Range and Habitat Selection of African Buffalo in South Africa

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Abstract

We used more than 10 years of data on buffalo herds 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 3 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 3 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 the ranges because 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 farther and range wider in the dry season than the wet. Habitat selection analyses on broad vegetation categories showed preference for Acacia *shrub veld and* Combretum-*dominated woodlands. We found no significant selection of habitat at a fine geographic and temporal interval using the remotely sensed normalized difference vegetation index (NDVI), but the index was correlated to ranging behavior at a larger geographic scale. We found that buffalo selected areas within 1 km 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 they may range farther in the dry season for higher-quality food. As KPNR has a higher density of water than the neighboring Kruger National Park (KNP), this study provides a comparison of buffalo response to water availability in a smaller reserve and important information to managing the buffalo population as part of the larger Greater Kruger Management Area (GKMA).* (JOURNAL OF WILDLIFE MANAGEMENT 70(3):764–776; 2006)

Key words

Recent studies of epidemic diseases, such as bovine tuberculosis (Bengis et al. 1996, Bengis 1999), persistent endemic brucellosis, and Rift Valley fever, and outbreaks of diseases, such as anthrax (De Vos 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 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. This information is vital for buffalo management and 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 (e.g., Sinclair 1977, Prins 1996). 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 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 (KNP), leading to a fission–fusion 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 our analysis, shows that a core group of females has been present in the focal herd (FH) of our 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 KPNR (Fig. 1) contained the range of 3 primary herds of buffalo. Although there appeared to be 3 foci of buffalo grouping, spatially explicit annual census data, collected outside of the breeding season from 1998–2001 (M. Peel, Arc-Range and Forage Institute, Nelspruit, South Africa, unpublished data) 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 showed that this population was increasing (Fig. 2). This was likely a combination of demography and additional growth, in the form of migration and supplementation. Stocking rates and trophy quotas for this private reserve were not available to our study, but we suspect this played only a minor role in population trends. In 1992, a severe drought, in combination with an anthrax outbreak (De Vos and Bryden 1996) caused approximately a 60% decline in the buffalo population of neighboring KNP (Mills et al. 1995). This decline appeared in the KPNR also; the count dropped by 53% between 1992 and 1993. The subsequent population growth may have reflected a recovery period in the data set; the geometric

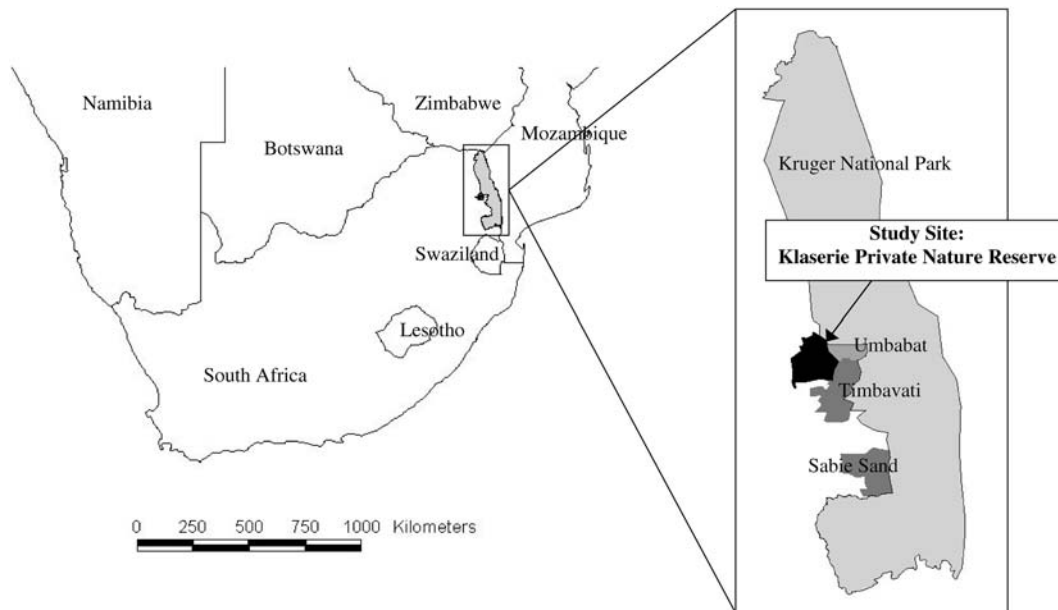[1] E-mail: sjryan@nature.berkeley.edu

Figure 1. Location of the study site: Klaserie Private Nature Reserve. Klaserie Private Nature Reserve is the location of the 3 herds of African buffalo (*Syncerus caffer*), one of which, the focal herd, was studied from 1993–2001, whereas the locations of all 3 herds were analyzed 1995–2000.

mean growth over the period 1992–2000 was 1.04, which indicated an annual growth rate of 4%. The fluctuating per-annum changes in population level may, in part, be due to migration between KPNR and KNP. It is important to note these background demographic and population trends when analyzing the range of buffalo herds because we must be aware of the potential for increased herd size to affect the range estimate.

The movement patterns of buffalo herds are hypothesized to shift with season as buffalo respond to available habitat. Prior studies hypothesized that the movement patterns of buffalo herds change seasonally, in response to available habitat. However, we found conflicting theories about 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). Two previous long-term studies have 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

Figure 2. Census data for African Buffalo (*Syncerus caffer*) in Klaserie Private Nature Reserve, 1992–2000 (M. Peel, Arc-Range and Forage Institute, South Africa, unpublished data).

perennial water. In a small reserve, movements of the herd are likely restricted by fence lines in addition to expected inter-herd and intra-herd interactions in optimizing habitat choice. To assess these restrictions in the context of our current understanding, we initially quantified the home ranges of the 3 herds and the annual range of the main FH. We then tested the hypotheses that buffalo in KPNR in the wet, compared with the dry, season 1) optimize energetic requirements by ranging closer to water; 2) move less, as shown by shorter travel distances and smaller ranges; and 3) form larger herds (reflecting the easing of the trade-off between defensive factors and foraging constraints). We also hypothesized that buffalo within KPNR 4) exhibit a herd size limit (i.e., an increase in population size in the reserve does not lead to an increase in herd size); 5) demonstrate overall preference for habitat in close proximity to water; 6) demonstrate preference for certain habitat types; and 7) select greener areas of the reserve, as indicated by increased normalized difference vegetation index (NDVI) values. If the latter holds, then NDVI provides a temporally consistent habitat surrogate with which to predict buffalo occurrence, which appears to be the case in the larger neighboring KNP (Ryan et al. 2006).
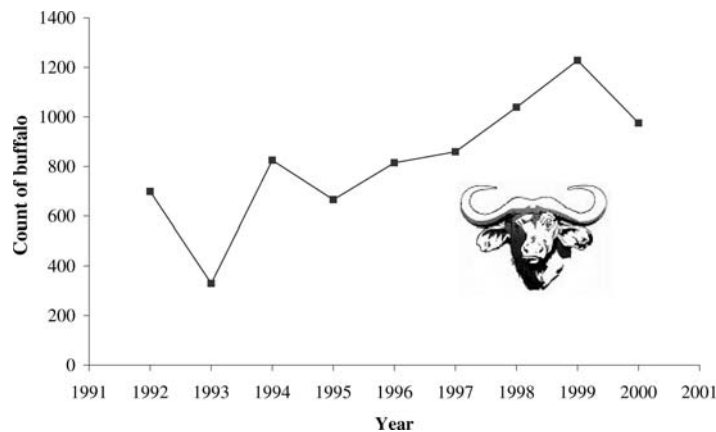
Study Area

The KPNR was located in the low-veld area of the Limpopo Province of South Africa, bordering the KNP on its western boundary (24°3–22′S, 31°2–19′E; 303–535 m above sea level [asl]; 57,800 ha; Fig. 1). The reserve comprises multiple private properties, formerly used as farms, and it was physically separated from KNP in 1961 with the erection of fences along the western boundary to prevent spread of FMD to domestic cattle (Witkowski 1983). Before that, KPNR provided dry season feeding and breeding grounds for many herbivores from KNP (Witkowski 1983). The KPNR now represents part of the Greater Kruger National Park Management Area, although it remains separated by fences from neighboring private reserves. Since 1990,
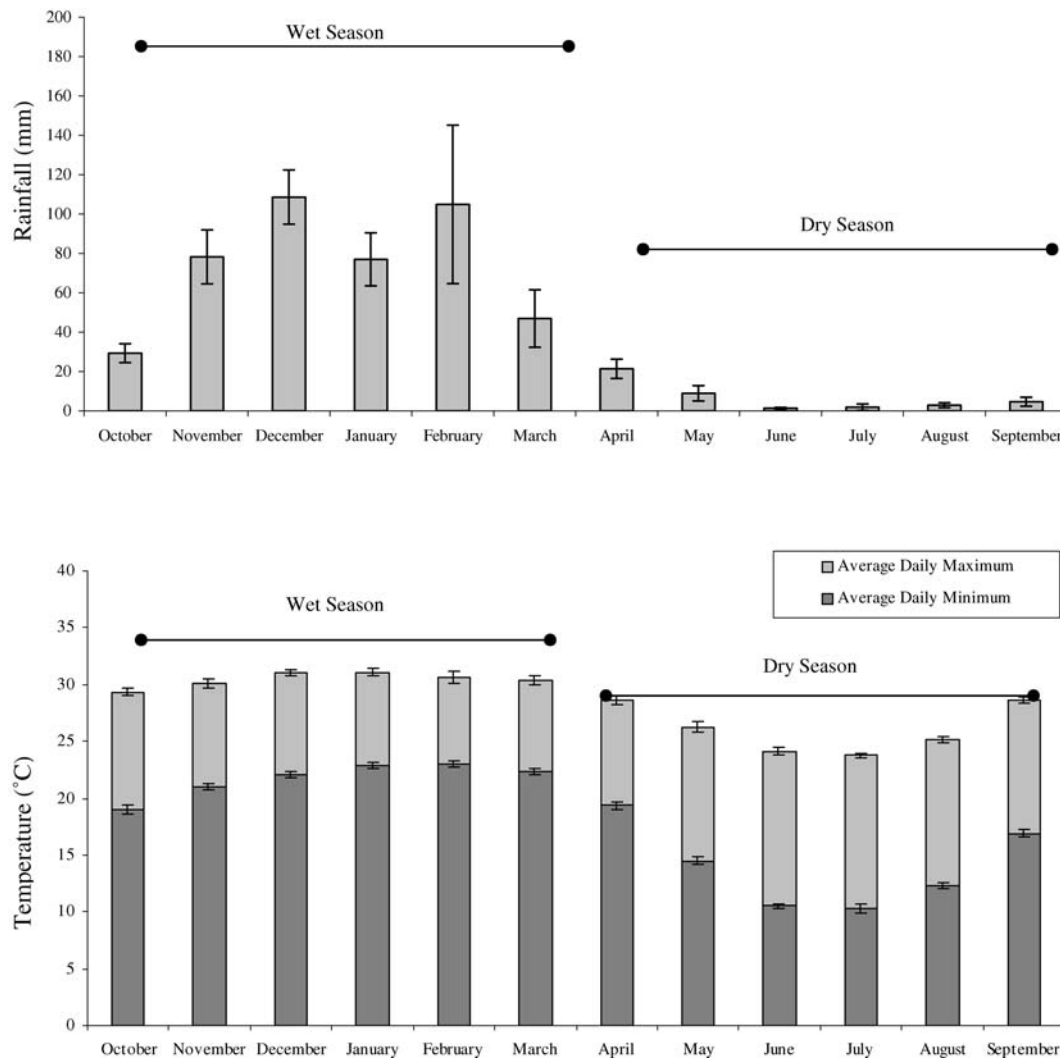
Figure 3. Klaserie Private Nature Reserve (KPNR) rainfall and temperature, showing seasons (adapted from Ryan and Getz 2005).

there has been a gradual removal of the western boundary fence of KNP, 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 the 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 and Witkowski 1999). The seasonality of KPNR follows a subtropical savanna pattern: both temperatures and rainfall follow a unimodal distribution annually (Fig. 3); mean annual rainfall from 1992–2000 was 486 mm. We define 2 main seasons based on rainfall and temperature records of the reserve for the decade in which we collected data: 1) a hot, wet summer season from October to March, and 2) a cool, dry winter season from April to September.

Methods

Data Acquisition

Buffalo herd locations in the KPNR were tracked over a period of more than 10 years as part of a long-term behavioral study of the central FH (C. U. Knechtel, Centre for Wildlife Management,

Pretoria, South Africa, unpublished data). Tracking of the FH was conducted by direct observation from a vehicle or by following spoor, whereas locations of the other herds were recorded opportunistically, often with the help of wardens and rangers in the reserve. All observations and research were conducted in compliance with the laws of the countries in which they were executed. The reserve was 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 was inevitable in a study spanning a decade, and we describe systematic resampling of the data in a following section.

We plotted the locations, over a period of 5 years (1995–2000), of 3 primary buffalo herds in the KPNR on hand-drawn surveyor's property maps of the reserve (origin unknown). These herds are a northern herd (NH), a southern herd (SH), and a central FH. We scanned these maps using a desktop scanner (HP ScanJet XPA, Hewlett Packard, Palo Alto, California), and then the image files were orthorectified and georeferenced using the Image Analysis extension for ArcView 3.x© (ESRI, Redlands, California; Fig. 4). We rendered the locations in ArcView as point files, with attributes such as the herd's name and the date recorded into the attribute table. We recorded locations of the FH onto enlarged
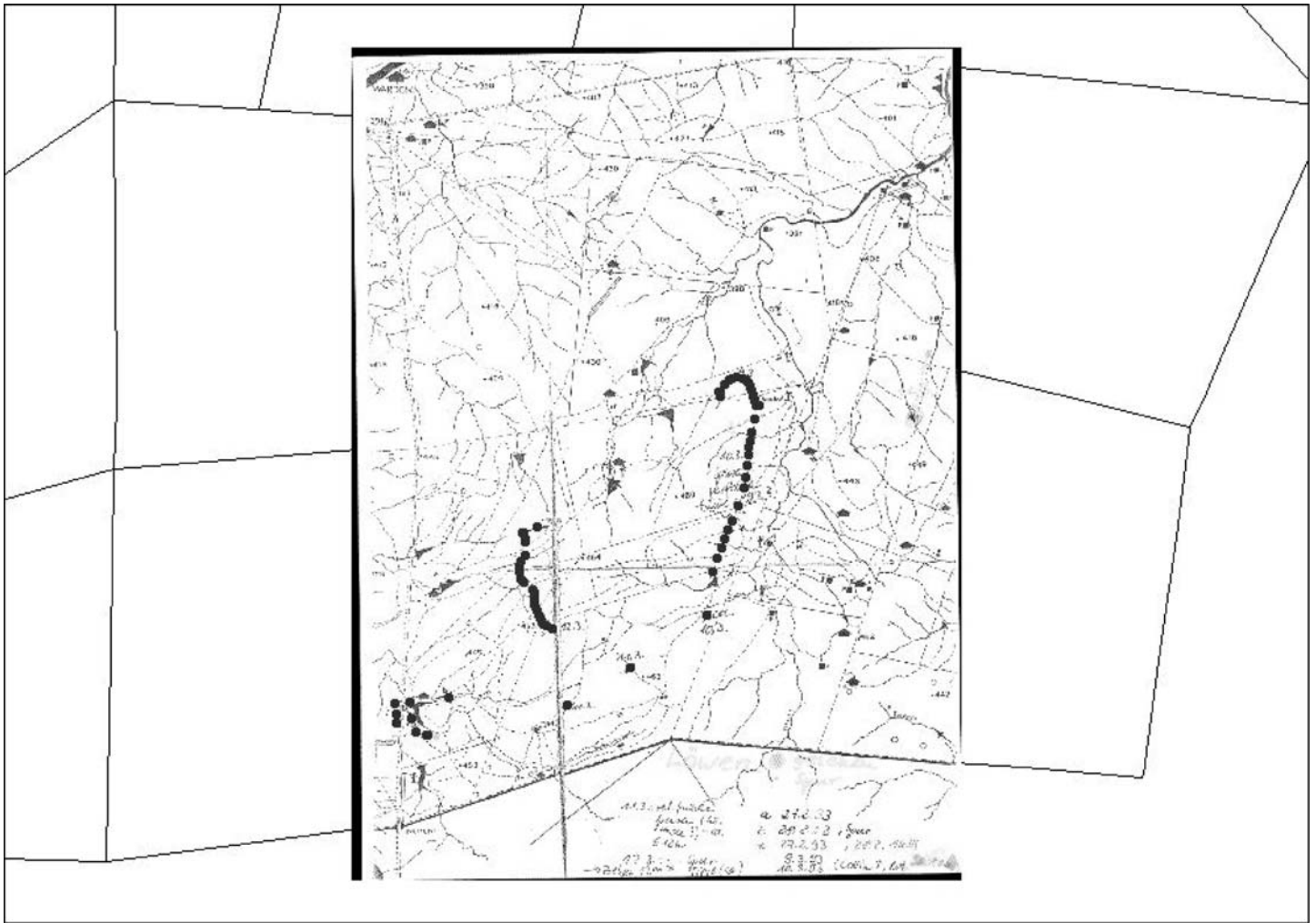
Figure 4. Scanned map image, showing transcription of buffalo group locations, which has been orthorectified and georeferenced to the Klaserie Private Nature Reserve (KPNR) in an ArcView shapefile.

sections of the surveyor's map, from 1993–2001, with an average of 247 (range: 180–290) days per year represented. These data were far more detailed, including tracking routes for multiple continuous days per map sheet. We processed these data in the same way as described above for all 3 herds.

For our analyses, a single point represented a herd's location, approximating the herd's centroid. These herds were quite small; the number of individuals in these herds varied between ~100 and 400 individuals, depending on season, and occupied a space of less than 500 m^2 (C. U. Knechtel, Centre for Wildlife Management, Pretoria, South Africa, personal observation).

Range Calculations

Three herds.—We calculated home ranges using a subset of the data from the 3 herds. Because single days involved multiple tracking points, we chose a randomly selected point from each day to ensure that each point represented an individual date event. In addition, to ensure that the comparisons were between separate primary groupings, we only used maps on which more than 1 group was recorded at the same time. This yielded data sets of 148 points (FH), 63 points (SH), and 48 points (NH). We collected these data opportunistically, and they 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 NH and FH could have moved between KPNR and KNP as their ranges approach the fence line that 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. U. Knechtel, Centre for Wildlife Management, Pretoria, South Africa, personal observation), which may cause us to underestimate the total ranges of these herds.

For comparison, we used 3 methods to calculate home ranges. The first was the minimum convex polygon (MCP), calculated in the Animal Movement Extension© (Hoodge and Eichenlaub 1997) for ArcView, which has been widely used in analyses of home range (see Getz and Wilmers 2004). This method provided a maximum estimate of the area of home range by joining the outermost points of a distribution. Although 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 it can inflate the home range estimates dramatically with the presence of outliers.

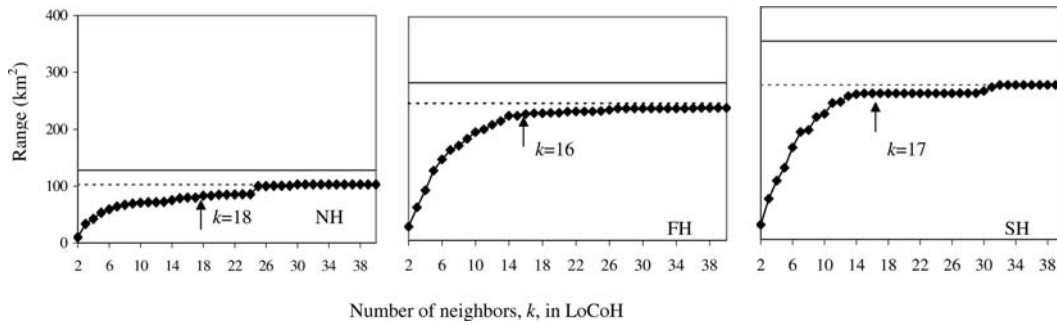The second method we used was the fixed-kernel home-range

Figure 5. Home-range estimates for the 3 herds: northern herd (NH), focal herd (FH), and southern herd (SH), collected in Klaserie Private Nature Reserve 1995–2000. Plots show comparisons of 3 methods: the local nearest-neighbor convex-hull (LoCoH; diamonds) construction method, the minimum convex polygon (MCP; dashed line) method, and the 95% fixed-kernel (H_{LSCV} 500-m grid; solid line) method.

estimator, using least-squares cross-validation (LSCV; see Seaman and Powell 1996) to obtain the smoothing parameter, H. This was also implemented in Animal Movement Extension (Hoodge and Eichenlaub 1997), with 5% probability contours generated on a 500-m grid. This method gave a clearer picture of internal areas of high use (cores) and generated 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 because of different frequencies of data collection between study periods, thereby masking actual trends with a methodological fallacy. Moreover, because technology advances permit the use of high-frequency data, such as Global Positioning System (GPS) locations, as frequently as 1 every hour, the apparent increase in area will become a considerable weakness in this method. This becomes problematic when trying to draw comparisons between studies or across years.

The third method, for which this analysis is its first application, was based on a local nearest-neighbor convex-hull construction (LoCoH; see Getz and Wilmers 2004, for details), which 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 and constructs isopleths by merging these local polygons, starting with the smallest and ending with the largest. LoCoH is useful for identifying unused areas within a range and, unlike kernel methods, converges to an estimation of area with the addition of data (Getz and Wilmers 2004). We implemented this method as an extension in ArcView, which differs slightly from the method described in Getz and Wilmers (2004), in that k neighbors, not $k - 1$ neighbors, are used in hull construction. To examine the potential areas used by buffalo, we ran this method for k values from 2 to 40 to find the plateau that gives a stable-area value across a range of k values to represent the area of the home range (Fig. 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.

The LoCoH method shows its superiority over earlier methods by being mathematically transparent, by converging to an estimate with the addition of data points, by uncovering lacunae (areas of

avoidance), and by allowing the examination of high-use areas using isopleth analyses.

Focal herd.—To calculate annual home ranges, we selected a randomly sampled location from each day that the herd was seen within each year, from 1993 to 2001. For each year, we ran the LoCoH method for $k = 1 \ldots 40$, and the optimal k was chosen (Table 1).

To make seasonal comparisons, we then resampled these data by available month to create 10 consecutive-day ranges within separate months. Each sample represented 10 consecutive days within a calendar month and was constrained to being at least 10 days from the previous sample. This yielded 85 samples across the entire data set. This set of 10-day ranges was reduced to 84 because closer examination of original field notes revealed one set to be the range of a small splinter group of the primary herd. We used these 84 10-day samples 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 for the minimum spurious hole covering (MSHC) method, as suggested by Getz and Wilmers (2004). We also used these 10-day samples to calculate 10-day trip lengths using the Create Polyline script in the Animal Movement Extension (Hoodge and Eichenlaub 1997) in ArcView, and we tabulated and assigned them to the wet season (Oct–Mar) and the dry season (Apr–Sep) to explore seasonal differences in movement.

Broad-Scale Habitat Selection

Three herds.—A habitat map created by N. Zambatis (*Scientific Services, KNP,* personal communication.) in 1984 describes 8

Table 1. Annual home-range estimates of the focal herd of African buffalo (*Syncerus caffer*) in the Klaserie Private Nature Reserve from 1993–2001 using local nearest-neighbor convex-hull (LoCoH) method.

Year	Area (km²)	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

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 6. Habitat types of the Klaserie Private Nature Reserve (adapted from Zambatis 1982). The numbered sections refer to the following habitat types: 1) *Acacia nigrescens* and *Grewia* sp.: open woodland; 2) mixed *Acacia* sp.: shrub-veld; 3) mixed woodland; 4) *Combretum apiculatum*, *Sclerocarya birrea*: open woodland; 5) *C. apiculatum*, *Sclerocarya caffra*, *Grewia* sp.: short woodland; 6) *C. apiculatum*, *Commiphora mollis*, *Grewia* sp.: closed short woodland; 7) *C. apiculatum*, *Colophospermum mopane*: woodland; and 8) *C. mopane*: woodland and shrub-veld.

broad-scale divisions of savanna woodland types (Fig. 6). The original map delineated major habitat divisions from aerial photographs, which were then subjectively ground-truthed by qualitative assessment of dominant-vegetation types. We scanned, orthorectified, and georeferenced this map from its paper format and rendered it as polygons in an ArcView shapefile. Although this is not a current map, it delineates major divisions of savanna and woodlands within the reserve. Small boundary alterations among habitat types may have occurred during brush manage-ment, but those would be unlikely to affect these analyses.

We tested habitat selection using the Neu method (Neu et al. 1974): a chi-square, goodness-of-fit, applying Bonferroni *Z*-statistics to establish confidence intervals for indications of the preference of particular habitat types (Neu et al. 1974, Alldredge and Ratti 1992). The herd locations were tested for selection across all months and separately for the dry season (Apr–Sep) and wet season (Oct–Mar).

We set up the analysis of selection for water availability using the distance of each herd location observed from the nearest-available water source. We buffered water points and river courses with 1-km bands in ArcView, yielding 5 distance classes, using the Geoprocessing Extension. For the wet season, it was assumed that the 2 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. A partial course for a third river, the Nsiri, 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 so that only water points for which water was actually present in the dry season and perennial portions of river courses were used (see Ryan and Getz 2005). We tested buffalo selection for water availability using the Neu method (Neu et al. 1974) analysis as described above, with the distance-to-water as a categorical choice.

Focal herd.—We conducted our analyses for habitat selection based on broad habitat types, and for water availability for the FH, similarly to the above methodology for the 3 herds, but the analysis was 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, we constructed isopleths as described in Getz and Wilmers (2004) to identify areas of high-observation density within the overall data set for the FH. The isopleths correspond-ing to deciles of data density are shown for all wet-season and all dry-season data (Fig. 7).

Seasonal Herd-Size Analysis

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

Habitat Selection Using Remotely Sensed Vegetation Data

To examine habitat selection on a more local scale, temporally and spatially, we used the FH data as described above in conjunction with remotely sensed vegetation data (NDVI). We made the assumption that the FH was excluded from access to resources across the entire reserve due to behavioral mechanisms of exclusion by the other 2 main herds present. This was a more conservative measure of selection than including the entire reserve, obviating bias due to potential exclusion from certain areas. Thus,
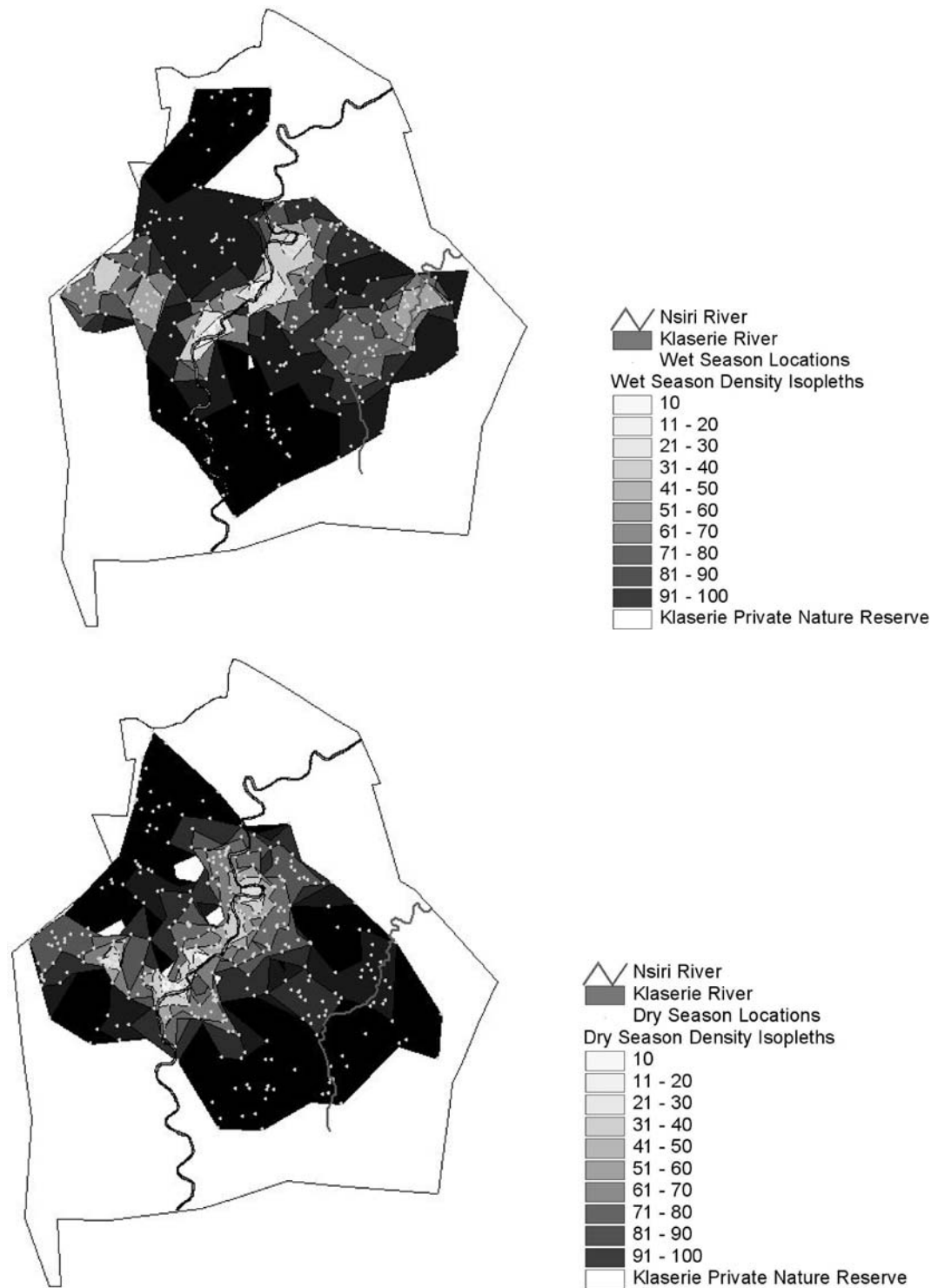
Figure 7. Seasonal differences in density isopleths of focal herd activity. The focal herd of African buffalo (*Syncerus caffer*) was studied 1993–2001.

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. We converted this to raster and used it to clip the vegetation layer to provide the series of cells on which the choice could operate.

Postprocessed NDVI data from the National Oceanographic and Atmospheric Association (NOAA) advanced very high resolution radiometer (AVHRR) 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 and 1995–2001, at a resolution of 1 km^2. A full description of the processing involved in this data before acquisition by this project can be found in Wessels et al. (2004). We used this data as a relative-scale measure of the change in vegetation quality in the reserve, not as absolute values. We

Table 2. Broad-scale habitat selection of African buffalo (*Syncerus caffer*) in the Klaserie Private Nature Reserve from 1995–2000 (3 herds) and 1993–2001 (focal herd).

	Across seasons						Wet season						Dry season					
	Proportion of area			χ² analysis			Proportion of area			χ² analysis			Proportion of area			χ² analysis		
Habitat	Obs[a]	95% CI[b]	sp[c]	Obs[d]	Exp[e]	χ²[f]	Obs[a]	95% CI[b]	sp[c]	Obs[d]	Exp[e]	χ²[f]	Obs[a]	95% CI[b]	sp[c]	Obs[d]	Exp[e]	χ²[f]
Three herds																		
1	0.04	0.01–0.08		14	12.7	0.1	0.04	−0.01–0.09		4	4.5	0.1	0.04	0.01–0.10		10	8.2	0.4
2	0.01	0.02–0.10	+	17	3.4	55.5	0.01	0.01–0.15		8	1.2	39.2	0.01	0.01–0.09		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		57	39.5	7.8	0.14	0.11–0.33		22	14.0	4.7	0.14	0.11–0.27		35	25.5	3.5
5	0.36	0.37–0.53	+	127	101.4	6.5	0.36	0.34–0.62		48	35.8	4.1	0.36	0.33–0.53		79	65.6	2.7
6	0.09	0.03–0.11		19	25.7	1.77	0.09	−0.01–0.09		4	9.1	2.8	0.09	0.03–0.14		15	16.6	0.2
7	0.08	0.05–0.15		29	23.9	1.17	0.08	0.02–0.18		10	8.4	0.3	0.08	0.04–0.17		19	15.4	0.9
8	0.04	0.00–0.00	−	0	12.3	12.3	0.04	0.00–0.00		0	4.3	4.3	0.04	0.00–0.00		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		190	168	2.9	0.20	0.21–0.33	+	110	80.0	11.3	0.20	0.13–0.23		80	88	0.7
5	0.47	0.46–0.55		424	394.8	2.2	0.47	0.38–0.51		181	188.0	0.3	0.47	0.49–0.61	+	243	206.8	6.3
6	0.04	0.01–0.04		23	33.6	3.3	0.04	0.00–0.03	−	5	16.0	7.6	0.04	0.02–0.06		18	17.6	0.01
7	0.08	0.04–0.08		49	67.2	4.9	0.08	0.04–0.11		31	32.0	0.0	0.08	0.02–0.06	−	18	35.2	8.4
8	0.00	0.00–0.00		0	0.0	0.0	0.00	0.00–0.00		0	0.01	0.0	0.00	0.00–0.00		0	0.0	0.0

[a] Observed proportion occurring in the habitat type.
[b] 95% confidence interval of area under a neutral-selection hypothesis. Adjusted α level for this analysis was 0.99, with a corresponding Z-value of 2.73 for the Bonferroni corrections.
[c] The significant preferences and avoidances are denoted + and −, respectively.
[d] Number of observations in habitat type.
[e] Expected observations
[f] Chi-square test.

manipulated this data in ARC/INFO 8.0 (ESRI, 2000) and ArcGIS 8.3 (ESRI, 2000), using ArcMap for visual assessment of available images. For viable images, we used 0–3 images per month to create monthly average grids of data clipped to the KPNR.

Because of the availability of viable NDVI images for this analysis, we reduced the data set 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. 2001). 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

We calculated the chi-square test statistics, with Bonferroni correction criteria in Excel© (Microsoft, Redmond, Washington); all other statistical tests were performed in S-PLUS© 6.0 Professional Release 2.0 (Insightful Corporation, Seattle Washington) or JMP© 4.04 Academic Version (SAS Institute, Cary, North Carolina).

Results

Range Calculations

Three herds.—The NH had an MCP of 102.76 km², a 95% fixed-kernel estimate of 196.91 km², and a LoCoH of 83.17 km² at $k = 18$. The FH had an MCP of 245.13 km², a 95% fixed-kernel estimate of 282.04 km², and a LoCoH of 226.19 km² at $k = 16$. The SH had an MCP of 266.05 km², a 95% fixed-kernel estimate of 341.50 km², and a LoCoH of 251.41 km² at $k = 17$ (Fig. 5).

Focal herd.—The average annual home range was 240.13 ± 16.77 km² (mean ± SE; Table 1). To test whether the number of points used in a year was introducing bias into the estimates, we regressed the estimated area 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 that for the year 1997, a higher-than-average number of points, an average k value, and a smaller-than-average home range was calculated. In addition, a regression of the k that resulted from 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 FH revealed that the buffalo travel significantly farther (27.81 ± 0.98 km dry season; 21.91 ± 1.03 km wet season; Welch-modified 1-way ANOVA: $t = 4.21$, df = 75.57, $P < 0.0001$) and range wider (33.80 ± 2.30 km² dry season; 17.61 ± 2.41 km² wet season; Welch-modified 1-way ANOVA: $t = 5.00$, df = 65.80, $P < 0.0001$) in the dry season.

Habitat Selection

Three herds.—The chi-square test 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

Table 3. Distance-to-water selection of African buffalo (*Syncerus caffer*) in the Klaserie Private Nature Reserve from 1995–2000 (3 herds) and 1993–2001 (focal herd).

Distance-to-water (km)	Area (km²)	Proportion of area			χ² analysis		
		Obs[a]	95% CI[b]	sp[c]	Obs[d]	Exp[e]	χ² [f]
3 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
3 herds, dry season							
0–1	227.3	0.46	0.37–0.56		85	72.0	2.4
1–2	252.8	0.42	0.33–0.51		77	80.1	0.1
2–3	76.2	0.09	0.04–0.15		17	24.1	2.1
3+	21.5	0.02	−0.01–0.05		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		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		182	204.6	2.5
2–3	43.8	0.15	0.08–0.15		51	64.2	2.7
3+	8.0	0.03	0.01–0.06		15	11.9	0.8

[a] Observed proportion occurring in the habitat type.
[b] 95% confidence interval of area under a neutral-selection hypothesis. The wet season adjusted α-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 α-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.
[c] The significant preferences and avoidances are denoted + and −, respectively.
[d] Number of observations in distance to water category.
[e] Expected observations.
[f] Chi-square test.

season, chi-square test 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-square test 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 0–1 km from water and selection against areas greater than 1 km from water. In the dry season, chi-square test 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-square test 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 season: $\chi^2 = 103.69$, df = 7, $n = 400$, $P < 0.001$; dry season: $\chi^2 = 205.84$, df = 7, $n = 440$, $P < 0.001$; Table 2). The FH 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, and selection against types 1, 3, 5, and 7, were indicated.

The FH showed significant distance-to-water selection in both seasons (wet season: $\chi^2 = 27.38$, df = 2, $n = 400$, $P < 0.0001$; dry season: $\chi^2 = 12.74$, 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 1 km 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-square test 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 the 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 FH 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 2 additional areas, including the Nsiri River, whereas in the dry season, it is more focused on the Klaserie River (Fig. 7).

Seasonal Variation in Herd Size

The effects of 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 ± 4.1) was nonetheless significantly smaller than the wet-season herd size (224.66 ± 4.17; 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 was $h = 0.40n - 68.60$). However, annual range was not significantly correlated with either average herd size or total census population size.

Discussion

Our results supported our hypotheses 1 and 5 regarding buffalo herd preference for close proximity to water; buffalo preferred areas at close proximity to water in the wet season; although we found no support for our prediction that herds would show preference for areas further from water in the dry season. However, the idea that buffalo might demonstrate a greater range and travel distance in the dry season (hypothesis 2) was borne out by our analyses. In support of hypothesis 3, we found seasonal differences in herd size, suggesting that perhaps social factors, not foraging constraints are at play in the fission–fusion herd structure in this reserve. However, contrary to hypothesis 4, we did not find evidence of a limiting herd size with increasing population size. We found that buffalo showed preference for certain habitat types (hypothesis 6), and although we found that there was a relationship between NDVI values and buffalo range distance at a seasonal scale, we did not find significant support for the

Table 4. Home-range estimates for African buffalo (*Syncerus caffer*) from several prior studies.

Location	Method	Description of range	No. of buffalo	Range (km^2)
Wankie National Park, Zimbabwe[a]	MCP	Wet season southern herd	123	170
	MCP	Wet season northern herd	24	233
	MCP	Dry season southern herd	123	128
	MCP	Dry season northern herd	259	214
	MCP	Overall southern herd		207
	MCP	Overall northern herd		286
Benoue National Park, Cameroon[b]	MCP	Wet season	50–55	46
	MCP	Dry season	50–55	61
Sabi Sand Wildtuin, South Africa[c]	95% cluster	Annual home range	248	120
	MCP; 95% cluster	Summer (wet)		127.76; 41.48
	MCP; 95% cluster	Winter (dry)		138.04; 120.94
	MCP; 95% cluster	Pre-summer (hot/dry)		114.93; 40.40
Sabi Sand Game Reserve, South Africa[d]	MCP	Overall	700	160
	MCP	Overall	350	90
Ruwenzori[e]	MCP			9.4–9.6
Voi Lodge, Tsavo[f]	MCP	A few weeks	350	85
Serengeti[g]	MCP	Moru (herd 3)	900	271.4
	MCP	Nyaboro (herd 2)	1500	296.3
	MCP	Banagi	800	143.8
	MCP	Seronera	700	178.4
	MCP	Northern (herd 1)	1100	83.5
	MCP	Northern (herd 4)	500	53.0
Momella Lakes[h]	MCP		200	10.9
Rwenzori[i]			130	10

[a] Conybeare 1980.
[b] Stark 1986.
[c] Funston 1994; 1,765 observations.
[d] Kruger 1996.
[e] Eltringham and Woodford 1973.
[f] Leuthold 1972.
[g] Sinclair 1977.
[h] Vesey-Fitzgerald, as cited by Sinclair 1977.
[i] Grimsdell 1969.

hypothesis (7) that herds selected for greener areas on a monthly basis; thus NDVI is perhaps not an appropriate habitat surrogate for a predictive model of buffalo ranging in this study site.

The analysis of the 3 herds' positions during our study demonstrates that although buffalo herd membership may be fluid and, therefore, hard to define, the herd foci occupy distinct areas of the reserve. Contrary to our hypothesis that a small reserve would induce herds to overlap ranges, the overlap of the ranges in our 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 it 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 2 major river courses with perennial portions and many permanent water points, suggesting that the herds' ranges need not overlap extensively due to water availability. Although we found that the 3 foci were in distinctly separate areas, because of the fission–fusion nature of buffalo herds, it is possible that unrecorded subgroups of the herds created overlapping ranges. This suggests that although 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. A previously published description (Prins 1996) and our observation of a consistent core group of females in the FH suggest that this mechanism is possible. The 3 home-range estimation methods that we use demonstrate the potentially different size estimates of the area of the ranges we can obtain using the same data sets. Both the MCP and kernel methods estimated 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 methodology and water distribution regimes and other abiotic factors that we are unable to control, 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, reexamination of that analysis reveals that the larger home-range area estimates also corresponded to larger herds, and there was no control for this factor in the Sinclair (1977) analysis. Both our findings and several other studies suggest that an upward limit of approximately 290 km^2 exists on range size (Fig. 5; Table 4), regardless of buffalo herd size. We compared the annual home range with average annual herd size, and we found that although 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 because it

suggests that the 3 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 in size and 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 because of 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 (e.g., Sinclair 1977, Prins 1996) 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 traveled farther and had larger 10-day ranges in the dry season than in the wet season. This suggests that in the dry season, the herd was either traveling farther 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 in wet season, because despite their reputation as "supreme bulk grazers" (Owen-Smith and 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 KPNR is a savanna ecosystem that is relatively well supplied with water: only 2.2% of the total area is greater than 4 km from water in the dry season. Buffalo herds have been reported in other studies to range 5 km 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 (e.g., Prins 1996), and our isopleth analysis supports this. C. U. Knechtel (Centre for Wildlife Management, University of Pretoria, Pretoria, South Africa, personal observation) noted that when 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 spending time drinking or standing in the riverbed. Water sources used for our analysis represent 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. It was surprising that our analysis of all 3 herds did not reveal a dry season preference for nearer distance to water categories. This may be an artifact of too few data points because it is contrary to the

findings of the FH. 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 KNP that were close to water on low-quality landscapes. 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, 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 our analysis are described by woody structure, the preference for habitat type 2 by all the herds and the FH across both seasons is likely confounded by the presence of reed beds along the Klaserie River at this point. C. U. Knechtel (Centre for Wildlife Management, Pretoria, South Africa, personal observation) suggests that when other areas of vegetation were already yellowish, grayish, or brownish, the river area was still green and greenish/yellowish. The guineagrass (*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 bushwillow (*Combretum* sp.) and other woody shrubs, which is observed more in the dry season, as has been noted in several other studies (Vesey-Fitzgerald 1974, Sinclair 1977, Stark 1986). 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 FH in the wet and dry season respectively is unsurprising, despite the apparent unpalatability of shrubland. The FH showed a preference for short or open woodland and scrub-veld, 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 nearly a decade before the onset of our study, and although 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 regrowth 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 (1 km^2) are hard to interpret for habitat quality. The reflectance values of water and canopy cover in a pixel obscured and lowered the overall value, yielding a low greenness value where there may be subpixel high-quality patches. Thus, a reclassification 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 KNP and the incorporation of KPNR into the Greater Kruger Management Area (GKMA) makes it essential to understand the use patterns and populations of wildlife in the reserve. We recommend that habitat types within KPNR be reclassified to be consistent with those in KNP, as NDVI is not useful for predicting habitat use by these buffalo. In addition, because buffalo prefer areas closer to water sources, we recommend monitoring the increasing buffalo population in KPNR to ensure it is not a response to the removal of water sources in KNP. We suggest that the evidence that buffalo herds do not have greatly overlapping ranges even in a small reserve be used to inform models of disease spread in KNP.

Acknowledgments

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