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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

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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.

Keywords: k-NNCH, LoCoH home range estimation, NDVI, Minimum Convex Polygon (MCP), Fixed Kernel Method, Habitat Selection, Kruger National Park
INTRODUCTION

Recent studies of epidemic diseases such as Bovine Tuberculosis (Begis et al., 1996; Bengis, 1999; e.g.), persistent endemic Brucellosis and Rift Valley Fever and outbreaks of diseases such as Anthrax (deVos and Bryden, 1996), and foot and mouth disease (FMD) (Vosloo et al. 1996; Bastos et al. 2000; Vosloo et al. 2001; Greyling et al. 2002) 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 et al., 2000).

African Buffalo (*Syncerus caffer*) are gregarious large herbivores that occur in herds of a few hundred to several thousand individuals (Sinclair, 1977; Prins, 1996, e.g.). 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 (deVos and Bryden, 1996) caused approximately a 60% decline in the buffalo population of neighboring Kruger National Park (KNP) (Mills et al., 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 (2005) 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 and Wilmers, 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, \( H \) (see Seaman and Powell, 1998), 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
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., 2005). 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, 1994; Sinclair, 1977). Previous studies have also shown that buffalo are a riverine species, preferring areas close to rivers or major lakes (Sinclair, 1977; Prins 1996); 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 (24°3-22’ S, 31°2-19’ 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 granulitic system underlying most of the country (Parker and 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 500m² (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, 1998) to obtain the smoothing parameter, H. This was also implemented in Animal Movement Extension© (Hoodge & Eichenlaub, 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 and Wilmers, 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 & Eichenlaub, 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, 1974); a \( \chi^2 \) Goodness of Fit, applying Bonferroni Z statistics to establish confidence intervals for indications of preference of particular habitat types (Neu et al., 1974; Alldredge and Ratti, 1992); 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, 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 km²) 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 1km². 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 8.0 (ESRI, 2000) and ArcGIS 8.3 (ESRI, 2000), 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., 2002). 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 $\chi^2$ 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 $240.13 \pm 16.77$ km$^2$ ($mean \pm S.E.$). 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 ($27.81 \pm 0.98$ km dry; $21.91 \pm 1.03$ km wet; $mean \pm S.E.$); Welch modified one-way ANOVA: $t = 4.21$, df $= 75.57$, $p<0.0001$) and range wider ($33.80 \pm 2.30$ km$^2$ dry; $17.61 \pm 2.41$ km$^2$ wet; $mean \pm S.E.$); Welch modified one-way ANOVA: $t = 5.00$, df $= 65.80$, $p<0.0001$) in the dry season.
Habitat Selection

Three Herds

The $\chi^2$ 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, $\chi^2$ 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 $\chi^2$ 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, $\chi^2$ 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 $\chi^2$ 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 $\chi^2$ 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 ($183.56 \pm 4.17$, ($mean \pm S.E.$)) was
nonetheless significantly smaller than the wet season herd size ($224.66 \pm 4.17$, ($mean \pm S.E.$))
(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 (1969), 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 $290\text{km}^2$ 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, 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 & Cumming, 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 (Sinclair, 1977; Mlosewski, 1983), 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 (Stark, 1986; Vesey-Fitzgerald, 1974; Sinclair,
1977, e.g.). 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 (1km²) 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 et al., 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.
ACKNOWLEDGEMENTS

Thanks to M. Fang, T. Kim and L. Wondolowski for tirelessly entering spatial data. Thank you also to N. Zambatis, C. Rowles, Warden of Klaserie Private Nature Reserve (KPNR) and to M. Peel at the Agricultural Research Center (ARC) in Nelspruit, S.A. for data and KPNR maps. In addition, thanks to D. Van Zyl of the ARC-ICSW for remote sensing data access and information. Thank you to SPC and ALB for comments on early drafts, and to two anonymous reviewers. NSF/NIH EID Grant DEB-0090323 to W.M Getz supported S.J. Ryan’s research and partially supported C. Knechtel and W.M. Getz’s research. S.J. Ryan’s research was additionally supported by EPA-STAR fellowship FP-916382. All observations and research were conducted in compliance with the laws of the countries in which they were executed.
LITERATURE CITED


Environmental Systems Research Institute (ESRI). 2000. ARC version 8.0.2. ESRI. Redlands, CA, USA.


Table and Figure Legends

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

Table 2: Broad Scale Habitat Selection

| a. Observed Proportion occurring in habitat type | b. 95% Confidence Interval of area under a neutral selection hypothesis* |
| c. Significant Preference for habitat type** | d. Number of Observations in habitat type |
| e. Expected Observations | f. $\chi^2$ |

*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

| a. Observed Proportion occurring in habitat type | b. 95% Confidence Interval of area under a neutral selection hypothesis * |
| c. Significant Preference for distance to water category** | d. Number of Observations in distance to water category |
| e. Expected Observations | f. $\chi^2$ |

*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 (adapted from Ryan & Getz, 2004)

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), Minimum 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
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<tr>
<td>1994</td>
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<tr>
<td>1995</td>
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</tr>
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<td>200</td>
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</tr>
<tr>
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</tr>
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<td>Proportion of Area</td>
<td>$\chi^2$ Analysis</td>
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<td>95% CI$^b$</td>
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<td>6</td>
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<td>[0.00-0.00]</td>
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<td>[0.02-0.06]</td>
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Table 3: Distance-to-water Selection

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<td>Obs⁷</td>
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<td></td>
<td></td>
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<td>95% CI³</td>
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<td></td>
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<td>All herds - Wet season</td>
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<td>All herds - Dry season</td>
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<td>2+</td>
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</tr>
<tr>
<td>Location</td>
<td>Method</td>
<td>Description of Range</td>
<td># of Buffalo</td>
</tr>
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<td>--------------------------------------</td>
<td>----------</td>
<td>-------------------------------------</td>
<td>--------------</td>
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<tr>
<td>Wankie National Park, Zimbabwe¹</td>
<td>MCP</td>
<td>Wet Season Southern Herd</td>
<td>123</td>
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<td>Overall Southern Herd</td>
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<td>Overall Northern Herd</td>
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<td>Wet Season</td>
<td>50-55</td>
</tr>
<tr>
<td>Benoue National Park, Cameroon²</td>
<td>MCP</td>
<td>Dry Season</td>
<td>50-55</td>
</tr>
<tr>
<td>Sabi Sand Wildtuin, South Africa³</td>
<td>95% cluster</td>
<td>Annual Home Range</td>
<td>248</td>
</tr>
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<td>Sabi Sand Wildtuin, South Africa³</td>
<td>MCP; 95% cluster</td>
<td>Summer (wet)</td>
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<td>Sabi Sand Wildtuin, South Africa³</td>
<td>MCP; 95% cluster</td>
<td>Winter (dry)</td>
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<tr>
<td>Sabi Sand Wildtuin, South Africa³</td>
<td>MCP; 95% cluster</td>
<td>Pre-summer (hot/dry)</td>
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<td>Overall</td>
<td>700</td>
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<tr>
<td>Sabi Sand Game Reserve, South Africa⁴</td>
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<td>Overall</td>
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<tr>
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<td>A few weeks</td>
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<tr>
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<td>MCP</td>
<td>Moru (Herd 3)</td>
<td>900</td>
</tr>
<tr>
<td>Serengeti⁷</td>
<td>MCP</td>
<td>Nyaboro (Herd 2)</td>
<td>1500</td>
</tr>
<tr>
<td>Serengeti⁷</td>
<td>MCP</td>
<td>Banagi</td>
<td>800</td>
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<td>Serengeti⁷</td>
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<td>Seronera</td>
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<td>Serengeti⁷</td>
<td>MCP</td>
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<td>MCP</td>
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<td><strong>Momella Lakes</strong>&lt;sup&gt;8&lt;/sup&gt;</td>
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<sup>1</sup> Conybeare, 1980; <sup>2</sup> Stark, 1986; <sup>3</sup> Funston, 1994; <sup>4</sup> Kruger, J, 1996; <sup>5</sup> Eltringham and Woodford, 1973; <sup>6</sup> Leuthold, 1972; <sup>7</sup> Sinclair, 1977; <sup>8</sup> Vesey-Fitzgerald, as cited by Sinclair 1977; <sup>9</sup> Grimsdell, 1969; in Grimsdell and Field, 1976
Figure 2

Year

Count of buffalo

0 200 400 600 800 1000 1200 1400
Figure 3

Rainfall (mm)

<table>
<thead>
<tr>
<th>Month</th>
<th>October</th>
<th>November</th>
<th>December</th>
<th>January</th>
<th>February</th>
<th>March</th>
<th>April</th>
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<td>100</td>
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<td>140</td>
<td>160</td>
<td>180</td>
<td>200</td>
<td>220</td>
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<tr>
<td>Average Daily Minimum</td>
<td>0</td>
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<td>30</td>
<td>50</td>
<td>70</td>
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Temperature (°C)

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<th>November</th>
<th>December</th>
<th>January</th>
<th>February</th>
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<th>June</th>
<th>July</th>
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<td>40</td>
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<td>40</td>
<td>45</td>
<td>50</td>
<td>55</td>
<td>60</td>
<td>65</td>
</tr>
</tbody>
</table>

Wet Season

Dry Season
Figure 4
Figure 5

Range (km$^2$) vs. Number of Neighbors, $k$, in LoCoH for NH, FH, and SH.
1. *A. nigrescens* and *Grewia sp.*: open woodland;
2. Mixed *Acacia sp.*: shrubveld;
3. Mixed woodland;
4. *C. apiculatum*, *S. birrea*: open woodland;
5. *C. apiculatum*, *S. caffra*, *Grewia sp.*: short woodland;
6. *C. apiculatum*, *C. mollis*, *Grewia sp.*: closed short woodland;
7. *C. apiculatum*, *C. mopane*: woodland;
8. *C. mopane*: woodland and shrubveld
Figure 8