improve their condition and then compete for mates in the breeding herd during the breeding season (Clutton-Brock *et al.*, 1979; Clutton-Brock *et al.*, 1982). The social ecology of seasonal aggregation depends largely on resource availability; there is a threshold at which the foraging cost of remaining in the group outweighs the reproductive opportunity (Turner, 2003; Turner, Jolles & Owen-Smith, 2005).

In accord with the principles of optimal foraging theory, to maximize reproductive output, an organism should maximize food quality; for herbivores this means maximizing protein intake (Kennish, 1997). For grazers in a semi-arid ecosystem, protein is a limiting nutrient (Bell, 1971; Owen-Smith, 1982; Owen-Smith & Novellie, 1982). While described as a "supreme bulk grazer", and therefore able to consume a high quantity of matter (Owen-Smith *et al.*, 1993), buffalo still lose condition as grass biomass increases, due to a decrease in the protein content of their diet. Prins (1996) found that African buffalo conceive at peak cow condition, and suggested the long gestation of buffalo *additionally* means that calving coincides with good nutritional condition, but a direct connection between maximum protein availability and conception has not previously been made for buffalo. African buffalo have birthing seasons reported to coincide with the wet season (Sinclair, 1977; Turner, 2003) and a gestation period with a mean of around 340 days (i.e. slightly over 11 months; see Sinclair, 1977). Therefore, we hypothesize that buffalo birthing seasons is adapted to coincide with peak protein content in the vegetation 11 months prior. We are able to demonstrate that this hypothesis is supported by the data we present, but insufficient variation and information exists to identify whether rainfall, protein content in forage, or some other environmental cue controls the time of conception. Further, an unusual inter-annual birthing event in our 7 years of data suggests that other factors may play an important role in the annual reproductive success of females including synchrony at the herd level as a response to predation.

In subtropical to tropical systems, periodic droughts will not only shift the onset of wet season, but can result in years of extremely low biomass production and palatability of standing grass. Plasticity of breeding in mammals subject to a highly variable climate may be greater than those that have evolved with reliable resource cues. As buffalo have an extended birthing season, this species may serve as an ideal candidate to test such a proximate response. In a study by Sinclair et al. (2000) and studies by Rutberg (1984, 1987), a dataset was summarized from a period in 1977 (Sinclair, 1977) in which 49 birth events were recorded. With a larger sample size of 385 births from a period spanning 1996-2001, we can explore the potential for a response to annual variations in ecological resource cues.

Methods

Study Site

The Klaserie Private Nature Reserve (KPNR) is located in the Limpopo Province of South Africa, bordering Kruger National Park on its western boundary (24º3-22' S, 31º2-19' E; 303-535m a.s.l.; 57,800ha) (Fig. 1). The main geological substrate is granitic gneiss, part of the extensive granalitic system underlying most of the country. The climate follows a subtropical savanna pattern: both annual temperature and rainfall follow a unimodal distribution (Ryan *et al.*, 2005). mean annual rainfall for this study period is 574mm. We define two main seasons based on rainfall and temperature: a hot wet "summer" season from October to March and a cool dry "winter" season from April to September. As this system is predicated upon the rainfall regime, our years are from October to October, with the year marked passing though the calendar year for January. KPNR contains the range of three main herds of buffalo. The range and habitat selection of these buffalo are summarized in a prior study (Ryan et al., 2005).

Birth Data

A dataset containing 488 calving events for one herd were recorded by one of us (CUK) between 1994 and 2001. This set was cropped to 385 births recorded between 1996-2001 to match the data for the resource availability and quality.

Rainfall Data

Mean monthly rainfall was taken from a maximum of seven stations throughout KPNR. These data were transcribed from logbooks into Excel© and monthly averages calculated to create a monthly distribution of rainfall through the study period.

Remotely Sensed Vegetation Data

Post-processed 1 km^2 NDVI (Normalized Differential Vegetation Index) data from NOAA's (National Oceanographic and Atmospheric Association) AVHRR (Advanced Very High Resolution Radiometer) sensor aboard weather satellites were made available to this project through the Agricultural Research Council, Institute for Soil, Climate and Water (ARC-ISCW) for the calendar years 1995-2001. A full description of the processing of these data prior to acquisition by this project can be found in Wessels et al. (2004). We use these data as a relative scale measure of the change in vegetation quality in the reserve, not as absolute values. These data were imported into ARC/INFO 8.0 (Environmental Systems Research Institute, 2000a) and ArcGIS 8.3 (Environmental Systems Research Institute, 2000b), using ArcMap for visual assessment of available images. For viable images, 0-3 images per month were used to create monthly average grids of data clipped to the KPNR. These monthly average values (on a scale of 0-255) were averaged across the reserve to derive a monthly mean value in a vegetation quality distribution.

Distribution of Protein Content

Ryan et al. (in prep) have established a strong relationship between the mean fecal nitrogen content, *N(t)*, of buffalo in month t and NDVI in month t-1,using samples and data from the neighboring Satara region of Kruger National Park, is part of the same ecosystem as KPNR . This relationship is (R^2=0.90, p<0.001):

$$N(t) = 0.82 + 0.005 * \text{NDVI}\ (t\text{-}1)$$

We refer to the fecal nitrogen estimate, which is an index of protein content, simply as protein from here on.

Annual Evenness of Births and Rainfall

To quantify the evenness of births and rainfall each year, we applied the method of Bronikowski & Webb (1996), which has been used in similar studies comparing ungulate behavioral responses to rainfall variability (Brashares & Arcese, 2002; Sinclair, Mduma & Arcese, 2000). The Evenness Index J' is given as

$$J_t^q = \frac{1}{\log 12}\sum_{i=1}^{12} p_i^q(t)\log p_i^q(t) \qquad \text{t=1996,\ldots,2001,}\quad q{=}b \text{ (births) and } r \text{ (rainfall)}$$

where $p_i^q(t)$ is the proportion of births (q=b) or rainfall (q=r) in the i^{th} month of the t^{th} year. (Note the year t=1996 begins in October 1995 and ends in 1996, and so on). Evenness ranges from zero (all births or rain occur in one month) to one (same levels each month).

Birth Timing

To find the peak of the birth distribution, monthly average proportions of births in the years 1996-2001 were compared using an ANOVA with a post-hoc Tukey-Kramer's HSD test for means. To test the hypothesis that the resource distribution predicts the timing of births, we compared the monthly distributions of rainfall and vegetation greenness to the birth distributions in both the current and proceeding year throughout the entire 6-year period. We cross-correlated the resource cue (rainfall or greenness) against the births by shifting the birth distribution one month at a time over 15 months of lag. To examine annual trends, we compared the temporal variability of the resource in the previous wet season to the current birth distribution. All statistics were run in SAS JMP© 4.04 (SAS, 1989-2002).

Results

Birth and Resource Distributions

The distributions of births, rainfall and NDVI values across the study period are shown in Figure 2. The average evenness, J_t^b, for births over the study period was 0.60 ± 0.06 (mean ± SE); for rainfall it was 0.72 ± 0.03 (Table 1). A Welch modified one-way ANOVA showed that the distribution of J_t^b values for births was not significantly different from that the distributions of J_t^r for rainfall (F_{ratio}=2.87, p=0.133).

Phenology:

We found that across this study period, January is the peak month of birthing as shown in Figure 3. An ANOVA with post-hoc means comparisons showed that the mean proportion of births occurring in this month is significantly higher than all other months except March (F=14.66, DF=11, p<0.0001; Tukey-Kramer HSD, α = 0.05). Cross-correlations of the birth distribution from 1996 to 2001 against monthly rainfall, greenness (NDVI) and protein for the same interval are shown in Figure 4. In this graph, the x-axis represents the number of months the resource cue in question precedes the individualized birth event. Correlations lost significance (and meaning) at a 14-month lag. The highest correlation (Pearson's r = 0.59, p<0.0001) of any resource cue with births is at a 12-month lag in the greenness index (1 year prior). For monthly rainfall, the highest correlation occurs at a 13-month lag (Pearson's r = 0.55, p<0.05). The positive correlations occur for all resource cues at a 0-2 (and 3, for rainfall) months lag, and between 10 and 13 (14 for rainfall), corresponding to the current and prior wet season months. These results support the idea that conception is tied to resources, but that the extended gestation implies that the same high quality conditions are realized at parturition a mean of 340 days later (Sinclair 1977).

Annual variability:

In years in which rainfall is low or has a very late onset, grass production and availability will also be low and/or late. As buffalo have evolved such that breeding season occurs during the wet season, years in which conception cues are not strong are likely to lead to less synchronized or disrupted birth patterns in the following year. The year 2000 had the highest rainfall of the entire study period. The birth distribution in 2001 had an early onset, with births occurring as early as November (Figure 2), which is unique in the dataset but anecdotal given that this could have happened by chance.

Although controls were not implemented in the original design to assess the number of calves per mature female each year, due to the fact that the Klaserie population is fluid, with individuals moving between this private reserve and the Kruger National Park at will, we noticed fewer births in 1999 and 2000 than in the other years. In fact, in 2000 there were only 24 births, of which 17 occurred in January alone; the entire birthing season was December-February. This dearth follows on from the lowest rainfall year in the study period, 1998 (Figure 2), suggesting a possible long-term maternal effect on reproductive success. The NDVI values in 1998 are lower than those in the following years, but similar to those in 1997 (Figure 5), suggesting that there may have been a two-year stretch of low-quality forage in the growing season; a 'mini drought' in the dataset.

The high of 87 births observed in 1998 turned out to be extremely anomalous for our data set. Specifically, an examination of the breeding success of all known females with complete records from 1994-2001—that is, 28 of 99 individuals—reveals that, in 1998, 89% reproduced, compared to a mean proportion of 43% for the seven-year period (Table 2). The data in Table 2 were bootstrapped 10,000 times by rearranging each of the rows at random (i.e. each females reproductive output for the 7 year period was held constant, but the years in which they had their calves was randomized). In none of these runs did 23 or more females reproduce at the same time in any of the seven years, and in only one did 22 females reproduce at the same time (the mode of this distribution is 12). This implies that the probability of observing 25 or more by chance of the 28 individuals reproducing is less than 0.0001.

Discussion

In savanna ecosystems the seasonality or variation of resource availability is largely predicated on rainfall. A cursory examination of figure 2 shows the close relationship between rainfall and vegetation greenness in this system. Vegetation greenness, measured as NDVI, lags the rainfall by one month; it is therefore unsurprising that the synchrony of the birth season is similar to that of rainfall. We found moderate values of birth synchrony for this period (J_t^b=0.60 ± 0.06, *mean* ± *S.E.*), slightly more synchronous than the value found by Sinclair et al. (2000) of 0.695. By comparison, the rainfall in our system was also more uneven, J_t^r = 0.72 ± 0.03 (*mean* ± *S.E.*), versus 0.935 in the western Serengeti (Sinclair et al., 2000)

The proposed mechanisms for birthing synchrony in ungulates (i.e. timing to good conditions for lactation, replenishing maternal reserves and providing high quality food for offspring) may all contribute to the synchrony and timing of births in this system. In a comparison of a suite of African ungulate species, Sinclair et al. (2000) posited that birthing synchrony in buffalo evolved as predator satiation. This echoed Rutberg (1984; 1987), who asserted that buffalo calves are precocious "followers" rather than "hiders", part of large groups in open habitat, promoting defense against predators. However, the observed length of the buffalo birthing season, both in this study and others (Prins, 1996; Sinclair, 1977; Sinclair *et al.*, 2000) is far longer than that of other "follower" species, corresponding to Rutberg's (1987) alternate hypothesis that the climate enables a longer birthing season, with peaks occurring at times of good nutritional condition. Moreover, Sinclair (1977) noted that buffalo calves tend to hide with their mothers, away from the herd, after birth. Thus it is more likely that the synchrony of buffalo parturition is driven by resource availability, meaning that we see a group of individual physiological responses, rather than selection cuing on seasonality alone. Moreover, as buffalo have individual behavioral adaptations to predation (hiding young calves) for protection of neonates, predator swamping is an unlikely explanation for birth peaks. We found that the availability and seasonality of resources around conception shape the birth distribution for this population. Due to such a long gestation period of over 11 months, buffalo can combine both income and capital strategies of breeding. The condition of the mother at both conception and during weaning will be maximized at vegetation quality peaks.

To examine the role of resource cues in conception timing, we correlated resource distributions with birth distribution (Figure 4). The highest correlation coefficient was taken as the strongest signal of a resource cue. This comparison included years in which the phenology both of births and resources varied both month to month and in relative frequency. Over the 6 years, births occurred in all months except September and October. The NDVI distribution is relatively even and does not change significantly for three months around its peak during the year, so we were cautious in making conclusive statements as to its role in cueing conception by specific month. However, we find that in our correlations with all resource cues, both in current and previous years, the strongest correlation corresponds to a one-year lag with greenness. This month represents the time at which buffalo breed, thus we infer that they come into breeding status when the forage condition is optimal. Peak rainfall lags the greenest month of the year by a month, meaning that we see a birth peak month followed by a rainfall peak month. This was also found in buffalo in Hluhluwe-Umfolozi Park, to the south of Klaserie (Turner, 2003), and is in fact the pattern seen in Sinclair et al.'s (2000) study in the Serengeti. In their study "green biomass" was predicted by rainfall, and births lagged peak biomass by one month. We suggest that rather than parturition *nearly* corresponding to biomass, the Serengeti buffalo actually conceived at the Serengeti "green biomass" peak, and parturition was observed 11 months later. With a longer period over which to examine this relationship, it is possible to distinguish between prior year conception and conditions at parturition. However, Sinclair et al. (2000) also found that the birthing peak for buffalo was around five months out of phase with the peak protein content of their forage. This is a very different pattern of protein availability than we find in our system, and we therefore do not find the corresponding lag. We posit that buffalo in our more subtropical system are reaching conception peak while the protein content of available grasses is highest, which coincides with the peak growing season.

While we infer from the consistency of the patterns in this and other studies that buffalo breeding ecology is strongly tied to resource seasonality, this is not a temporally static relationship. For example, the birth distribution in 2001 had an early onset, with births occurring as early as November, which is unique in the dataset. This indicates that buffalo might have come into peak condition earlier in 2000 than would be expected from average long-term trends, suggesting that buffalo respond to resource cues on the short term, and are not wholly constrained by the evolved timing of their breeding habits.

It is important not to discredit mechanisms other than maternal response that may be at play in this system. Our anomalous result of a highly synchronized birth year (1998) from an inter-annual perspective suggests that other factors might be at play. The population will likely reflect some abiotic effects that affect demography, even at this time scale. The lack of resources due to low rainfall years may drive prime breeding females either into non-reproductive condition, or cause them to leave the population, perhaps migrating to better habitat. This would likely result in fewer offspring in following years in this dataset, regardless of phenological resource pattern. In addition, it is not just breeding females that rely on the resources and resource cues. In a study on buffalo in Hluhluwe-Umfolozi, Turner (2005) suggests that males who join breeding herds face an energetic trade-off between obtaining sufficient food and engaging in reproductive activity. As the grass growing season tapers and the quality of food is reduced, it is likely that both sexes must face this trade-off. A habitat selection study (Ryan, Knechtel & Getz, 2006) showed that these buffalo range further in the dry season, most likely in search of forage that is still green. The combination of spending more time searching and more time ruminating would likely curtail reproductive activities after the wet season.

Our findings of the close relationship between buffalo breeding ecology and seasonal availability of resources have ramifications for breeding during periods of extreme conditions. Whereas it appears that buffalo can adjust their birthing regime in response to the onset of good forage conditions, the limits of this plasticity may be tested under future predicted climate changes. For instance, if as suggested global warming is altering rainfall regimes, either by increased dryness overall, or by creating more erratic and pronounced drought cycles, the pattern of resource availability will become skewed. The rainfall regime of this area is subject to oscillations due to the El Nino Southern Oscillation (ENSO) and temperature anomalies in the Atlantic and Indian Oceans (Ogutu *et al.*, 2003); these create an 18 year interdecadal oscillation, which may have overlaid upon it the effects of global warming. In the short-term, these disruptions may lead to lower rates of conception and ill-defined breeding seasons as females will not attain sufficient condition to be receptive to males. In the longer term, if a social system response is not elicited, and buffalo cannot adapt to dramatic climatic shifts, this may lead to lowered birthrates and could influence juvenile mortality via increasing predation risk due to asynchronous births and a lack of predator swamping. Current literature addressing the effects of global warming in ecological contexts include evidence of shifts in plant phenology (Post & Stenseth, 1999), which in turn affects coevolved herbivore population dynamics in the Northern (Coulson *et al.*, 1999; Forchhammer *et al.*, 2001; Langvatn *et al.*, 2004; Post *et al.*, 2001) and Southern hemispheres (Ogutu *et al.*, 2003). The mechanism by which climate change can affect population dynamics is most likely through the increased extremes of large scale climate phenomena driven by oscillations such as the North Atlantic Oscillation (NAO) and the El Nino Southern Oscillation (ENSO) (Ogutu *et al.*, 2003; Post *et al.*, 1999).

A study of Alaskan moose with highly synchronized parturition suggested that they have adapted timing and synchrony of births to long-term patterns of climate and could not adjust to proximate resource changes (Bowyer, Van Ballenberghe & Kie, 1998). The authors concluded that this lack of proximate adjustment in the face of global warming could compromise the long-term viability of the population. It has been argued that greater birthing synchrony and a shorter breeding season will occur in temperate or subarctic climates (Gaillard *et al.*, 1993b; Gaillard, Festa-Bianchet & Yoccoz, 1998; Rubenstein & Wikelski, 2003; Rutberg, 1987), whereas tropical and subtropical habitats enable longer birthing periods (Rutberg, 1987), except where predation provides a strong selective force (Estes, 1976). Under conditions of global warming, this may mean that buffalo, with their extended birth season and a demonstrated capacity to adjust to the onset of seasonal forage availability will not suffer such dramatic impacts as their northern counterparts. However, at the extremes of such resource shifts, the signals of disruption that we noticed in 2000 after a low rainfall year, and the early onset of births in 2001 could become more pronounced and ultimately affect population viability.

Despite the luxury of more data than in prior studies of buffalo birth seasonality, this still represents a short period for this system. The study period reflects the wetter second half of a interdecadal rain cycle (Ogutu *et al.*, 2003), yet has considerable annual variation in rainfall within the study period. This may create noise in the study system from which it is hard to untangle behavioral breeding responses. In addition, buffalo may not breed in every year, and at this low sample size, this may confound some of the findings. In low rainfall years, cows may build condition on any and all available biomass and then conceive towards the end of the breeding season. This may in turn cause disruption in consecutive years, due to having dependent yearling calves during the next mating opportunity. Another possibility is that some cows may ‘skip’ a year in a bad year and be in high condition very early in the following mating season. Evidence for this strategy has been observed by CUK, wherein mothers will calve for two consecutive years, followed by a non-calving year (*unpublished data*).

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Tables and Figures

Table 1 Number of births, yearly rainfall and Evenness indices (J_t^q) measuring synchrony for births and rainfall each year.

Table 2 A description of the proportion of females giving birth each year in a record of 28 females from 1994-2001. Records are binary results of observations of mothers calving in the given year (CUK), column totals of births and the proportion of mothers calving (denoted Calving) are given. The age estimate for each mother at the end of the study period, in years is also given for reference.

Figure 1 The study site showing Klaserie Private Nature Reserve

Figure 2 Distribution of Births, Rainfall (mm) (top panel) and NDVI (bottom panel) across the study period, by month.

Figure 3 Average monthly proportion of births (mean ± SE) from 1996-2001.

Figure 4 Cross-correlations of the birth distribution against the Rainfall (hatched), NDVI (dark grey) and Protein (light grey) distribution for the period 1996-2001. The X-axis gives the lag, or months prior in which the resource cues occur. Significance is denoted with asterisks: * denotes $p<0.05$, ** denotes $p<0.0001$.

Table 1

Year	Births	J_t^b	Rainfall (mm)	J_t^r
1996	65	0.58	739.43	0.76
1997	64	0.70	401.33	0.82
1998	87	0.66	199.29	0.64
1999	59	0.63	680.29	0.77
2000	24	0.29	870.07	0.69
2001	86	0.72	556.03	0.63
Mean ± S.E.	385	0.60 ± 0.06	574.41 ± 99.50	0.72 ± 0.03

Table 2

Mother ID	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	***Age in 2002***	**# Calves**
Anita	0	1	1	0	1	0	1	16-18	4
Anka	0	0	0	0	1	0	0	12	1
Anoa	0	0	0	0	1	1	0	10	2
Arkadia	0	1	0	0	1	0	1	16-18	3
Aurora	1	0	0	0	1	1	1	16-18	4
Bjelaja	0	0	0	1	1	0	1	12	3
Claudia	1	1	1	0	1	0	0	20	4
Diana	1	0	0	1	1	0	1	18-20	4
Dreipunkt	0	1	1	0	1	0	0	20	3
Gabane	0	1	0	1	1	1	0	16	4
Gabikro	0	0	0	0	0	0	1	12-14	1
Hella	0	0	1	0	1	1	1	14-16	4
Horni	0	0	1	0	1	0	0	12-14	2
Jambila	0	0	1	0	1	0	1	16-18	3
Katanga	0	1	0	0	0	1	1	20+	3
Liberia	0	0	1	0	1	0	0	14-16	2
Mandy	1	0	1	1	1	0	0	20	4
Messina	1	1	0	0	0	0	0	14-16	2
Mitumi	1	0	1	0	1	0	0	18-20	3
Quadri	1	0	1	0	1	0	0	14-16	3
Quiba	0	0	1	1	1	0	0	18-20	3
Rodentia	1	0	1	0	1	0	1	16	4
Ruanda	1	0	1	0	1	0	0	14-16	3
Sambia	1	0	1	1	1	0	0	20-22	4
Simone	1	0	1	0	1	0	0	14-16	3
Tailcut I	0	0	1	0	1	1	0	12-14	3
Weike	1	1	0	0	1	0	0	14-16	3
Zianka	1	0	0	0	1	0	0	18-20	2
Total Calves	13	8	16	6	25	6	10		84
Calving	0.46	0.29	0.57	0.21	0.89	0.21	0.36		

Figure 1

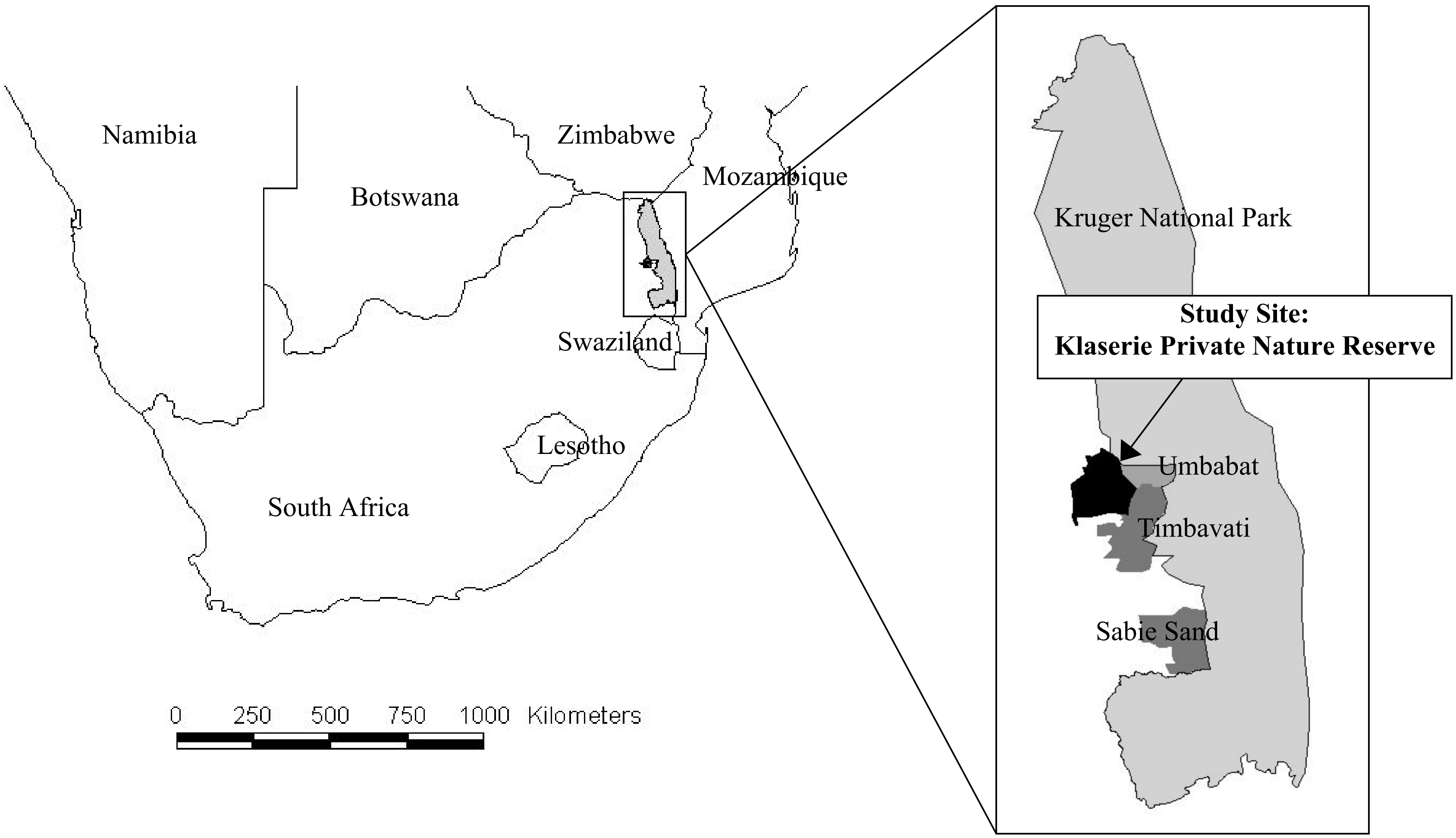
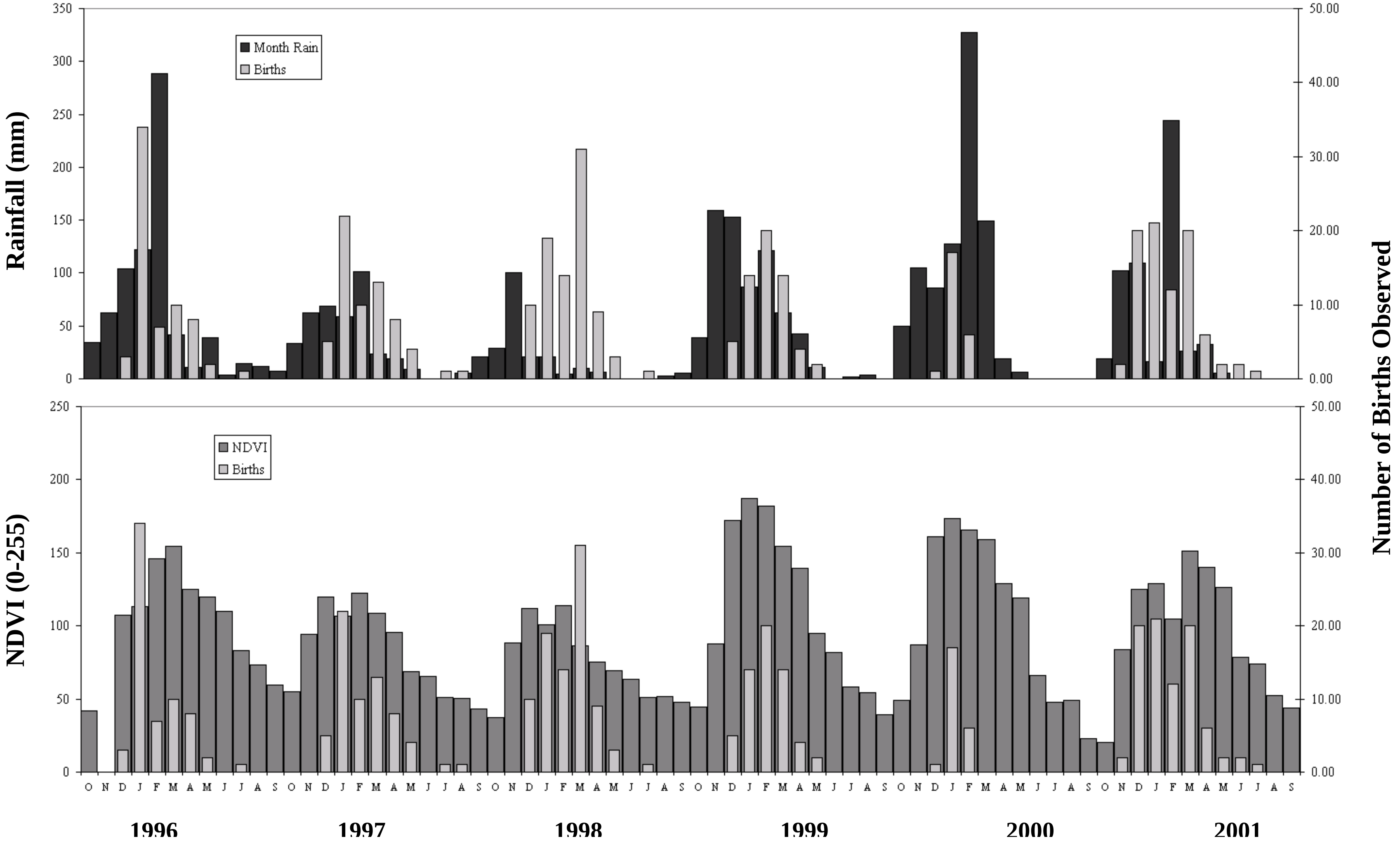

Namibia
Botswana
Zimbabwe
Mozambique
Swaziland
Lesotho
South Africa
0 250 500 750 1000 Kilometers
Kruger National Park
Study Site:
Klaserie Private Nature Reserve
Umbabat
Timbavati
Sabie Sand

Figure 2



Rainfall (mm)
350
300
250
200
150
100
50
0
Month Rain
Births
50.00
40.00
30.00
20.00
10.00
0.00
Number of Births Observed
NDVI (0-255)
250
200
150
100
50
0
NDVI
Births
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1996
1997
1998
1999
2000
2001

Figure 3

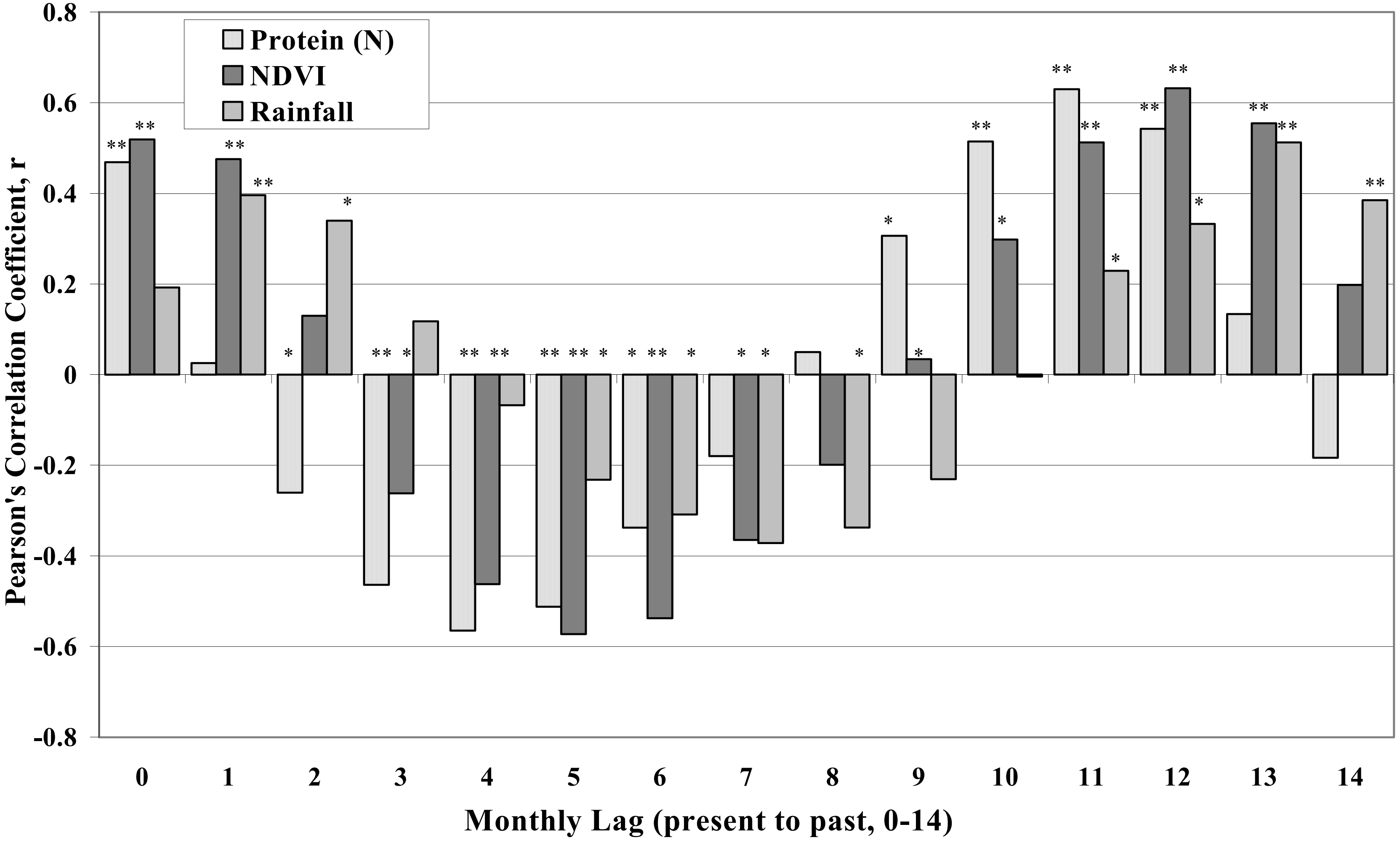
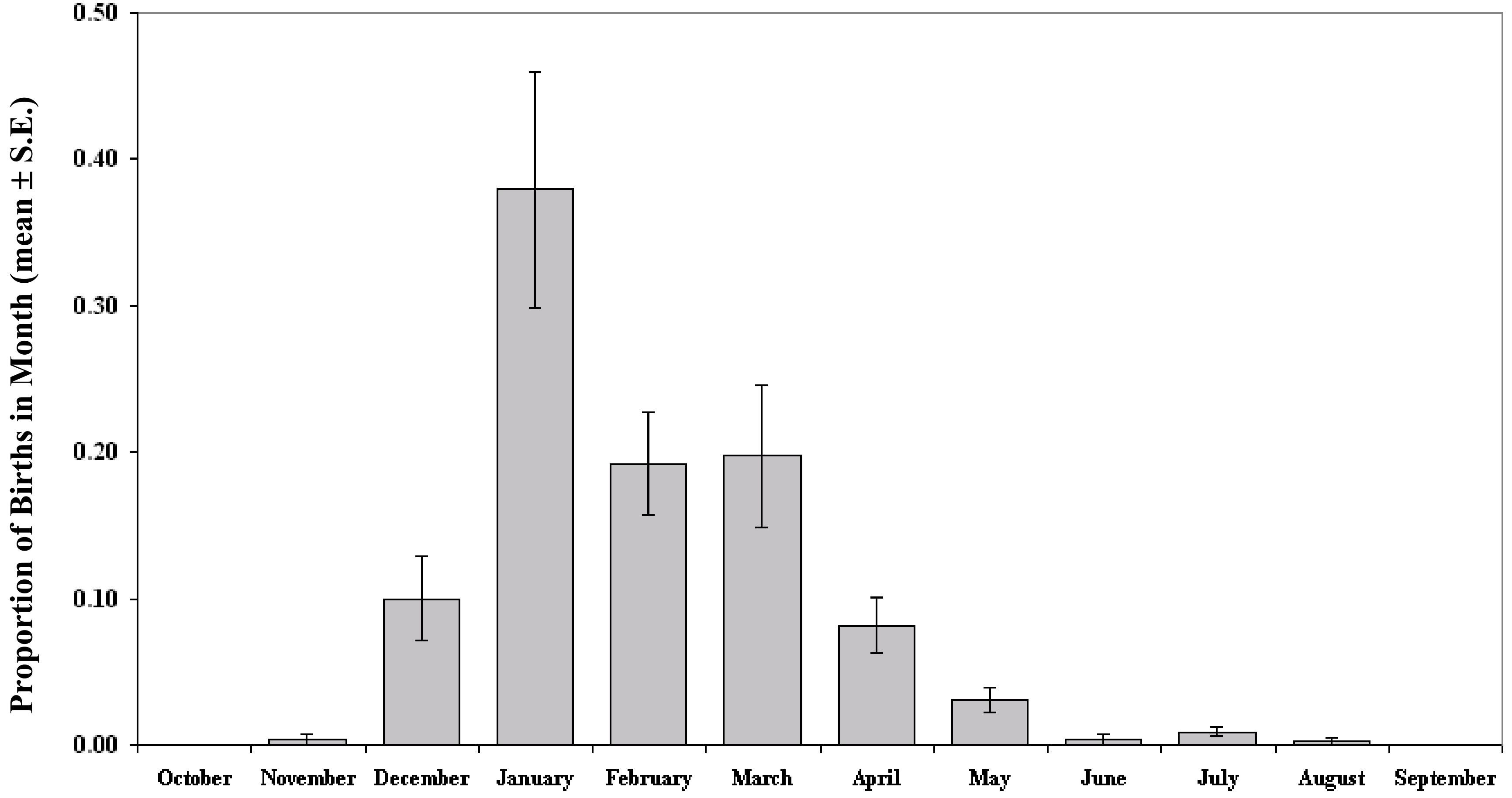

Protein (N)
NDVI
Rainfall
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
Pearson's Correlation Coefficient, r
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Monthly Lag (present to past, 0-14)
**
*

Figure 4.


Proportion of Births in Month (mean ± S.E.)
0.50
0.40
0.30
0.20
0.10
0.00
October
November
December
January
February
March
April
May
June
July
August
September

Chapter 4: Spatio-temporal indicators of diet and habitat quality for African buffalo

ABSTRACT

Fecal samples were collected from African Buffalo *(Syncerus caffer)* in Kruger National Park, South Africa and analyzed for phosphorus and nitrogen content using standard laboratory procedures as well as near infrared spectroscopy (NIRS). The resulting fecal nitrogen (N_f) and fecal phosphorus (P_f) measurements were examined with respect to a distribution of monthly average values of remotely sensed vegetation quality (NDVI) to establish a temporally explicit predictive measure of vegetation quality for herbivores in a savanna ecosystem. We demonstrated that both N_f and P_f measures are affected by large-scale landscape differences. Distinguishing between basalt-derived and granite-derived soils showed that while granite was predicted to be less nutrient-rich than basalt, levels of N_f on both soils were higher in the north of the park than the south, but P_f was highest on southern basalts. We also found a seasonal effect on the levels of N_f and P_f on southern granites and basalts, suggesting differential retention of protein and minerals by the vegetation. This suggests that buffalo face trade-offs in habitat selection that may change with season with respect to these limiting nutrients. We found a significant positive relationship between N_f and a monthly average NDVI of the prior month, and a significant positive relationship between NDVI and herd condition scores. We found no significant relationship between P_f and NDVI, or between P_f and herd condition. These results suggest that NDVI can provide a surrogate measure of habitat quality for buffalo with regards to crude protein, but may not be a good measure for the limiting mineral phosphorus. We discuss the utility of establishing measures of dietary quality that can be related to remotely sensed data for research and management of savanna herbivores.

KEYWORDS: Savanna, African Buffalo, Remote sensing, fecal analysis, NIRS

INTRODUCTION

Diet quality is fundamental to understanding habitat quality and population dynamics. These relationships, in turn, are important to management of free ranging wildlife populations in managed settings, such as parks and reserves (Grant *et al.*, 2000). Determining diet quality for free ranging ruminants, however, is difficult. Fistulation is impractical, sampling the species consumed is expensive, and it is difficult to acquire contemporaneous samples at a landscape scale. Even if these samples were obtainable, they may not always accurately reflect dietary quality. Fecal indices are attractive for several reasons. They are easy to acquire, relatively inexpensive to analyze, and they reflect the actual dietary decisions of target species. Application of the analysis of fecal indices to wild ruminants began in the 1970s (Arman, Hopcraft & McDonald, 1975; Erasmus, Penzhorn & Fairall, 1978; 1973; Sinclair, 1977), but their usefulness has been debated (Hobbs, 1987). They have been shown recently to be a useful adjunct to existing methods for assessing range quality in South Africa (Grant *et al.*, 2000).

Even a facile and inexpensive measure can become impractical in application and analysis over the long-term, due to logistics and finances. Therefore we sought to quantify the relationship between a readily available remotely sensed vegetation index (NDVI) and a study of fecal indicators of dietary quality to create a spatially explicit, regular, long-term predictor of vegetation quality from the perspective of a large herbivore in a savanna ecosystem.

Grant et al., (2000) conducted a study of fecal indices in this study area, using samples collected opportunistically between 1991 and 1998 for buffalo, impala and wildebeest. They found considerable large-scale landscape effects on fecal nitrogen and phosphorous measurements, and also saw considerable seasonal effects on these indices. Furthermore, they were able to correlate these indices with body condition scoring in buffalo and impala. This suggests that using fecal indices as the basis for a distinct habitat quality predictor on a spatial (landscape-level) and temporal (seasonal and annual) scale is feasible. Mutanga et al. (2004) conducted a study of grass nutrient patterns in Kruger National Park, South Africa, relating physical variables such as slope, aspect, elevation and soil texture to grass-nutrient patterns. The motivation for the study was the need to understand the spatial distribution of vegetation quality to understand the spatial distribution of herbivores. Their study was based on a very short-term, albeit intensive, dataset (approximately 1 month). We build on these prior studies, scaling up from local fecal indicators of quality to remotely sensed indicators, and from a short time window to a long-term predictive measure of dietary quality.

Limiting Nutrients

Protein, expressed as nitrogen, is the most limiting nutrient for grazers (Bell, 1971; Owen-Smith *et al.*, 1982), and phosphorous is the most limiting mineral in South African and Namibian pastures (Du Toit, Louw & Malan, 1940; Grant, Biggs & Meissner, 1996a). Fecal nitrogen (N_f) is highly correlated with forage digestibility (Bartiaux-Thill & Oger, 1986; Greenhalgh & Corbett, 1960; Leslie & Starkey, 1985), dietary protein concentration(Holechek, Vavra & Arthur, 1982; Irwin *et al.*, 1993; Moir, 1960a; Mould & Robbins, 1981; Wofford *et al.*, 1985), intake quantity (Arnold & Dudzinski, 1963), and changes in live mass of cattle (Grant *et al.*, 1996b). However, the applicability of N_f appears bounded. Irwin et al. (1993) found that, in Bighorn sheep, fecal nitrogen-dietary nitrogen associations deteriorated when dietary nitrogen (DN) levels exceeded 2.4%. In cattle, below DN concentrations of 1.1 to 1.2%, metabolic nitrogen continues to be excreted irrespective of intake (Sinclair 1977). The quality of vegetation declines considerably in the dry season in semi-arid savanna ecosystems, with large proportions of available forage lignified and hard to digest. The protein content of this forage declines below 1.1%, failing to provide sufficient dietary protein and leading to visible decline in body condition. Thus N_f may not be as good an indicator of diet quality during the dry season as in the wet season, making it difficult to use this variable to identify habitats of high and low diet quality when resources are most limiting.

Several studies have shown that fecal phosphorus (P_f) concentration is a good predictor of dietary phosphorous (DP) and phosphorous (P) deficiency in cattle and wildlife (Belonje, 1980; Belonje & van den Berg, 1980; Holechek *et al.*, 1985; Moir, 1960b, 1966; Wrench, Meissner & Grant, 1997). Studies of cattle have found that phosphorus can have a large effect on daily weight gain, and where P deficiency occurs, growth and reproduction in large mammalian herbivores are hampered (Grasman & Hellgren 1993). The relationship between phosphorus and body condition is complicated, however, by the nitrogen budget of the animal. Grant et al. (1996b) found that phosphorus supplementation increased average daily gain of cattle only when N concentrations were above 1.2%, and Bortolussi et al. (1996) found that low nitrogen intakes depressed P absorption at low P intakes. One would thus expect that P supplementation could resolve this problem in cattle, but Van Niekerk and Jacobs (1985) showed that if DN was limiting, then increases in DP may have a negative effect on feed intake and live mass change of cattle. Therefore it appears that there is a balance between

DN and DP that must be achieved to maintain herbivores, the bounds of which are likely tested in nutrient limited landscapes, particularly during the dry season and during periods of drought.

Feeding ecology of buffalo

African buffalo *(Syncerus caffer)* are primarily grazers, and due to their body size and ruminant gut morphology have been called *supreme bulk grazers* (Owen-Smith *et al.*, 1993), implying that they are bulk grazers whose feeding strategy is to maximize biomass intake. Yet in a savanna ecosystem, as the season progresses, available graze lignifies and becomes unpalatable, such that even a bulk grazer will become selective (Macandza, 2004). They will occasionally browse on woody shrubs, particularly in the dry season (Stark, 1986; Vesey-Fitzgerald, 1974). Habitat selection studies in Kruger National Park (Redfern *et al.*, 2003) and a neighboring reserve, Klaserie Private Nature Reserve (Ryan *et al.*, 2006) show that buffalo are most often found in areas near water, but they will range further from water in the dry season in order to forage on higher quality vegetation.

Buffalo in Kruger National Park represent a major herbivorous component of the savanna ecosystem; their population has been maintained at between 25,000-30,000 individuals (DeVos, 1983). Buffalo occur in groups of a few hundred to several thousand individuals (Prins, 1996; Sinclair, 1977); with herds in this study comprising 250-800 individuals (Ryan *et al.*, 2006). Buffalo exhibit seasonal social ecology in which they aggregate into large mixed herds during the breeding season, splitting into mixed herds and bachelor groups for the rest of the year. This social ecology means that the membership of a ‘herd’ varies considerably on multiple temporal and spatial scales

(Cross *et al.*, 2005). The factors determining seasonal grouping behavior may include intragroup resource allocation conflicts leading to smaller groups forming for foraging. Given that there is such a seasonal difference in grouping, and thus strategies to optimize dietary quality and intake, it is important to analyze dietary indicators in both seasons.

Remote Sensing and Vegetation quality

Remotely sensed vegetation indices, or measures of greenness have been widely used to assess large scale patterns in vegetation growth and quality (Loe *et al.*, 2005). The utility of indices such as NDVI (Normalized Differential Vegetation Index) to measure biomass, however, has been questioned (Moreau *et al.*, 2003). NDVI is a measure of greenness—the photosynthetic capability of the plant cover—the actively productive plant parts cause red reflectance, and higher values of measured greenness. In a semi-arid system, much of the ground biomass is unproductive for many months of the year. Recent studies have examined the capacity of NDVI to quantify leaf area index (LAI) as a surrogate for biomass, and the results have been mixed (Moreau *et al.*, 2003). In this study, we are interested in the quality of vegetation as it will be perceived by a herbivore, and in savanna landscapes, a large part of the flux in NDVI value is grass growth (Scanlon *et al.*, 2005). Despite the fact that our study focuses on a bulk grazer, since these herbivores are protein limited, it is the digestibility and protein content of the vegetation that interests us most. Thus, red reflectance is a good indicator of precisely these qualities of vegetation that we deem "good" for herbivores. Moreover, we recognize that the vegetation heterogeneity at a small scale means that multiple species are represented by a single measure. Thus we simplify to a single signal of ‘green’, which is useful, regardless of standing biomass.

METHODS

Study Area

In this study, fecal samples were collected on a North-South transect of the Kruger National Park (KNP) and more intensively in the Satara Region of KNP and the Klaserie Private Nature Reserve (KPNR) (Figure 1). This area has an underlying geology comprising an east-west division of basaltic derived soils (east) and granite derived soils (west) (Figure 1). The main geological substrate of KPNR is granitic gneiss, part of the extensive granalitic system underlying most of the country (Parker and Witkowski, 1999). This is the same landscape as the western portion of the Satara region, and thus we include KPNR samples in granitic landscape samples. Granitic landscapes form sandy soils, which have high permeability and infiltration (Venter & Gertenbach, 1986); in KNP this leads to broad-leaf savanna and a herbaceous layer of moderate quality in the uplands, a dense herbaceous layer with few trees in the midslopes, and a productive grass layer with thorny shrubs on the footslopes of drainages (Grant *et al.*, 2000). Basaltic soils, on the other hand, are mineral rich, clayey and have low infiltration; in KNP the vegetation found on this soil type is mopane shrubland (*Colophospermum mopane*) in the north and knobthorn (*Acacia nigrecens*) and marula (*Scelocarya birrea*) savanna in the south (Gertenbach, 1983). Basaltic areas have higher grass production than the granitic, leading to more frequent burning (Grant *et al.*, 2000).

In addition to the geology and soil, a North-South rainfall gradient contributes to landscape heterogeneity at a large scale in KNP, with the south receiving more rain than the north. The mean annual rainfall in this area is 450–550mm (Gertenbach, 1980); rainfall and temperature for this area are described in more detail elsewhere (Ryan *et al.*, 2005; Ryan *et al.*, 2006). In this study, we describe 4 seasons: an early wet season (Oct-December), late wet (Jan-Mar), early dry (April-June) and late dry (July-September).

Fecal Samples

Two fecal sample datasets were used in this study:

1. A set of fecal samples (10 dung samples pooled per herd from 27 herds = approx. 270 total samples), ranging from North-South in KNP. These were collected from July-September, 2001 as part of prior study examining the relationship between parasite load, disease status and condition. Collection protocols are described in more detail elsewhere (Caron, Cross & Du Toit, 2003).
2. The second dataset (10 dung samples per herd from 23 herd collection opportunities (repeated samples) = 230 samples) were collected from February 2001- December 2002, a longer time span, but restricted to the Satara Region of KNP and KPNR. This sample spans granite and basalt substrates from the eastern limit of KNP at the Lebombo mountains to beyond the western park boundary at KPNR (see figure 1). We collected 10 fecal samples per mixed herd or bachelor group during the wet season (8-15 March), early dry season (15 July – 11 August), and late dry season (9 September - 15 November).

As both sets of data were collected and analyzed with the same protocol and equipment, we are comfortable conducting similar analyses on both datasets without being subject to collection bias. To ensure consistent measurement, all samples were collected within 12 hours of deposition (Leite & Stuth 1994) and samples already contaminated with dung beetles or fly larvae were not used. Samples were air dried until they could be transported to an oven where they were dried to a constant weight at 60^0C.

Near Infrared Spectroscopy (NIRS)

NIRS technique is far less expensive and more rapid than traditional wet-lab methods for analyzing fecal samples. Near infrared spectral data of each sample was collected using a NIRSystems model 5000 monochromator, scanning a range from 11000 to 25000 nm using 2 nm increments. Fecal samples were ground using a Recth model SM1 mill with a 1mm sieve, and samples were scanned in twice and an average value was taken with a RMS limit of 35 between duplicates. The spectral boundaries for each set of samples were computed, resulting in 7 samples with extreme spectra that were eliminated for calibration purposes.

Eighty samples were used for calibration of the NIR instrument. Wet lab nitrogen and phosphorous values for the 80 calibration samples were obtained by the combustion method for nitrogen and by Molybdovanadate colourmatic method for phosphorous (Wenzel & Likens, 1991). Using WinISI version 1.5 (Infrasoft International, 2005) for chemometric calibration analysis, the best calibration equation was chosen. A modified partial least squares (MPLS) regression with a detrend scatter correction, first derivative treatment of the spectral data points and a segment and gap of 4 each was chosen for nitrogen. The calibration equation for phosphorous was MPLS regression with standard normal variate (SNV) scatter correction, first derivative data treatment, and segment of 10 with gap set at 5. All remaining fecal samples were then processed for nitrogen and phosphorous and the content derived using the calibration equation for nitrogen and phosphorous respectively.

N_f and P_f as surrogates for dietary N and P

In addition to fecal samples, a vegetation sample was collected and analyzed to ascertain whether the fecal samples were representative of the feeding patch on which they were obtained. The data collection methodology for this part of the study is described in Macandza et al. (2004), wherein the authors conducted a study of forage species selection in KNP during the dry season. The samples were collected during three short study periods, on a total of 40 days between July and October 2002. Concomitant with this study, the samples of forage, both grazed stems and representative samples of ungrazed stems, were analyzed for nitrogen and phosphorous content. These samples were pooled by month for comparisons with fecal sample data.

Metabolic fecal nitrogen (MFN)

There is a contribution to fecal nitrogen comprising metabolic nitrogen (derived from sloughed intestinal cells and rumen products), which is not part of dietary input. Regressing fecal nitrogen, $N_{f,}$ (or protein) on vegetation nitrogen, N_v, (or protein), one can estimate metabolic fecal nitrogen at the intercept (Jhala, 1997). Conversely, the opposite regression and corresponding intercept can be used to estimate forage protein from fecal protein.

Remotely Sensed Vegetation Greenness

Remotely sensed vegetation data was derived from the 1km AVHRR (Advanced Very High Resolution Radiometry) imagery collected by NOAA (the National Oceanic and Atmospheric Association) polar orbiting satellites. The daily imagery was processed at the Agricultural Research Council, Institute for Soil, Climate and Water (ARC-ISCW), as described in Wessels et al., (2004). The scale is 8-bit (2^8 binary storage), 0-255, with 255 omitted as a cloud and atmospheric interference layer. The details of the methods used to derive the average monthly distribution of vegetation greenness are described in Ryan et al., (2006). The distribution of NDVI values across seasons represents pixel-wise monthly means derived from imagery in the timeframe 1995-2001, at a resolution of 1km^2, which are then averaged over the region in question. The methods differ from the prior study (Ryan *et al.*, 2006) only in that the spatial coverage of the dataset is KNP and KPNR, and we use a more recent time-series.

Landscape patterns in NDVI –effects of an unanticipated drought

We conducted a brief exploratory examination of the NDVI data in our defined landscapes—North vs. South and East vs. West (Soil types)—during the time period of fecal sample collection. This was motivated by an unanticipated period of extremely low rainfall, constituting a minor drought in KNP, occurring in the wet season of 2002. To understand how this unanticipated disruption of seasonality might confound our expectations, we simply plotted the NDVI values across the entire time period, spatially averaging by 4 quadrants defined by a North-South and East-West split of the study area (Figure 6). This provides a simple visual comparison of the greenness values' temporal pattern in the 4 quadrants between the drought year and the two years preceding and following.

Herd Condition Data

Measures of herd condition from the Satara region collected on a monthly basis from February 2001 - December 2002 were also used in this analysis. The condition scoring method was adapted from that of Prins (1996), using a 1-5 condition scoring scale where 1 is poor and 5 is good. The condition assessments are based on visual observations of skeletal protrusions at the pelvis, flank, ribs, neck and spine (Caron *et al.*, 2003). To eliminate the confounding relationship between condition and age, the scores used in this study are arithmetic averages of the quality of females in the age >5 category. Although the condition scores were not collected directly in conjunction with fecal sample collection, they are condition measures of the herds providing the samples. Thus we used this data to represent the temporal effects of forage quality on body condition.

Statistics

A linear regression was used to examine the relationship between average $\mathrm{NDVI}_{(t-1)}$ and the N_f and P_f measures. A simple least-squares linear regression was also used to test the relationship between NDVI and body condition measures.

Two separate 2-way ANOVAs with post-hoc Tukey's Honest Significant Difference (HSD) tests were used to examine the effects of region (North and South), season and substrate (Granite or Basalt) on N_f and P_f.

All stats were performed in JMP version 5 Academic (SAS Institute, 1989-2002)

RESULTS

NIRS Method calibration

The lab technique using NIRS was shown to capture a significant and high proportion of the variance of the wet-lab measured nitrogen (r^2=0.98, n=77, p<0.0001; Standard Error of Calibration (SEC) = 0.0419, Standard Error of calibration validation (SECV) = 0.0504) and phosphorous (r^2=0.85, n=74, p<0.0001; SEC=0.0406, SECV=0.0481). This high level of fit allowed the calibration equation to be used to establish N_f and P_f with a high degree of accuracy.

N_f and P_f as surrogates for dietary N and P

The relationship between N_f and %N in the vegetation samples collected was also strong and highly significant (r^2=0.95, *df*=8, *p*<0.0001), the relationship between P_f and %P in the vegetation samples captured slightly less of the variance, but was still significant (r^2=0.72, *df*=8, *p*=0.004). This implies that the N_f and P_f are appropriate surrogates for dietary N and P.

Metabolic Fecal Nitrogen (MFN)

Using an orthogonal regression (to account for variation on both axes) of N_f against percent nitrogen in the vegetation (N_v) to derive the equation $N_f = 0.93N_v + 0.50$, we find a metabolic fecal nitrogen (MFN) value of 0.5% or 3.13% protein. This gives us a baseline of N_f output that is not contributed by dietary intake.

Temporal relationship between N_f and P_f and NDVI

The relationship between the prior month's NDVI value and the month's mean measured N_f was positive and significant ($r^2=0.90$, $n=12$, $p<0.001$). The equation relating these is: $N_{f(t)} = 0.82 + 0.005^* \text{ NDVI}_{\ (t\text{-}1)}$. In contrast, the relationship between the prior month's NDVI value and the month's mean measured P_f was not significant ($r^2=0.27$, $n=12$, $p=0.082$). This suggests that whereas dietary N is related to measurable greenness, dietary P is not.

Landscape patterns in NDVI –effects of an unanticipated drought

The wet season of 2002 following the rapid north-south sampling was highly irregular; the first few months of the calendar year had extremely low rainfall; there was essentially no wet season that year. In figure 5, the monthly rainfall in the Satara region (where most of the long-term fecal sample data were collected) is shown for 2002, superimposed on the average monthly rainfall since 1933. When we look at this longer data collection period (February 2001 – December 2002) it appears from the NDVI patterns (figure 6), that the north was less resilient to the effects of wet season drought effects, in terms of greenness.

Body Condition

The average monthly observed body condition of cows and the greenness measure (avg. 5 yr $NDVI_{(t-1)}$) were highly and significantly correlated ($r^2=0.72$, $n=23$, $p<0.0001$). The condition scores and associated greenness values (NDVI) for the Satara region of KNP where the cows were observed is shown in figure 4.

Landscape effects on N_f and P_f

Using the dataset collected in a North-South gradient (from July-September, 2001), we found that there was a significant effect of latitude (N/S) on N_f and P_f on granite and basaltic landscapes (G/B) (ANOVA: N_f $F_{3,215}=29.59$, $p<0.0001$; N/S $F=14.14$, $p=0.0002$; G/B $F=72.92$, $p<0.0001$; N/SxG/B $F=17.3097$, $p<0.0001$; P_f $F_{3,215}=23.02$, $p<0.0001$; N/S $F=2.62$, $p=0.10$; G/B $F=72.92$, $p<0.0001$; N/SxG/B $F=17.04$, $p<0.0001$). Specifically, N_f was higher on granite landscapes than basaltic in both the North and the South. A Tukey's Honest Significant Difference (HSD) test of means showed that this difference is significant in the north, but not the south. P_f was higher on granite landscapes in the North, but lower in the South. Another Tukey's HSD showed that this difference is significant in the south, but not the north (Figure 3a).

Using the longer dataset, we examined seasonal effects of this landscape difference and found there was a significant effect of season (S_{1-4}, from early wet to late dry) within and across substrate (G/B) (ANOVA: N_f $F_{7,1038}=107.31$, $p<0.0001$; S_i $F=204.89$, $p<0.0001$; G/B $F=17.12$, $p<0.0001$; S_ixG/B $F=21.63$, $p<0.0001$; P_f $F_{7,1038}=69.32$, $p<0.0001$; S_i $F=114.58$, $p<0.0001$; G/B $F=44.37$, $p<0.0001$; S_ixG/B $F=12.86$, $p<0.0001$). N_f was higher on granite landscapes than basaltic in the early wet season and throughout the dry season, but not in the late wet season. A THSD shows that this difference is only statistically significant in the early wet season. P_f was higher on granite landscapes than basaltic in the early wet season, and lower in all other seasons, this difference is significant in all seasons except the early wet season (Figure 3b).

DISCUSSION

We found that the remotely sensed vegetation index, NDVI, may be a useful surrogate for habitat quality where crude protein is important. In contrast, assessing the limiting mineral phosphorous, is likely more appropriately measured directly via directly sampling vegetation, or P_f. We found that N_f and P_f were appropriate measures of dietary N and P; that N_f followed vegetation greenness values in a predictable manner, but P_f did not; we found that buffalo body condition was highly correlated with this greenness index also, and that both N_f and P_f are influenced by latitude, season and landscape.

Reliability and utility of techniques

NIRS, with which rapid analysis of a large number of samples was feasible, was shown to be a reliable technique for analyzing N_f and P_f content, compared to robust chemical analyses. In addition, we found that using N_f and P_f as surrogates for the nutrient content in the specific vegetation consumed by buffalo was valid and reliable. This alleviates the fconcern of misinterpretation of fecal indicators as the botanical composition of intake changes (Leite & Stuth, 1990). The strong validity of these field and lab techniques allowed us to extrapolate fecal indicators to represent local indices of habitat quality in this savanna landscape.

Habitat heterogeneity

We found that the differences in the landscape due to geological substrate were reflected in the fecal indicators of habitat quality. The northern half of KNP experiences lower rainfall than the south (Gertenbach, 1980), which one would expect to result in lower plant productivity and thus lower values in the greenness index. A closer examination of greenness index values during the period of time wherein we contrast the north and south samples (July-September, 2001), we found that the north maintained higher greenness levels than the south (figure 6 insert), and that both N_f and P_f were higher on granites in the north than the south. This suggests that as the dry season progresses, the north declines more slowly in quality than the south, perhaps retaining some areas of higher quality forage on granites later in the season. We found that N_f was also significantly higher on northern granites than basalts, although P_f was not. This finding for N_f was unexpected, as basalt derived soils are nutrient rich soils that promote high productivity (Gertenbach, 1983; Grant *et al.*, 2000). As a result, we would expect that if the north is generally less susceptible to drying effects than the south, then we would find higher levels of nutrients on its basaltic soils, not on granites. This suggests that there is a more complex interaction of vegetation and rainfall allowing retention of greenness in spite of the geological (soil type) substrate.

In addition, during this sampling period, we noted an unanticipated drought period, essentially meaning there was no wet season in 2002. Whereas in 2001, as the dry season progressed, we saw an expected pattern of the north retaining higher greenness than the south (rainfall gradient) and the granites retaining more greenness than the basalts (soil infiltration) (Figure 6 insert). During the 2002 dry season, however, we see that the south west (and even the south east for a few months) reach and retain higher values of greenness than the north, although all four sections decline to similarly low values by the end of the dry season. This apparent lack of green retention or resilience in the north, despite predictions that the eastern, basalt soils are more productive and nutritious, may offer further explanation for the unexpected distribution of nutrients.

Habitat seasonality

We found that there was a seasonal pattern to N_f that echoed the growing season as predicted, lagging the remotely sensed greenness by one month. This peak in fecal nitrogen with peak growing season has been seen in many studies of ruminants on semi arid and arid landscapes, including domesticated cattle on rangeland (Senft, Stillwell & Rittenhouse, 1987) and desert (Becerra *et al.*, 1998) and tropical ruminants in parks (Jhala, 1997; Padmalal, Takatsuki & Jayasekara, 2003). The peak in greenness reflects the early green growth of plants, which is low in tannins and high in digestible fiber and allows uptake of plant crude protein. However, it does not represent a biomass peak; we suggest that a combination of accumulated growth and improvement of cow condition accounts for the month's lag. Although we were not able to these buffalo, the body condition index of cows was our proxy and was highly correlated with the time-lagged greenness measure. The positive relationship between N_f and condition in buffalo was well established by Grant et al. (2000), and has been measured more directly in cattle as correlated with weight gain (Grant *et al.*, 1996b).

Since protein is approximately 16% nitrogen, another means of understanding N_f is to express it in terms of crude protein (CP = 6.25*N). Sinclair (1975) measured fecal nitrogen in buffalo for 5 samples, with values ranging from 5-10% protein (N_f = 0.8-1.6), which is within the range of our study. The N_f values found in this study (0.9-2.3) were slightly lower than those found in cattle. In free-roaming cattle in Oregon, USA, N_f ranged from 1.5 to 3.4 (Holechek *et al.*, 1982), and in hardy cattle breeds in the Chihuahuan desert, Becerra et al.(1998) found values of 1.09 to 2.85.

To understand the needs of herbivores on a given feeding range we can compare crude protein of the vegetation with fecal output. Sinclair (1975) combined his analysis of buffalo with a study of wildebeest in the Serengeti to quantify the minimal requirements of dietary protein at between 5-6% (DN = 0.8-0.9) (Sinclair, 1975; Sinclair, 1977). We found a metabolic fecal nitrogen (MFN) value of 0.5% or 3.13% protein. The dry season value of N_f which persists at approximately 1.2% (see figure 2), suggests a DN value of 0.7% or 4.4% protein. We suggest that buffalo are living at or below their minimum dietary protein requirement during this period and will be visibly losing condition (see figure 4).

Although P_f was not predicted well by NDVI across the entire year, the interaction of N and P became apparent during the dry season. The increased excretion of phosphorus during the late dry season (Figure 2) may be due to a combination of dietary phosphorus (DP) deficiency and of buffalo living at the boundary of protein availability, which depresses P absorption and increases fecal output. This may also provide another explanation for the unexpected lower values of nutrients found on northern basaltic landscapes. The level of N_f was at the apparent minimum dietary level in the dry season (approximately 1.2) in both the north and south on basaltic landscapes. This may leave the buffalo with lowered absorption of P, even where it was available, meaning higher values of P_f. These results suggest that both nitrogen and phosphorus are important factors in predicting diet quality in sub-Saharan Africa and that the paradigm of using N_f as an indicator of diet quality may need to be revised to include the complicating role of limiting minerals.

A remotely sensed index that can serve as a proxy for habitat quality for herbivores in a large, managed landscape such as KNP would provide a useful management tool. Many of the management initiatives in this, and other parks are based on concepts of carrying capacity and stocking rates. Understanding the seasonality and spatial components of resource availability and limitation is essential to this type of management. In this study, not only did we establish a more cost-effective means of predicting protein availability on the landscape than direct analysis of vegetation, but we also uncovered the effects of minor droughts on the spatial distribution of that availability. In addition, we uncovered inconsistencies between accepted predictions of soil types and vegetation quality, which arise with the interaction of weather. Furthermore, we found that even with extensive sampling and strong correlations between N_f and remotely sensed data, the complex role of the limiting mineral P cannot be simply quantified in the same manner and requires direct sampling.

Figure 1. Location of Kruger National Park, Klaserie Private Nature Reserve (KPNR), and map showing quadrants of the park defined along the Granite-Basalt geology and the North-South rain gradient.

Figure 2. Temporal distribution of dietary indicators N_f and P_f (monthly average % across herds +/- standard error) and prior month NDVI values (as a 5 year mean monthly average +/- standard error); note that nitrogen follows a similar seasonality to vegetation greenness, peaking in the wet season (Oct-Mar), whereas phosphorus shows no clear relationship to greenness or the wet season, rising to a peak in the mid-dry season

Figure 3a. N_f and P_f values vs. North and South, Basalt and Granite landscapes (2-way ANOVA least squares means +/- standard errors). Tukey's HSD of means was performed: the same letter denotes a lack of significant difference.

Figure 3b. N_f and P_f values vs. season on Basalt and Granite (2-way ANOVA least squares means +/- standard errors). Tukey's HSD of means was performed: the same letter denotes a lack of significant difference.

Figure 4. Herd Condition (measured for females aged 5+, with and without calves) and the prior month's vegetation greenness.

Figure 5: Satara Rainfall (reproduced from figure 1, Macandza et al., 2004)

Figure 6: Monthly averaged NDVI values for the four divisions of KNP, Northeast (NE), Northwest (NW), Southeast (SE) and Southwest (SW), January 2001- December 2002. (Boxed area is for the period July-September 2001.)

Figure 1.

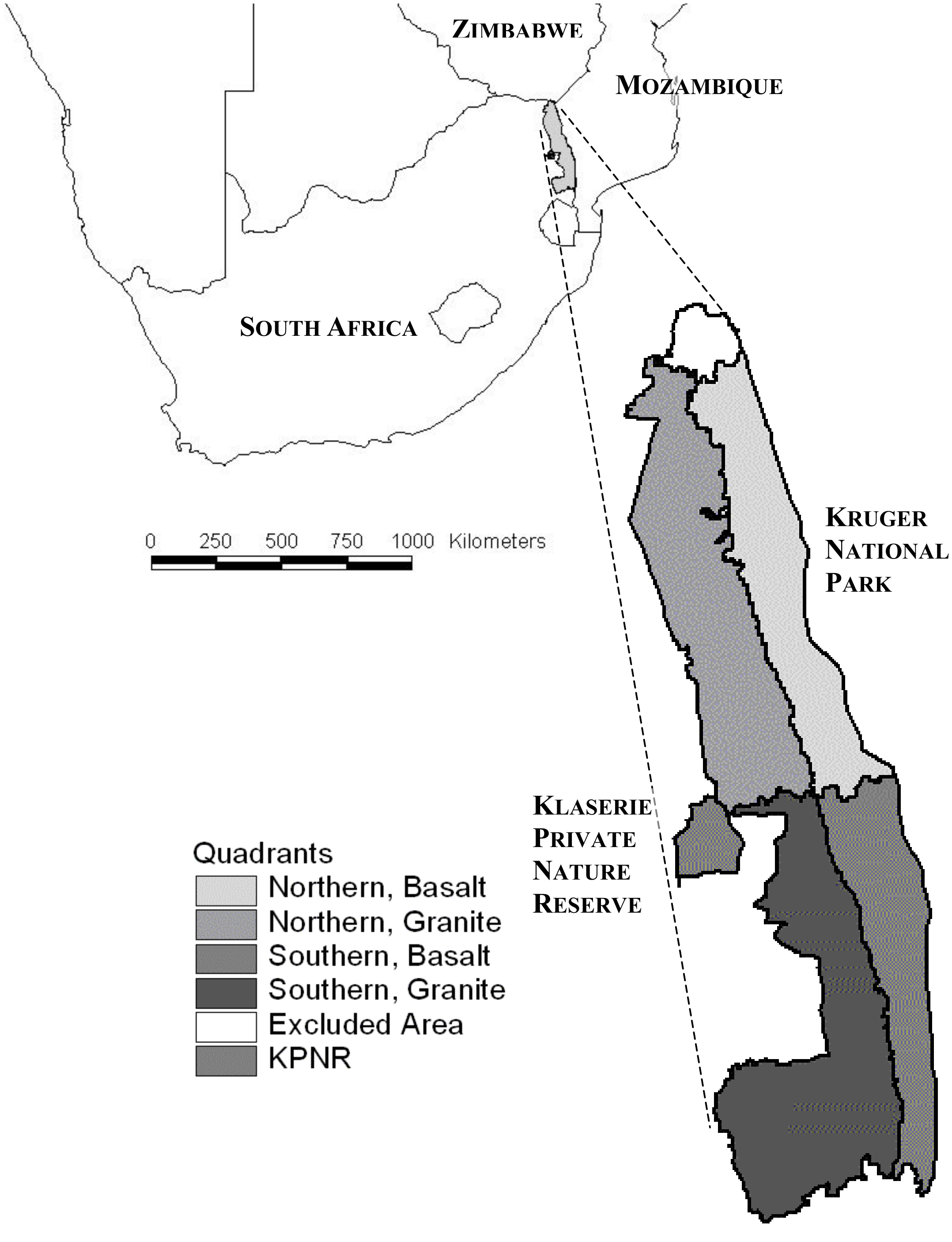
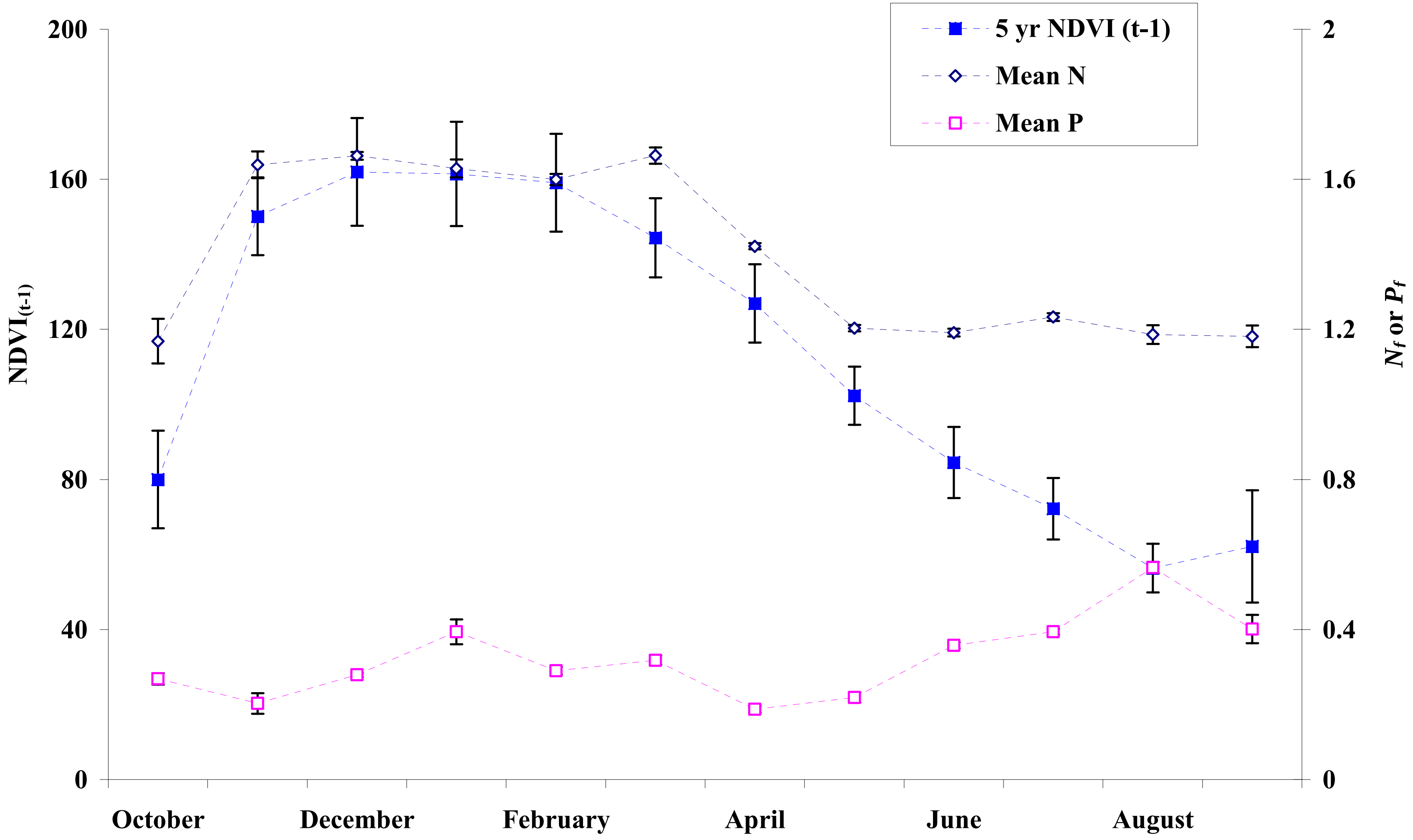
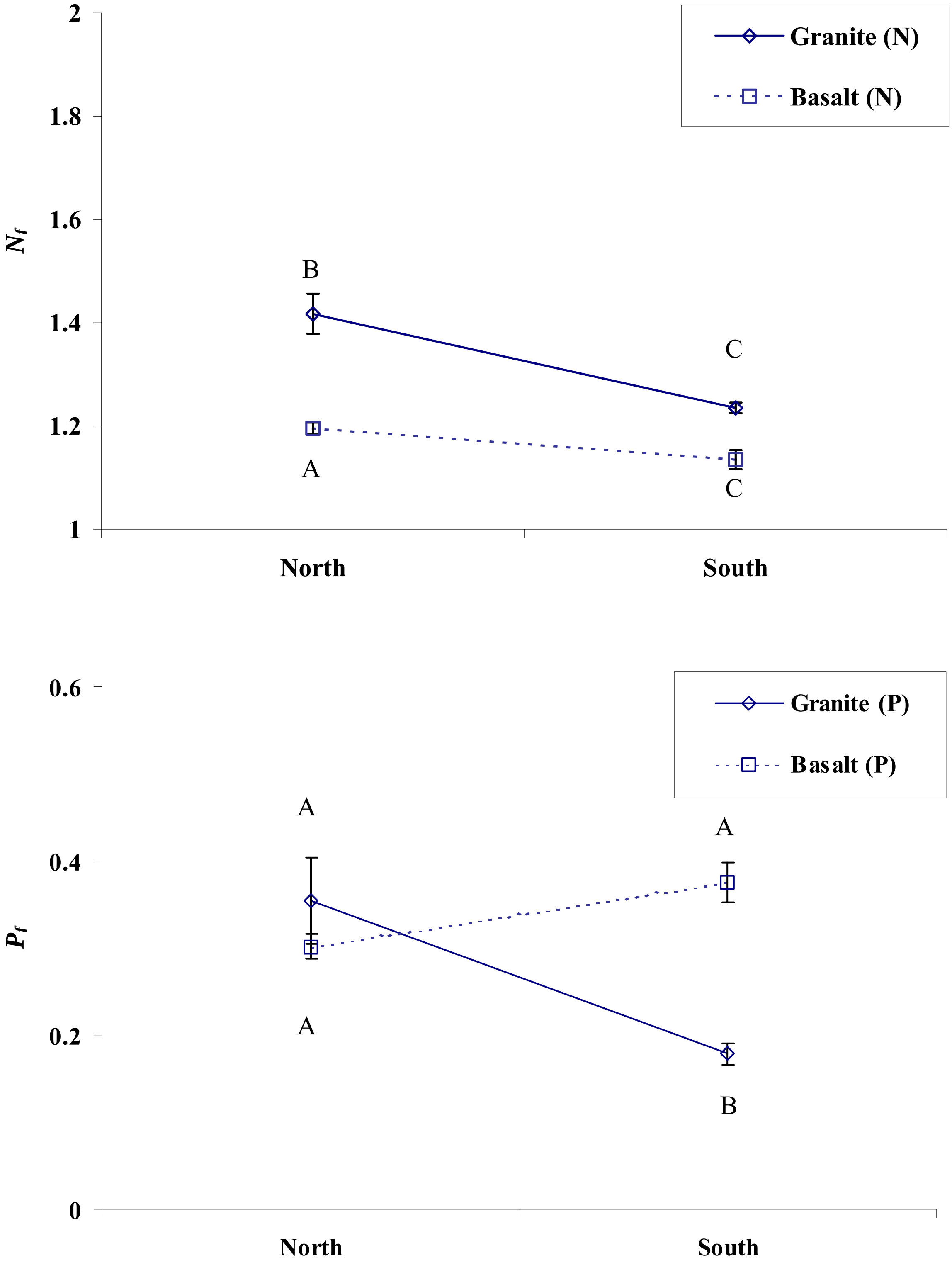

ZIMBABWE
MOZAMBIQUE
SOUTH AFRICA
0 250 500 750 1000 Kilometers
KRUGER NATIONAL PARK
KLASERIE PRIVATE NATURE RESERVE
Quadrants
Northern, Basalt
Northern, Granite
Southern, Basalt
Southern, Granite
Excluded Area
KPNR

Figure 2



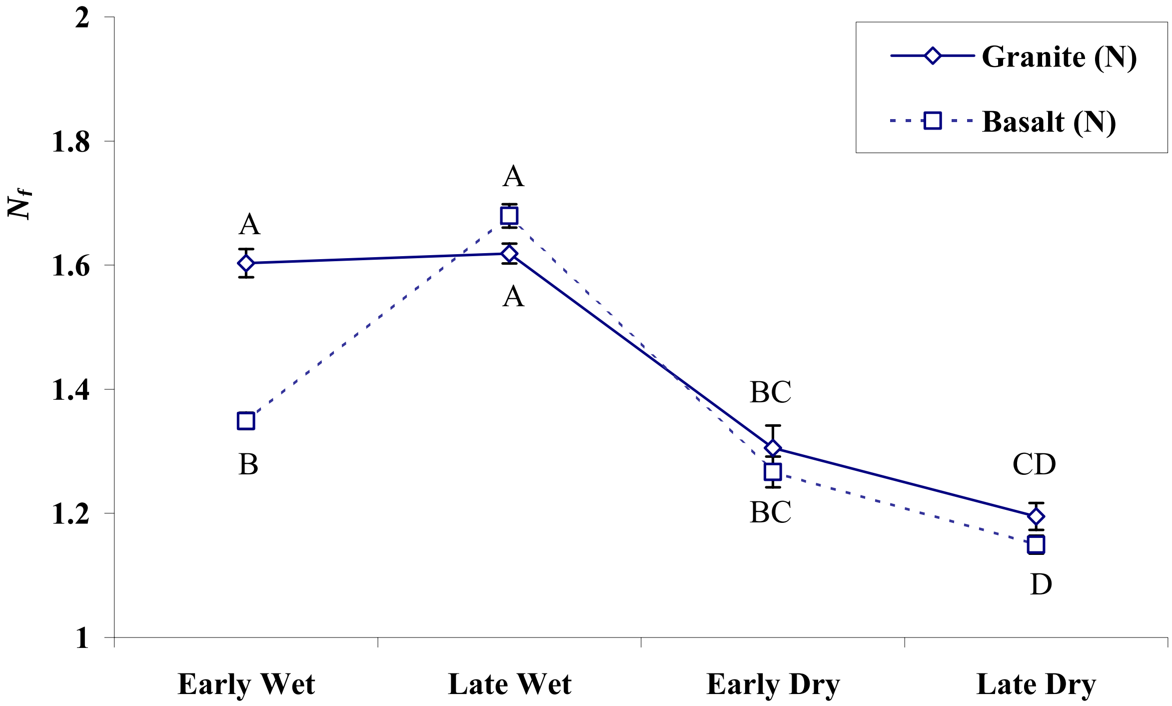
5 yr NDVI (t-1)
Mean N
Mean P
$NDVI_{(t-1)}$
200
160
120
80
40
0
N_f or P_f
2
1.6
1.2
0.8
0.4
0
October
December
February
April
June
August

Figure 3a.

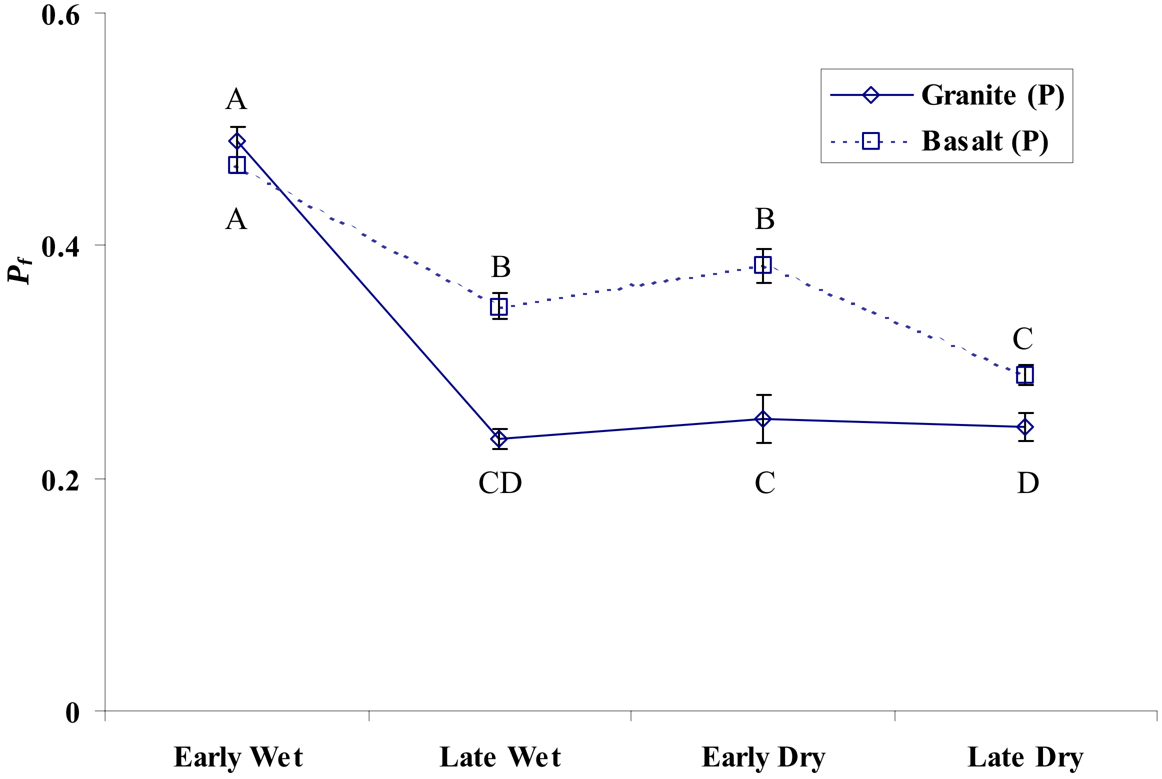


2
1.8
1.6
1.4
1.2
1
N_f
Granite (N)
Basalt (N)
B
C
A
C
North
South
0.6
0.4
0.2
0
P_f
Granite (P)
Basalt (P)
A
A
A
B
North
South

Figure 3b.



2
1.8
1.6
1.4
1.2
1
N_f
Granite (N)
Basalt (N)
A
A
A
B
BC
BC
CD
D
Early Wet
Late Wet
Early Dry
Late Dry



0.6
0.4
0.2
0
P_f
Granite (P)
Basalt (P)
A
A
B
CD
B
C
C
D
Early Wet
Late Wet
Early Dry
Late Dry

Figure 4.

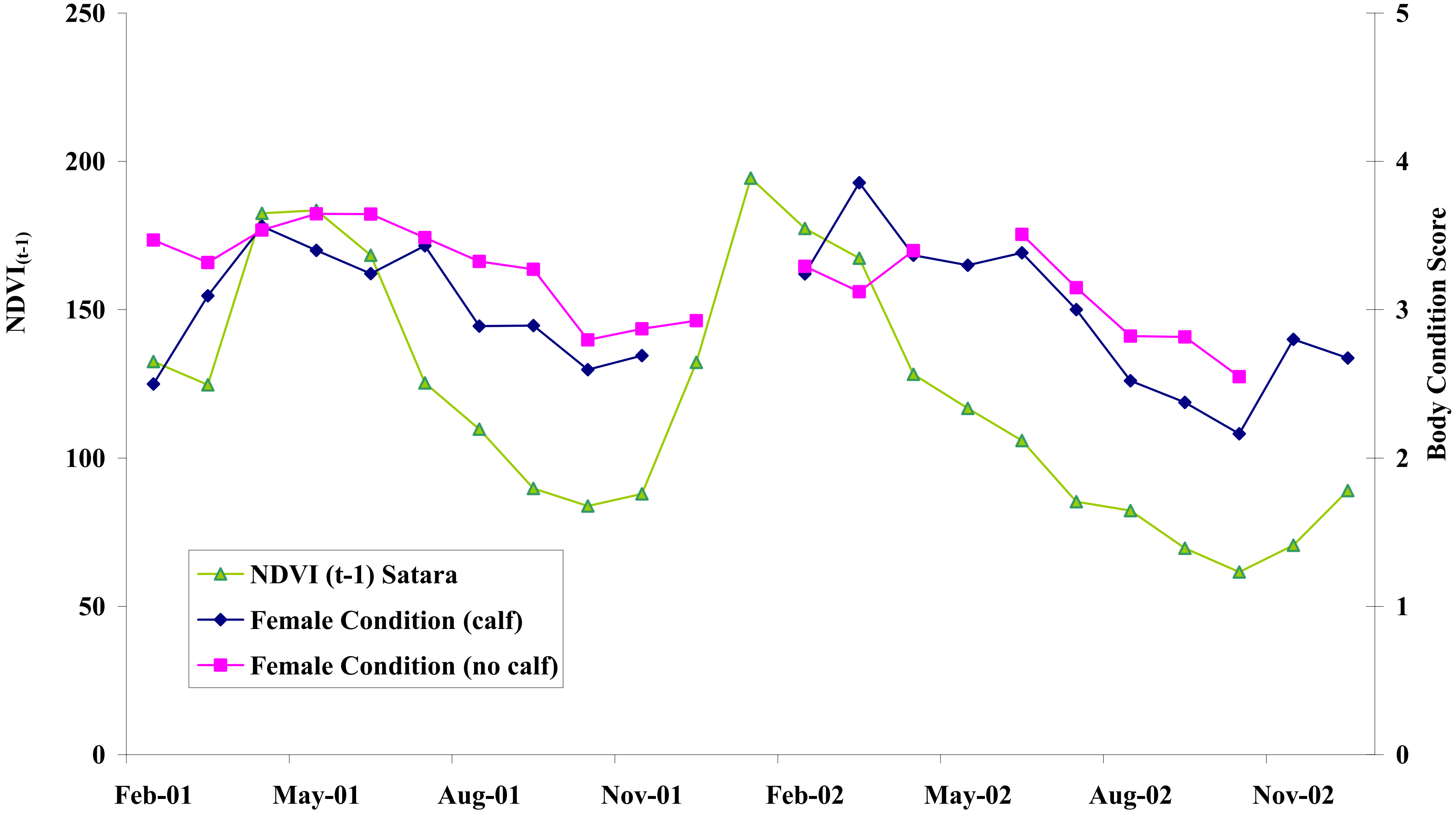

250
200
150
100
50
0
NDVI$_{(t-1)}$
5
4
3
2
1
0
Body Condition Score
Feb-01
May-01
Aug-01
Nov-01
Feb-02
May-02
Aug-02
Nov-02
NDVI (t-1) Satara
Female Condition (calf)
Female Condition (no calf)

Figure 5

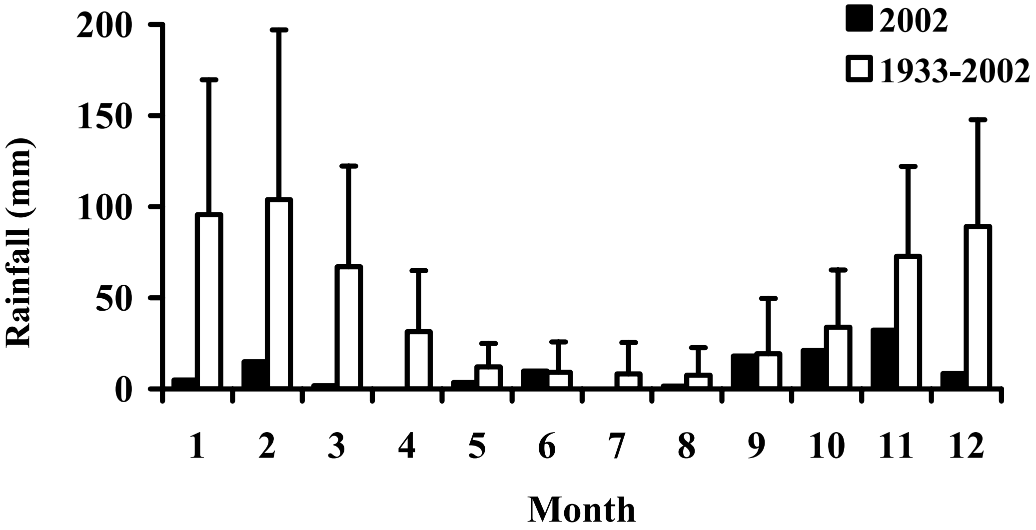
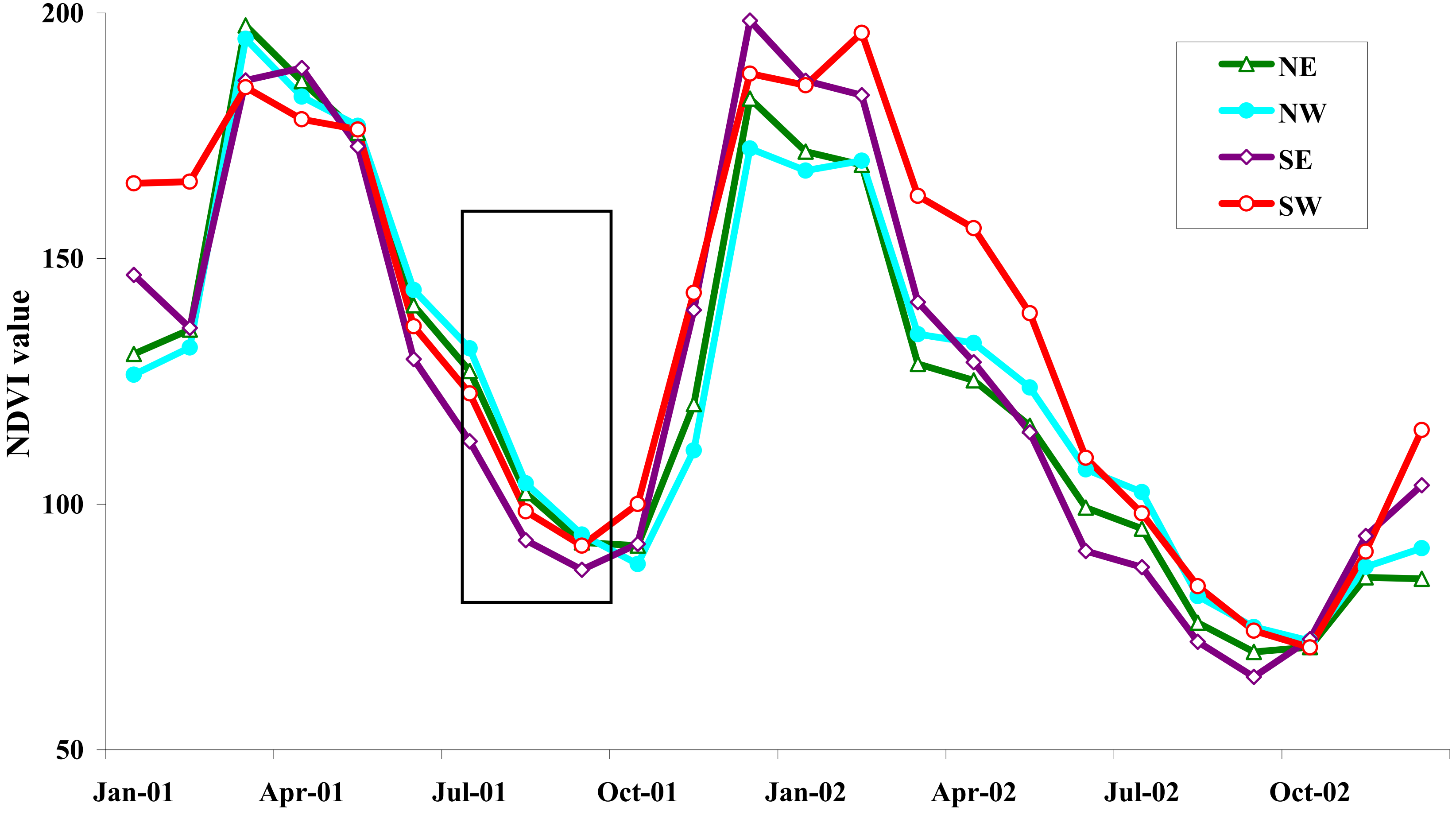

■ 2002
□ 1933-2002
Rainfall (mm)
200
150
100
50
0
1
2
3
4
5
6
7
8
9
10
11
12
Month

Figure 6.


NDVI value
200
150
100
50
Jan-01
Apr-01
Jul-01
Oct-01
Jan-02
Apr-02
Jul-02
Oct-02
NE
NW
SE
SW

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