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HABITAT QUALITY AND HETEROGENEITY INFLUENCE DISTRIBUTION AND BEHAVIOR IN AFRICAN BUFFALO (*SYNCERUS CAFFER*)

John A. Winnie, Jr.,[1,4] Paul Cross,[1,2] and Wayne Getz[3]

[1]*Ecology Department, Montana State University, Bozeman, Montana 59717 USA*
[2]*Northern Rocky Mountain Science Center, USGS, Bozeman, Montana 59717 USA*
[3]*Department of Environmental Science Policy and Management, University of California, Berkeley, California 94720-3112 USA*

Abstract. Top-down effects of predators on prey behavior and population dynamics have been extensively studied. However, some populations of very large herbivores appear to be regulated primarily from the bottom up. Given the importance of food resources to these large herbivores, it is reasonable to expect that forage heterogeneity (variation in quality and quantity) affects individual and group behaviors as well as distribution on the landscape. Forage heterogeneity is often strongly driven by underlying soils, so substrate characteristics may indirectly drive herbivore behavior and distribution. Forage heterogeneity may further interact with predation risk to influence prey behavior and distribution. Here we examine differences in spatial distribution, home range size, and grouping behaviors of African buffalo as they relate to geologic substrate (granite and basalt) and variation in food quality and quantity. In this study, we use satellite imagery, forage quantity data, and three years of radio-tracking data to assess how forage quality, quantity, and heterogeneity affect the distribution and individual and herd behavior of African buffalo. We found that buffalo in an overall poorer foraging environment keyed-in on exceptionally high-quality areas, whereas those foraging in a more uniform, higher-quality area used areas of below-average quality. Buffalo foraging in the poorer-quality environment had smaller home range sizes, were in smaller groups, and tended to be farther from water sources than those foraging in the higher-quality environment. These differences may be due to buffalo creating or maintaining nutrient hotspots (small, high-quality foraging areas) in otherwise low-quality foraging areas, and the location of these hotspots may in part be determined by patterns of predation risk.

Key words: African buffalo; behavior; distribution; forage heterogeneity; foraging; herd size; home range; hotspots; predation; Syncerus caffer.

INTRODUCTION

Herbivores are important components of African savanna that shape the plant communities they depend upon, and are in turn strongly influenced by the spatiotemporal variation in the quantity and quality of forage. At foraging sites, plant quantity, quality, and structure can influence herbivore intake rates (Ungar and Noy-Meir 1988), selectivity (Sinclair and Gwynne 1972), and overall diet quality (Prins 1996, Macandza et al. 2004). Grazers and browsers respond to coarser-scale spatial and temporal variation in food quality and quantity through local, short-term shifts in foraging locations (Fryxell et al. 2004), and larger scale seasonal migrations (Sinclair 1977, Fryxell et al. 1988). Herbivores, in turn, can influence soil nutrient distribution and cycling rates at both local (McNaughton 1988, Frank et al. 1994) and landscape scales (McNaughton 1984, McNaughton et al. 1997, Polis et al. 1997, Frank and Groffman 1998), affecting plant growth rates, distribution, quantity, and quality (McNaughton 1984, Polis et al. 1997, Sinclair 2003).

The top-down effects of predators on herbivore behavior (Underwood 1982, Scheel 1993, Creel and Winnie 2005), distribution (Heithaus and Dill 2002, Winnie and Creel 2007), and population dynamics (Sinclair 1977, Sinclair and Arcese 1995, Creel et al. 2007) have been extensively explored. Recently, however, several authors have presented evidence that populations of Africa's largest herbivores are regulated primarily from the bottom up (Sinclair et al. 2003, Radloff and Du Toit 2004, but see Ogutu and Owen-Smith 2005), and if this is the case, variation in food quality and quantity may not only be important drivers of large-herbivore distribution on the landscape (Sinclair 1977, Morgantini and Hudson 1985, Prins 1996), but also influence both individual and group behaviors. We are not implying that predation risk is unimportant to these animals. Individual large herbivores doubtless do not care whether predation is additive or compensating at the population level, and can reasonably be expected to behave in ways that reduce personal risk. Indeed, predation has been identified as the leading cause of adult mortality in some populations of large herbivores (Sinclair 1977, Prins 1996, Ogutu and Owen-Smith

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[4] E-mail: jwinniejr@msn.com

2005), but because of the demographics of the victims (often a small percentage of newborns, and a larger percentage of individuals near senescence), predation can have little effect on population dynamics relative to other variables such as weather (Sinclair 1977, Mills et al. 1995, Prins 1996, Sinclair et al. 2003, Radloff and Du Toit 2004).

African buffalo (*Syncerus caffer*; see Plate 1) is a common species of large herbivore (+450 kg) in African savanna that shape the plant communities they graze, and through their influence upon forage species, indirectly affect the spatiotemporal distribution of other grazers (Sinclair 1977, McNaughton 1985, Prins 1996). Buffalo are prey for lions (Sinclair 1977, Prins 1996, Radloff and Du Toit 2004), food, and trophies, for subsistence and sport hunters, and are one of Africa's "Big Five," widely promoted as tourist attractions. In Kruger National Park, South Africa (KNP), buffalo are also reservoirs for bovine tuberculosis (BTB) (Rodwell et al. 2000), and due to their dietary preference for grasses (Sinclair 1977, Prins 1996, Gagnon and Chew 2000, Macandza et al. 2004), are likely to come in contact with domestic cattle, and through cattle indirectly infect humans (AHEAD GLTFCA Working Group 2006). The identification of variables that drive buffalo distribution and behavior is important to understand the dynamics of intra- and interspecific disease transmission and overall savanna ecosystem function.

The western two-thirds of the KNP is underlain primarily by granite substrates, while the eastern portion of the KNP is primarily basalt (Gertenbach 1983). These geological substrates are strong drivers of coarse-scale savanna heterogeneity (Scholes et al. 2003, Venter et al. 2003). Granite areas are generally less fertile than basalt, with sandier soils harboring small nitrogen pools that tend to turn over slowly. In contrast, areas underlain with basalt tend to have more fertile, clayey soils, larger nitrogen pools, and higher nutrient turnover rates (Scholes et al. 2003, van Wildgen et al. 2003; but see Mutanga et al. 2004). These differences in geologic substrate lead to fundamental differences in savanna plant communities in KNP (Venter 2003), thus indirectly influencing the quality, quantity, and distribution of forage for grazers and browsers. Indeed, Bell (1982) suggested that the influence of substrate on plant communities is so important that plant–soil relationships should be incorporated into studies of community interactions and treated no differently than trophic interactions.

In KNP, individual buffalo often move from one herd to another, resulting in frequent changes in herd sizes, and both herds and individuals move freely between areas underlain by granite and basalt (Cross et al. 2005). The variables that influence these herd dynamics have not been well studied. Because individuals behaviorally adapt to environmental conditions in real time, geologic heterogeneity that leads to plant community (forage) heterogeneity may indirectly influence animal behavior from the bottom up as they move from one area to another.

Buffalo behavioral responses to forage heterogeneity may in turn influence: the intra- and interspecific transmission and persistence of diseases (Cross et al. 2004, 2005); the quantity (Murray and Illius 2000) and quality of forage available to other grazers (McNaughton 1984, 1985); the distributions and population dynamics of other herbivores (Sinclair 1977, McNaughton 1984, McNaughton et al. 1988); intraspecific interactions, including influencing the strength and nature (linear vs. nonlinear) of density dependence (Chesson and Rosenzweig 1991, Getz 1996); and feedback to influence savanna plant community dynamics (McNaughton 1985, Scholes 1990, Polis et al. 1997, Sinclair 2003). To explore these possibilities, it is first necessary to establish the basic responses of buffalo to the variation in quality and quantity of their food sources, a heterogeneity that in KNP is largely driven by geologic substrate (Scholes et al. 2003, Venter et al. 2003). Here we examine differences in spatial distribution, home range size, and grouping behaviors of African buffalo as they relate to geologic substrate (granite and basalt), and variation in food quality and quantity. In this study, we used satellite imagery, forage quantity data, and three years of radio-tracking data to assess how forage quality, quantity, and heterogeneity affect the distribution, individual, and herd behavior of African buffalo.

Hypotheses

Prior research suggests that buffalo will be more selective in areas and times when forage is abundant (Sinclair and Gwynne 1972). Thus, in addition to testing the hypothesis that forage quality and quantity in granite areas will be of uniformly lower quality and quantity than in basalt areas, we also test the hypothesis that measures of forage quality at buffalo locations will not only be higher on basalt than on granite, but on basalt, buffalo locations will be above the average quality of basalt areas (i.e., buffalo will be more selective while on basalt).

Prior work indicates that buffalo range more widely to meet their daily foraging needs when forage quality is low (Ryan et al. 2006). We test the hypothesis that lower overall quality forage on granite substrates will lead to larger individual buffalo home ranges as compared to home ranges on basalt.

Elgar (1989) suggested that animals in groups may be converging on preferred forage, and offered this as a possible alternative to grouping as predator defense. Given the generally low predation pressure on buffalo (Mills et al. 1995, Sinclair et al. 2003, Radloff and Du Toit 2004), and the large herds common to buffalo (Sinclair 1977, Prins 1996), converging on resources offers a possible explanation for group formation. Thus, we test the hypothesis that group sizes will be larger on granite than on basalt because buffalo will converge on a limited number of high-quality areas. Buffalo in basalt areas will not need to converge on resources because the forage will be of uniformly higher quality. Alternatively, if group size on granite soils is primarily driven by intraspecific competition for limited quantity and quality of forage, we may expect herds to be smaller on granite than basalt substrates.

Finally, because areas nearer to rivers and water holes support greater plant growth throughout the year, we test the hypothesis that buffalo locations will be biased in favor of these areas in both granite and basalt areas, but will be more pronounced in the overall lower-quality granite areas. We also test the related hypothesis that there will be no difference in distance to artificial water sources (boreholes) due to their ubiquity in both regions of the park (Redfern et al. 2003; SANPARKS [South Africa National Parks; *unpublished data*]).

Methods

Study area

Kruger National Park, South Africa, is located along the north end of the border between Mozambique and eastern South Africa. The substrate underlying Kruger is divided east–west between granite (1 255 943 ha) and basalt (643 026 ha), respectively (Fig. 1). The annual wet season extends from roughly November through April, but the precise beginning and end dates vary from year to year, and delays in plant responses to changes in precipitation further blur the boundaries between seasons within and between years. Data for this study were gathered from mid-2001 through 2003, and we delineated wet and dry season based on the above range of dates.

African buffalo

In KNP, African buffalo numbers ranged from ~23 000 to 25 500 during the study period (SANPARKS, *unpublished census data*). Throughout the study, buffalo were often found in large, mixed-gender herds, ranging up to 1000 individuals in a single herd. Smaller herds and singles are generally breeding-age (and sometimes older, postbreeding-age) bachelor males that periodically rejoin the larger herds in attempts to breed (Sinclair 1977, Prins 1996). Kruger helicopter census counts indicate that more buffalo are on granite than basalt (averaging ~14 000 on granite and 10 000 on basalt per year during this study), but buffalo density is lower on granite than on basalt (0.011 buffalo/ha on granite; 0.016 buffalo/ha on basalt) (KNP annual Megaherbivore Censuses, 2001–2003).

As part of a study addressing the spread and persistence of bovine tuberculosis (Cross et al. 2004, 2005) from 2001 to 2003, we randomly selected 134 individuals from representative age and sex classes and fitted them with VHF radio collars (MOD-600 transmitter, Telonics Incorporated, Mesa, Arizona, USA). We attempted to distribute these collars evenly across granite and basalt in the central portion of KNP. However, buffalo frequently moved between herds and from one substrate to the other, thereby disrupting the equal distribution of radio collars across the two substrates (Cross et al. 2005). Field personnel radio-tracked focal herds once per week year-round, and if an individual went missing for over one month it was relocated using fixed-wing aircraft. These individuals yielded 14 980 locations for these analyses. In addition to date, time, and coordinates, we assigned a season (wet, dry) depending on the date of the fix, to each buffalo location. For this study, we defined the study area as the intersection between the minimum convex polygon (MCP) around the entire set of buffalo locations (Convex Hulls around Points v. 1.22, Jeness Enterprises, Flagstaff, Arizona, USA) and the area within Kruger National Park (Fig. 1).

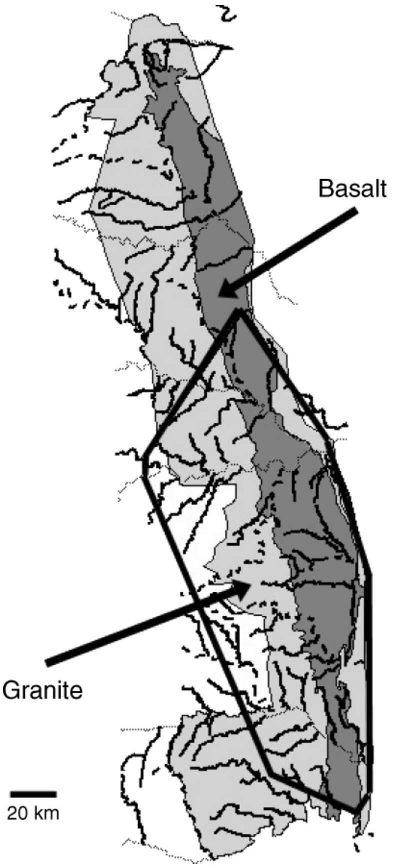

Fig. 1. The shaded areas are Kruger National Park, South Africa, with light gray areas underlain by granite and dark gray areas underlain by basalt. The study area is the intersection of the heavy polygon and shaded areas, and the irregular lines are rivers.

To determine differences in the sizes of individual buffalo home ranges between granite and basalt, we made two comparisons. First, for individuals with ≥40 locations on both substrates, we compared the area on each substrate using 90% LoCoH (Local Convex Hulls) ($k = 5$ [see Getz and Wilmers 2004, Getz et al. 2007]) to determine home range sizes in square kilometers. (Larger values for k yield larger home range estimates, encompassing areas that buffalo are likely to have used, whereas smaller values of k, particularly when combined with lower percentage isopleths, yield tight, conservative home range estimates. That is, we can be more certain that areas within a $k = 5$, 90% LoCoH were used than for a higher k, higher percentile LoCoH isopleth as the home range boundary [see Ryan et al. 2006].) Second, we compared home range sizes of individuals that spent most of their time on one substrate, vs. individuals that spent most of their time on the other substrate (in effect comparing residents of one substrate vs. the other). We defined *most of their time* as five times as many fixes on one substrate vs. the other, with a minimum of 40 locations on the home substrate. We chose 40 as a minimum number of locations needed to define a home range based on exploratory regressions that showed an asymptote in the relationship between the number of points used to build a home range and the total area of the home range occurring between 20 and 40 fixes. As a final check, we regressed home range size against the number of locations used for all home ranges built using 40 or more locations, and found no significant differences in area as number of fixes increased ($r^2 = 0.012$, $P = 0.32$). For the construction of home ranges, we used all the buffalo locations available to us (unlike our evaluations of buffalo location characteristics [see *Forage quality, Landsat data, and buffalo location characteristics*]). For analysis of the resulting home range data, we used single-factor ANOVA with home range size in square kilometers as the dependent variable and substrates (granite, basalt) as independent factors.

Group size

To compare group size between substrates we used two different sources of data. Kruger National Park's annual megaherbivore census is a comprehensive helicopter census of all large herbivores and takes place in the late dry season (typically in late August to early September). Second, we used data from our own field counts (begun in early 2002) while locating radio-collared buffalo throughout the year. Counting buffalo from the ground can be surprisingly difficult, particularly in areas of tall, dense grass, so we used mark–resight Lincoln-Peterson estimates (Chapman 1951, Pollock et al. 1990), and were only able to count herds that were near, or in the process of crossing, roads. When tracking buffalo using VHF telemetry, we determined how many collared individuals were in a herd. Then we counted the herd, recorded how many of the collared individuals we saw, and used the proportion of collared individuals seen to correct the herd count, yielding an estimate of overall herd size. Lincoln-Peterson estimates assume a closed population, no loss of marks, and equal chances of resighting. In this case, where the marked individuals are known to be present, these assumptions are met for the brief period during which we sampled a herd.

For our analysis of the KNP megaherbivore census data we used single-factor ANOVA, with herd size as the dependent variable and substrate (granite, basalt) as the independent variable. For our count data, we used factorial ANOVA with herd size as the dependent variable and substrate (granite, basalt) and season (wet, dry) as the independent variables. As is typical of group size distributions, these data are right-skewed by a few very large herds. Fixed-effect ANOVA is very robust to violations of both normality and homogeneity of variance (Zar 1999).

In addition to the herd size comparisons just described, for both the KNP census data and our own counts, we calculated the herd size experienced by typical buffalo on both granite and basalt by weighting each herd observation by herd size as per Jarman (1974).

Forage quality, Landsat data, and buffalo location characteristics

To assess forage quality at buffalo locations we used Normalized Difference Vegetation Index (NDVI) derived from 30-m resolution Landsat satellite Environmental Thematic Mapper (ETM) data. NDVI is a measure of greenness that gives a coarse measure of photosynthetic activity (NASA, Earth Observatory), which is in turn positively correlated with vegetation quality (nutrient content) (Sinclair 1977, McNaughton 1985, Prins 1996) and net primary productivity (Rasmussen 1998). NDVI values can range from −1 to 1, with higher values indicating greener, more photosynthetically active areas.

Mutanga et al. (2004) found low overall nutrient (Ca, K, Mg, N, Na, P) content across grass species (e.g., <1% of each element) in northern KNP at the wet–dry season transition (April and May), and that nutrient content varied in response to both local geography (slope, aspect, elevation, and soil texture) and landscape-scale geology (areas underlain by granite vs. basalt). Variation in vegetation quality at these spatial scales has been demonstrated to influence African buffalo diet quality (Sinclair and Gwynne 1972, Sinclair 1977, Macandza et al. 2004). In turn, NDVI has been shown to reflect measures of plant quality important to herbivores, including crude protein concentration (percentage of crude protein) and NDF (neutral detergent fiber) (Starks et al. 2006), and nitrogen concentration (Kruse et al. 2006). For elephants (*Loxodonta africana*) in northern Kenya, NDVI is positively correlated with pregnancy rates (Wittemyer et al. 2007), and possibly juvenile survival (Rasmussen et al. 2006), indicating that NDVI captures vegetation characteristics that influence herbivore fitness.

The use of NDVI is problematic in that it is a function of both individual plant greenness and biomass. NDVI values increase as both greenness and biomass increase, and once full coverage of the ground occurs, it is mainly

Table 1. Normalized Difference Vegetation Index (NDVI) values at random points within each satellite view.

NDVI date and season	NDVI value on basalt			NDVI value on granite		
	Mean	SD	CV	Mean	SD	CV
2001_04_28 WET	0.34	0.14	40	0.31	0.08	25
2001_10_05 DRY	−0.19	0.23	121	−0.20	0.08	40
2002_09_22 DRY	−0.23	0.24	105	−0.24	0.09	36
2003_05_04 DRY	−0.05	0.22	395	−0.06	0.10	154

Note: CV = coefficient of variation.

differences in plant greenness that are reflected in changing values. Thus, we also include measures of biomass (see *Forage quantity*, below), to help us infer the degree to which NDVI reflects differences in forage greenness vs. quantity.

Some studies using satellite spectral data rely upon relatively low spatial resolution data (e.g., 1-km MODIS) in exchange for high temporal resolution (daily or eight-day intervals). Because we wished to determine fine-scale differences in forage quality, and coarse-scale temporal changes in habitat use (wet vs. dry season), we chose high spatial, but low temporal, resolution data (30-m Landsat ETM). Implicit in this approach is the assumption that the NDVI value of a location is representative of that site's quality for that season, regardless of date within that season. The lack of high temporal resolution available in Landsat imagery limited our opportunities to acquire clear views (<2% cloud cover) of the study area from November through April, and we obtained only one clear wet-season view during the study period from 2001. We used the latest dry-season view we could obtain in each year (2001–2003); the dates of these views are in Table 1. We used Idrisi GIS (Clark Laboratories, Clark University, Worcester, Massachusetts, USA) to build 30-m resolution NDVI layers from the original Landsat ETM data using the standard formula (NASA, Earth Observatory):

$$\mathrm{NDVI} = \frac{(\mathrm{Band}\ 4 - \mathrm{Band}\ 3)}{(\mathrm{Band}\ 4 + \mathrm{Band}\ 3)}.$$

We imported the buffalo location data and NDVI data layers into ArcView GIS (ESRI, Redlands, California, USA) and using additional data layers obtained from SANPARKS (*unpublished data*), extracted the type of substrate (granite, basalt), distance to nearest river (including all primary, secondary, and tertiary watercourses), water hole, and borehole (artificial water source) for each buffalo location. We also extracted the NDVI value at each buffalo location from the temporally nearest NDVI data from the same year. For example, if a location in 2001 was designated as a dry-season location, we extracted the NDVI value at that location from the 2001 dry season satellite view.

We used autoregression on NDVI values at buffalo locations to check the data for autocorrelation. We sorted the locations on their x and y coordinates and by year (lowest to highest), without regard to individuals, and offset the data, regressing the NDVI values of the sorted locations against the NDVI values of the nearest neighbors. We repeated this process in single increments out to 16 lags (original locations' NDVI values regressed against their 16th nearest neighbors). At 14 lags, we achieved an r^2 value of 0.1. Before we reached 14 lags, r^2 values fell by several percent per lag, but after 14 lags, r^2 fell by single percentage points or less per lag. We decided that the smaller decreases in correlation that occurred beyond 14 lags were not warranted when weighed against the substantial losses in sample size. Based on this result, we subsampled every 14th entry within the sorted buffalo locations, reducing these data from 14 980 to 1070 locations. This technique simultaneously addresses both between- and within-individual autocorrelation in the data, thus addressing units of measure (herd vs. individual) while allowing for individual movements between herds.

To assess buffalo selectivity, we generated 14 980 random points across the study area (equal to the original number of buffalo locations) and randomly assigned 25% of the points to each of the four NDVI layers. We checked for independence in these data by looking for autocorrelation between the NDVI values at nearest spatial neighbors using autoregression, as we previously did for buffalo locations. For these autoregressions we further divided the data into four groups based on substrate and season (granite, wet; granite, dry; basalt, wet; basalt, dry) and regressed nearest neighbors against each other within each group. The resulting single-lag regressions indicated very low autocorrelation between NDVI values at random locations and their nearest neighbor (granite wet $r^2 < 0.0001$, $P = 0.99$; granite dry $r^2 = 0.0004$, $P = 0.13$; basalt wet $r^2 = 0.015$, $P < 0.001$; basalt dry $r^2 = 0.047$, $P < 0.001$). The significant P values on basalt despite very small r^2 values in the random location data illustrate a problem with using large numbers of random points or animal locations for analyses (and in turn inferences): effects sufficiently small to be of little biological interest yield significant P values when sample sizes are sufficiently large. This issue, common among imagery and animal location data, applies to several of our analyses. To offset this problem, we stress results with both significant P values and large (we believe biologically significant) effects in our results and discussion. We further addressed the high degrees of freedom in the

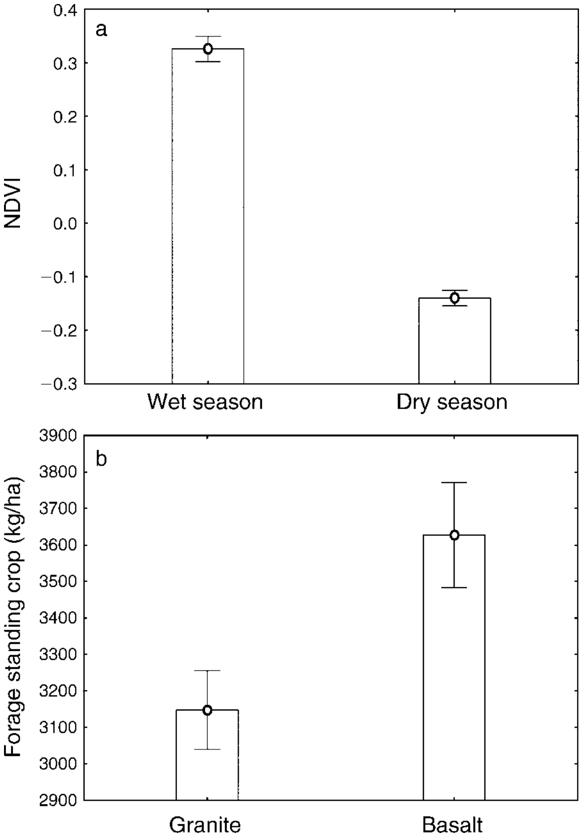

FIG. 2. (a) Normalized Difference Vegetation Index (NDVI) values at random locations in Kruger National Park were higher during the wet season than the dry season, and (b) standing crop of forage at Veld Condition Assessment (VCA) sampling sites was higher on basalt than on granite substrates. Vertical lines through the means denote 95% confidence intervals.

random locations by randomly subsampling these data from 14 980 down to 1070 locations (the same number of points we arrived at for the buffalo locations). This raised the issue of Type 2 errors due to sample size reduction. To address this, in parallel with running analyses on the reduced data sets, we ran all analyses with the full data sets (14 980 random points and 14 980 buffalo locations). All relationships were consistent between the two analyses, but data reduction did broaden confidence intervals, leading to more conservative evaluations of the data.

We merged the random location data with the buffalo location data, allowing the comparison of buffalo locations to random points in the same analyses. We used multifactor and single-factor ANOVA for these analyses, with location NDVI values and distance to rivers, water holes, and boreholes as the dependent variables, and type of point (buffalo vs. random location), substrate (granite, basalt), and season (wet, dry) as the independent factors.

To assess heterogeneity of NDVI values on granite and basalt, we generated 196 438 random points across the study area, and for each point, extracted NDVI values from the same four layers we used to acquire NDVI values at buffalo locations. (We started with 200 000 random points, but some fell on data seams in the GIS layers and were deleted. No points with values that fell within the possible range of NDVI values, −1 to 1, were deleted.) We calculated the mean, standard deviation, and coefficient of variation (CV) within each of these four data sets (NDVI layers), and used differences in CV between granite and basalt as indicators of NDVI (forage quality) heterogeneity.

Forage quantity

Each year KNP staff conduct Veld Condition Assessments (VCA) at ~533 fixed sampling sites across the KNP (SANPARKS, *unpublished data*). The time of the surveys varies slightly from year to year based upon variation in rainfall, and other management activities, but the surveys typically occur in the wet season during peak standing biomass, and depending on site accessibility and staffing, not all sites are sampled all years. Personnel walk four 50-m transects from each sampling site, sampling with a disk pasture meter every 2 m, taking 25 sample readings per transect, yielding 100 points per sampling station. These data are then compiled, and an estimate of standing biomass in kilograms per hectare is calculated for each site. For these analyses, we used single-factor ANOVA with biomass as the dependent variable and substrate (granite, basalt) as the independent variable.

RESULTS

Mean NDVI values at random points were significantly lower during the dry season than in the wet season ($F_{1,1064} = 1097.9$, $P < 0.001$) (Fig. 2a) and lower on granite substrates than on basalt in all satellite views ($F_{1,1064} = 9.12$, $P = 0.003$) (Table 1). The geology by season interaction was not significant ($F_{1,1064} = 0.002$, $P = 0.97$).

Standing crop in kilograms per hectare was higher on basalt than on granite as measured during the annual Kruger Veld Condition Assessments ($F_{1,1357} = 27.42$, $P < 0.0001$) (Fig. 2b).

In each satellite view, there was less variation in NDVI values within random points on granite than within random points on basalt, indicating that granite is a *uniformly* lower-quality foraging environment than basalt (Table 1).

Despite the higher mean NDVI values of random points on basalt areas compared to granite (Fig. 2a), buffalo locations on granite had higher average NDVI values than on basalt, and buffalo selected for areas of higher than average NDVI within granite areas, but lower than average NDVI within basalt ($F_{1,2129} = 11.39$, $P < 0.001$) (Fig. 3).

Buffalo locations averaged ~300 m farther from rivers in the wet season compared with the dry season ($F_{1,1065} = 4.79$, $P = 0.029$). Buffalo locations averaged

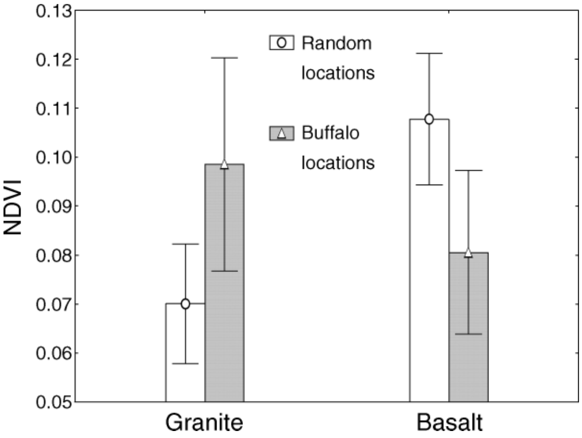

FIG. 3. NDVI values at African buffalo locations compared with random locations for different types of geological substrate (granite and basalt). Vertical lines through the means denote 95% confidence intervals.

~1 km farther from rivers on granite than on basalt ($F_{1,1065} = 60.6$, $P < 0.001$) (Fig. 4a), while random points did not differ significantly in their distance to rivers between granite and basalt ($F_{1,1067} = 0.44$, $P = 0.51$). The season by substrate interaction for buffalo locations was not significant ($F_{1,1065} = 0.999$, $P = 0.31768$).

Buffalo location distances from boreholes in the wet and dry seasons did not differ significantly ($F_{1,1065} = 0.27$, $P = 0.6$), and the season by substrate interaction was not significant ($F_{1,1065} = 0.27$, $P = 0.6$). Buffalo locations on granite averaged ~500 m farther from boreholes than buffalo locations on basalt, and random points on granite and basalt were similar distances to boreholes ($F_{1,1066} = 0.0002$, $P = 0.99$) (Fig. 4b).

Buffalo locations were closer to water holes in the wet seasons than in the dry season ($F_{1,1065} = 63.4$, $P < 0.001$). The season by substrate interaction was significant ($F_{1,1065} = 30.4$, $P < 0.001$), driven by buffalo on granite moving closer to water holes in the wet season (mean distance 8.9 km from water holes in the dry season vs. 4.8 km in the wet season), although overall, buffalo locations on granite and basalt averaged similar distances from water holes ($F_{1,1067} = 0.48$, $P = 0.49$) (Fig. 4c). Random points were farther from water holes on granite than on basalt ($F_{1,1066} = 105$, $P < 0.001$) (Fig. 4c).

Mean herd sizes on granite from the annual KNP dry season Megaherbivore Censuses were approximately half the mean size of herds on basalt ($F_{1,634} = 26.042$, $P < 0.001$) (Fig. 5a). There was no significant effect of year (2001 to 2003) on herd size ($F_{2,634} = 0.97150$, $P = 0.37908$), nor was the year by geology interaction significant ($F_{2,634} = 1.6770$, $P = 0.19$).

Similarly, from our year-round count data, the mean herd size on granite was approximately half that of basalt ($F_{1,117} = 17.314$, $P < 0.001$) (Fig. 5b). There was no significant effect of season on herd size (determined from field count data) ($F_{1,117} = 0.48$, $P = 0.49$), nor was the season by substrate interaction significant ($F_{1,117} = 1.17$, $P = 0.28$). Year (2002 and 2003) was not significant as a main effect on herd size ($F_{1,110} = 0.73$, $P = 0.39$), nor in interactions with season ($F_{1,110} = 2.45$, $P = 0.12$), or geology ($F_{1,110} = 0.15$, $P = 0.7$). Note that the mean herd sizes from our field counts are substantially higher than the Kruger dry season counts. We believe this is because our field counts were based upon herds with radio

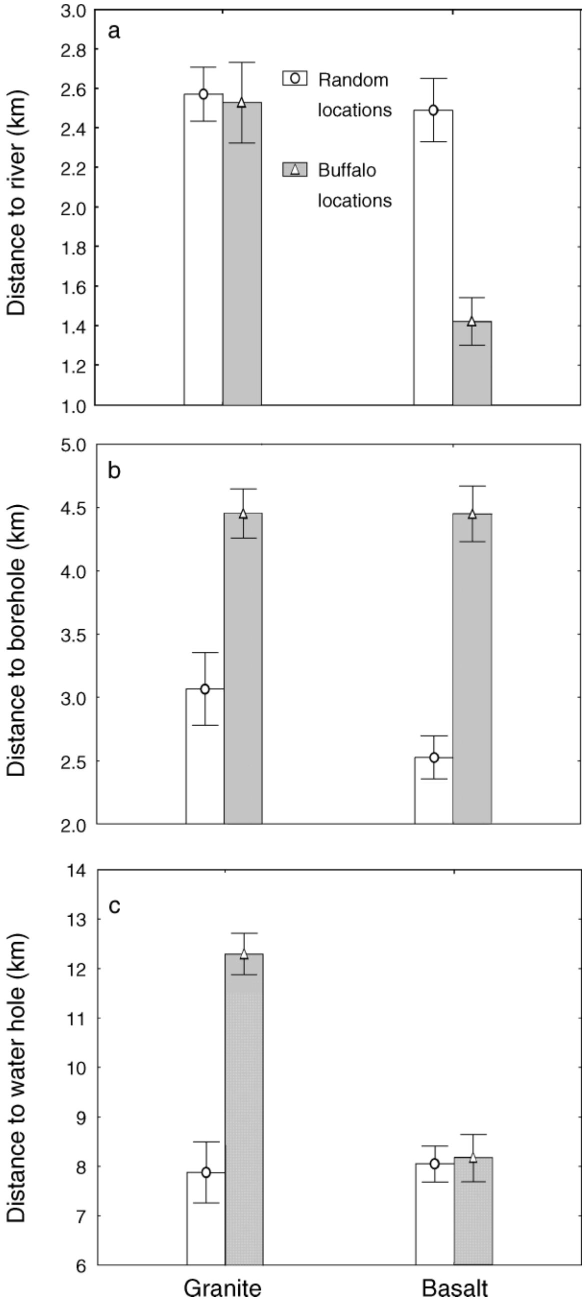

FIG. 4. Comparison of buffalo and random location distances to (a) rivers, (b) boreholes, and (c) water holes for granite and basalt substrates. Vertical lines through the means denote 95% confidence intervals.

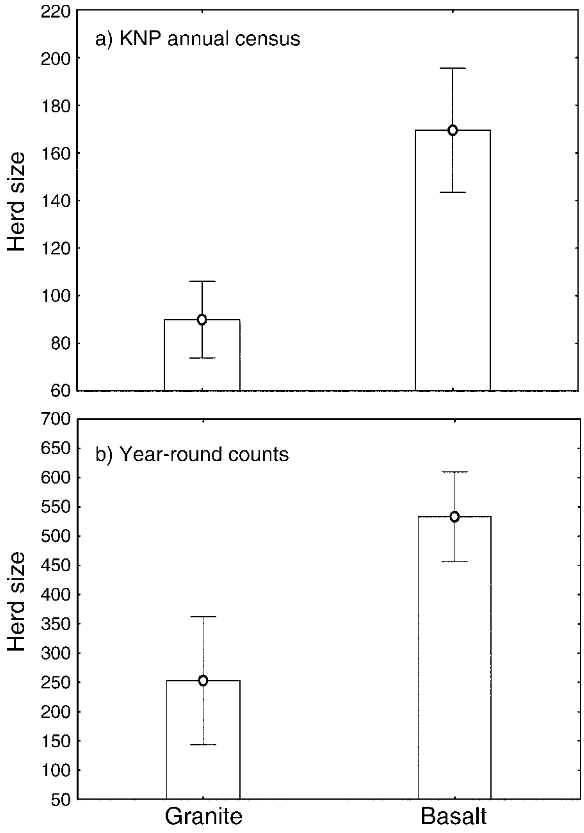

FIG. 5. African buffalo herd size comparisons between granite and basalt substrates, from (a) Kruger National Park (KNP) annual census data and (b) our year-round counts. Vertical lines through the means denote 95% confidence intervals.

collars present, and larger herds were more likely to contain radio collars. Because we are looking for a relative effect on herd size between granite and basalt, and between seasons, we chose to keep these counts in these analyses. In addition, our field counts are based upon herds within the study region, while the aerial census data includes the entire KNP.

The herd sizes observed for typical buffalo mirrored the above results. From the KNP census data, the herd size characteristic of typical buffalo on granite was 343 individuals, and on basalt 473 individuals. From our field counts, the herd size characteristic of typical buffalo on granite was 453 individuals, and on basalt 790 individuals.

Mean home range sizes on granite were approximately half as large as on basalt for individuals that divided their time between both substrates (>40 locations on both granite and basalt) ($n = 42$, $F_{1,82} = 9.04$, $P = 0.004$) (Fig. 6).

There was a similar, but not as strong, difference between individuals that spent most of their time (≥5:1 ratio) on one side vs. the other, with home ranges for individuals frequenting granite averaging approximately two-thirds the size of home ranges of individuals frequenting basalt ($n = 24$ individuals: 4 on granite, 20 on basalt; $F_{1,22} = 3.96$, $P = 0.059$). Unfortunately, for both of these home range size analyses we did not have enough locations to further divide the data by season (yielding a home range size by season by substrate multifactor ANOVA).

DISCUSSION

Our results show that basalt areas have higher biomass than granite areas (Fig. 2b). However, biomass estimates on both substrates are quite high, averaging >3 Mg/ha, and we suggest that from the perspective of an herbivore, the forage quantity differences between the two substrates are not meaningful. Thus, we infer that the differences we see in NDVI values are driven primarily by differences in plant greenness. Granite areas have overall lower quality (as determined by NDVI, Fig. 2a), and forage quality of granite areas appeared less variable than basalt as indicated by a lower coefficient of variation in NDVI values at random points (Table 1). Granite areas in KNP have higher tree densities than basalt areas (Eckhardt et al. 2000). This observation does not confound our results, because any greenness contributed by trees would result in our overestimating grass quality on granite, bringing mean NDVI values on the two substrates closer together. Given that we found granite areas to have significantly lower NDVI values than basalt, the presence of trees does not lead to a Type 2 error.

Buffalo appear to forage in higher-quality areas when they are on granite, a substrate that is on average, lower quality than basalt (Fig. 3). This surprising result, when combined with the smaller average home range sizes on granite (Fig. 6), suggests that buffalo are more selective foragers when they are on granite than when they are on basalt. Alternatively, it is possible that while in the

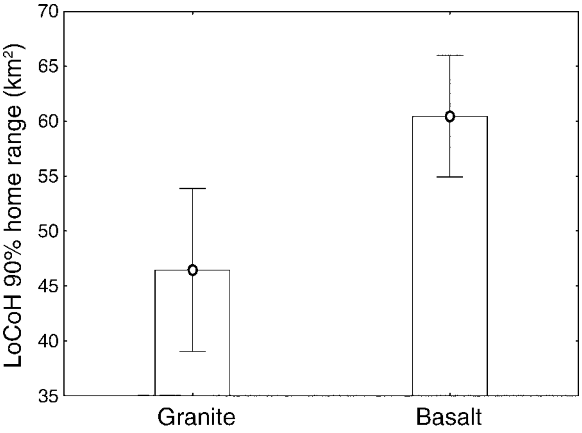

FIG. 6. Comparison of buffalo home range sizes between granite and basalt substrates, using the Local Convex Hulls (LoCoH) method (see *Methods: African buffalo*), for individuals with >40 locations on both substrates. Vertical lines through the means denote 95% confidence intervals.

PLATE 1. African buffalo *Syncerus caffer*. Photo credit: W. Getz.

overall higher-quality basalt areas, buffalo are still selecting the best forage from these more abundant pastures (Sinclair and Gwynne 1972), but that selection is occurring at a finer scale than we can detect using NDVI. However, Ryan (2006) found that buffalo fecal nitrogen content was higher on granite than on basalt (even when body condition was good, precluding the likelihood that their observations were due to catabolic N), further supporting the conclusion that buffalo diets are of higher quality on granite.

Another surprising result is that within the basalt areas, buffalo locations are lower quality than random points (Fig. 3). Mean forage quality and (to a lesser extent) quantity are both relatively high on basalt (Fig. 2), and this combination may more than offset the extra effort needed to be selective while foraging, causing buffalo to become less selective bulk foragers, as suggested by Prins (1996). The shift from selective to bulk foraging observed by Prins (1996) was temporal, as forage quality changed from dry to wet season, respectively. In the case of this study, we appear to see a similar response, but to spatial variation in food quality and quantity. In essence, if forage overall is of sufficient quality and plentiful, it may not matter where buffalo graze as long as they are able to keep their rumen filled. If this is the case, while buffalo are on basalt, decision-making about foraging locations may be driven by factors other than forage quality and quantity. Factors we do not address here, such as predation risk from lions, ease of movement, whether an area has recently been grazed by conspecifics or other species, could all lead to buffalo using locations that are *good enough*, but also below average quality. Prins (1996) suggests that *good enough* (i.e., a maintenance diet that meets both protein and energy needs) is a diet containing roughly 8% protein and 14 600 kJ/d for a 500-kg buffalo, but this may vary considerably based on lactation, breeding status, gender, and environmental stresses.

Granite areas had uniformly lower mean NDVI values and somewhat lower biomass than basalt areas (Table 1, Fig. 2b). While on granite, buffalo appear to be keying-in on areas of exceptionally high quality (Fig. 3), and these areas are not near rivers or water holes as we expected (Fig. 4a, c). This result raises the interesting possibility that buffalo are contributing to the creation or maintenance of high-quality areas on granite by influencing nutrient cycling and distribution, a process that has been documented elsewhere in South Africa. Scholes (1990) summarized a group of studies examining soil fertility and nutrient cycling in sandy soils similar to KNP's granite areas, identifying areas of high fertility on otherwise depauperate substrates that appeared to be created and maintained by animal activity (the interaction of grazers and browsers with plant life), and referring to these places as *nutrient hotspots*. McNaughton et al. (1997) experimentally demonstrated that nutrient hotspots are in part the result of a positive feedback loop: the use of these areas by grazers enhances plant growth and quality, creating places that are better for, and more attractive to, grazers, and the grazers in turn use these areas more. The possibility that this is occurring in KNP is supported by our result that buffalo locations on granite are far from rivers and water holes (Fig. 4a, c) and farther from rivers and boreholes than buffalo locations on basalt (Fig. 4a, b). When on granite, buffalo are *not* using the areas that are most commonly documented to have highest forage quality, i.e., near natural water sources (Sinclair 1977, Prins 1996). However, the places they are using on granite are of exceptionally high quality when compared both within granite, and between granite and basalt (Fig. 3). The set of hypotheses that we introduced in this paper, as well as the data we used, do not directly address the possibility of nutrient hotspots. However, we offer a nutrition hotspot hypothesis as a plausible explanation for the distribution patterns we see in KNP buffalo and as an interesting area for further research.

It is important to note that the above patterns may also arise due to differences in competition or predation between the two landscape types. Few data exist on predation rates in the two landscapes, and variation in the nature of spatial predation risk between granite and basalt could also lead to the patterns we are seeing. For example, although plant biomass differences between substrates may not be important from a feeding perspective, biomass is higher on basalt than on granite (Fig. 2b). This in turn may yield a more uniform distribution of lion predation risk (because lions are ambush predators that approach prey closely under cover of vegetation before launching their final attacks [Schaller 1972]). More dense vegetation may make it difficult for buffalo to discern areas of high vs. low risk, so buffalo distribution on the landscape is minimally influenced by spatial variation in risk in basalt areas. Granite supports ~20% less dense vegetation (Fig. 2b), and places of high risk may be more predictable, such as near rivers or water holes, so buffalo may seek to avoid these areas while on granite. This raises the possibility of important relationships between substrate and the spatial distribution of risk, as well as the way in which buffalo responses to risk influence both their own distribution and plant distribution. If buffalo are avoiding areas of high risk on granite, and these areas tend to be near natural water sources because of the way that substrate influences vegetation, we can hypothesize that buffalo risk avoidance leads to the creation of alternate foraging areas through enrichment, that is, the creation of nutrient "hotspot" foraging areas away from places of highest risk. We cannot test this hypothesis here for lack of suitable data. However, it suggests a future area of research that should help broaden our understanding of the importance of trade-offs between optimal foraging from a purely consumption point of view and predator avoidance.

Herd size differences between granite and basalt areas (Fig. 5) may be a result of interactions among volume and quality of forage locally available per individual, and forage heterogeneity. Because overall forage density and quality are lower on granite, buffalo key-in on areas of very high-quality forage on granite and restrict their movements to these places, as reflected in the reduced home range sizes (Fig. 6). Smaller home ranges suggest that these higher-quality areas are small (at least in comparison to those seen on basalt), so the local consequences of intraspecific competition may force reductions in group size. This may partially explain the fission–fusion patterns in buffalo group dynamics observed by Cross et al. (2005). As buffalo move through heterogeneous environments they adjust group size to accommodate variation in forage distribution (in both quantity and quality), leading to smaller herds on granite and larger herds on basalt. It should be noted that overall density is lower on granite than basalt, and that these are two adjoining areas over which a single population roams. Thus differences in density do not result from two separate populations of buffalo contained in two separate areas; instead, the animals respond to differing environmental characteristics as they move freely about the region.

Given our attempts to evenly distribute collars between granite and basalt areas, fewer collared animals than we expected made granite their primary residence (4 animals on granite, 20 on basalt). We did not anticipate this in our original hypotheses, but a possible explanation is that we managed to relocate animals less often while they were on granite due, in part, to the larger area, and also because some individuals frequently left KNP to the west, entering private game reserves. Thus, individuals that would otherwise have been included in the analyses were excluded by the minimum number of fixes that we required for home range analyses (40, see *Methods*). This potential bias would influence the number of individuals labeled as residents, but should not lead to a bias in home range size estimates between the two substrates (see *Methods*), and so should not influence the interpretation of our result that home range sizes are smaller on granite than on basalt.

Our results suggest that buffalo selectivity depends on the nature of forage heterogeneity at a variety of spatial scales. Sinclair and Gwynne (1972) found that when individual buffalo foraged in large enclosures of high-quality sward they were very selective (but these individuals were unencumbered by conspecifics). Other authors have identified landscape-scale responses to environmental heterogeneity (Sinclair 1972, Prins 1996). We can not directly address selectivity within foraging areas on granite or basalt, but our results show that while on granite buffalo are choosing to forage in exceptionally high-quality areas, and this suggests that they are responding to an intermediate scale of heterogeneity, well below landscape and well above that necessary when making bite choices. The differences we see here between granite and basalt areas in distribution (distance to water sources), forage selection, group size, and home range size, further suggest that to understand buffalo herd dynamics, distribution, and ultimately population dynamics (Chesson and Rosenzweig 1991), it will be necessary to consider buffalo responses to this intermediate scale of forage heterogeneity.

Considered in parallel with the work of others, our results show that buffalo foraging and grouping behavior is surprisingly complex and strongly influenced from the bottom up. Buffalo respond to different forage quality and quantity by altering their home range size (Fig. 6) and group size (Fig. 5a, b); respond to lower overall forage quality by becoming more selective in their foraging sites (Fig. 3); respond to low densities and high-quality forage by becoming more selective in their diet (Sinclair and Gwynne 1972); and appear to respond to high densities and overall higher-quality forage by becoming less selective in their foraging (Prins 1996), earning the title, "supreme bulk grazers" (Owen-Smith and Cumming 1993) (Fig. 3).

Herbivores respond to variation in forage quality and quantity at a variety of spatial and temporal scales. Most documented responses involve local or large-scale movements that track areas of highest-quality forage (Sinclair 1977, Fryxell et al. 1988, Fryxell et al. 2004), or individual selectivity at very fine scales (Sinclair and Gwynne 1972, Macandza et al. 2004). Here we have identified several unexpected behavioral responses to forage heterogeneity that appear to ultimately be driven by coarse-scale differences in geologic substrate. Substrate appears to drive overall forage quality as well as heterogeneity, and buffalo respond to these differences by distributing themselves in unexpected ways with respect to water, and altering individual home range size and group size. For a group-living species with a well established need for water (Sinclair 1977, Prins 1996, Redfern et al. 2003) to fundamentally alter its distribution and group dynamics in response to changes in forage, suggests that forage heterogeneity is a strong driver of behavior. Our results further suggest that to better understand top-down and bottom-up influences on animal behavior and distribution, it is necessary not only to address trophic interactions, but also to consider how abiotic components, through their influence on plant community heterogeneity, indirectly influence the distribution of predation risk.

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Literature Cited

AHEAD-GLTFCA Working Group 2006. AHEAD-GLTFCA Working Group–Sixth Meeting. 9–10 March 2006, Pestana Kruger Lodge, Malelane, South Africa. ⟨http://www.wcs-ahead.org/workinggrps_limpopo.Html⟩

Bell, R. H. V. 1982. The effects of soil nutrient availability on community structure in African ecosystems. Pages 193–216 *in* B. J. Huntley and B. H. Walker, editors. The ecology of tropical savannas. Springer-Verlag, Berlin, Germany.

Chapman, D. G. 1951. Some properties of the hypergeometric distribution with applications to zoological censuses. University of California Publications in Statistics 1:131–160.

Chesson, P., and M. Rosenzweig. 1991. Behavior, heterogeneity, and the dynamics of interacting species. Ecology 72: 1187–1195.

Creel, S., D. Christianson, S. Liley, and J. Winnie, Jr. 2007. Predation risk affects reproductive physiology and demography of elk. Science 315:96.

Creel, S., and J. Winnie, Jr. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. Animal Behaviour 69:1181–1189.

Cross, P. C., J. O. Lloyd-Smith, J. A. Bowers, C. T. Hay, M. Hofmeyr, and W. Getz. 2004. Integrating association data and disease dynamics in a social ungulate: bovine tuberculosis in African buffalo in the Kruger National Park. Annales Zoologici Fennici 41:979–892.

Cross, P. C., J. O. Lloyd-Smith, and W. M. Getz. 2005. Disentangling association patterns in fission-fusion societies using African buffalo as an example. Animal Behaviour 69: 499–506.

Eckhardt, H. C., B. W. van Wilgen, and H. C. Biggs. 2000. Trends in woody vegetation cover in Kruger National Park, South Africa, between 1940 and 1988. African Journal of Ecology 38:108–115.

Elgar, M. A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. Biological Review 64:13–33.

Frank, D. A., and P. M. Groffman. 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. Ecology 79:2229–2241.

Frank, D. A., R. S. Inouye, N. Huntly, G. W. Minshall, and J. E. Anderson. 1994. The biogeochemistry of a north-temperate grassland with native ungulates: nitrogen dynamics in Yellowstone National Park. Biogeochemistry 26(3): 163–188.

Fryxell, J. M., J. Greever, and A. R. E. Sinclair. 1988. Why are migratory ungulates so abundant? American Naturalist 131(6):781–798.

Fryxell, J. M., J. F. Wilmhurst, and A. R. E. Sinclair. 2004. Predictive models of movement by Serengeti grazers. Ecology 85:2429–2435.

Gagnon, M., and A. Chew. 2000. Dietary preferences in extant African Bovidae. Journal of Mammalogy 81(2):490–511.

Gertenbach, W. P. D. 1983. Landscapes of the Kruger National Park. Koedoe 26:9–121.

Getz, W. M. 1996. A hypothesis regarding the abruptness of density dependence and the growth rate of populations. Ecology 77:2014–2026.

Getz, W. M., S. Fortmann-Roe, P. C. Cross, A. J. Lyons, S. J. Ryan, and C. C. Wilmers. 2007. LoCoH: non-parametric kernel methods for constructing home ranges and utilization distributions. PLoS One 2(2):e207.

Getz, W. M., and C. C. Wilmers. 2004. A local nearest neighbor convex-hull construction of home-ranges and utilization distributions. Ecography 27:489–504.

Heithaus, M. R., and L. M. Dill. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83:480–491.

Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. Behaviour 48(3–4):215–267.

Kruse, J. K., N. E. Christians, and M. H. Chaplin. 2006. Remote sensing of nitrogen stress in creeping bentgrass. Agronomy Journal 98:1640–1645.

Macandza, V. A., N. Owen-Smith, and P. C. Cross. 2004. Forage selection by African buffalo in the late dry season in two landscapes. South African Journal of Wildlife Research 34(2):113–121.

McNaughton, S. J. 1984. Grazing lawns: animals in herds, plant form, and co-evolution. American Naturalist 124(6):863–886.

McNaughton, S. J. 1985. Ecology of a grazing system: the Serengeti. Ecological Monographs 55:259–294.

McNaughton, S. J., F. F. Banykwa, and M. M. McNaughton. 1997. Promotion of the cycling of diet-enhancing nutrients by African grazers. Science 278:1798–1800.

McNaughton, S. J., R. W. Ruess, and S. W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. BioScience 38(11):794–800.

Mills, M. G., H. C. Biggs, and I. J. Whyte. 1995. The relationship between rainfall, lion predation and population trends in African herbivores. Wildlife Research 22:75–88.

Morgantini, L. E., and R. J. Hudson. 1985. Changes in diets of Wapiti during a hunting season. Journal of Range Management 38:77–79.

Murray, M. G., and A. W. Illius. 2000. Vegetation modification and resource competition in grazing ungulates. Oikos 89:501–508.

Mutanga, O., H. H. T. Prins, A. K. Skidmore, S. van Wieren, H. Huizing, R. Grant, M. Peel, and H. Biggs. 2004. Explaining grass-nutrient patterns in a savanna rangeland of southern Africa. Journal of Biogeography 31:819–829.

Ogutu, J. O., and R. N. Owen-Smith. 2005. Oscillations in large mammal populations: are they related to predation or rainfall? African Journal of Ecology 43:332–339.

Owen-Smith, N., and D. H. M. Cumming. 1993. Comparative foraging strategies of grazing ungulates in African savanna grasslands. Proceedings of the International Grassland Congress 17:691–697.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28:289–316.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107:1–97.

Prins, H. H. T. 1996. Ecology and behaviour of the African Buffalo: social inequality and decision making. Chapman and Hall, London, UK.

Radloff, F. G., and J. T. Du Toit. 2004. Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. Journal of Animal Ecology 73: 410–423.

Rasmussen, H. B., G. Wittemyer, and I. Douglas-Hamilton. 2006. Predicting time-specific changes in demographic processes using remote-sensing data. Journal of Applied Ecology 43:366–376.

Rasmussen, M. G. 1998. Developing simple, operational, consistent NDVI-vegetation models by applying environmental and climatic information: Part I. Assessment of net primary production. International Journal of Remote Sensing 19(1):97–117.

Rodwell, T. C., N. P. Kriek, R. G. Bengis, I. J. Whyte, P. C. Viljoen, V. De Vos, and W. M. Boyce. 2000. Prevalence of bovine tuberculosis in African buffalo at Kruger National Park. Journal of Wildlife Diseases 37:258–264.

Ryan, S. J. 2006. Spatial ecology of African buffalo and their resources in a savanna ecosystem. Dissertation. University of California, Berkeley, California, USA.

Ryan, S. J., C. U. Knechtel, and W. M. Getz. 2006. Range and habitat selection of African buffalo in South Africa. Journal of Wildlife Management 70(3):764–776.

Schaller, G. 1972. The Serengeti lion: a study of predator-prey relations. Wildlife Behaviour and Ecology Series. University of Chicago Press, Chicago, Illinois, USA.

Scheel, D. 1993. Watching for lions in the grass: the usefulness of scanning and its effects during hunts. Animal Behaviour 46:695–704.

Scholes, M. C., R. J. Scholes, L. B. Otter, and A. J. Woghiren. 2003. Biogeochemistry: the cycling of elements. Pages 130–148 *in* J. T. Du Toit, K. H. Rogers, and H. C. Biggs, editors. The Kruger experience: ecology and management of savanna heterogeneity. Island Press, Washington, D.C., USA.

Scholes, R. J. 1990. The influence of soil fertility on the ecology of southern African dry savannas. Journal of Biogeography 17:415–419.

Sinclair, A. R. E. 1977. The African buffalo: a study of resource limitation of populations. University of Chicago Press, Chicago, Illinois, USA.

Sinclair, A. R. E., and P. Arcese. 1995. Population consequences of predation sensitive foraging: the Serengeti wildebeest. Ecology 76:882–891.

Sinclair, A. R. E., and M. D. Gwynne. 1972. Food selection and competition in east African buffalo (*Syncerus caffer* Sparrman). East African Wildlife Journal 10:77–89.

Sinclair, A. R. E., S. Mduma, and J. S. Brashares. 2003. Patterns of predation in a diverse predator-prey system. Nature 425:288–290.

Starks, P. J., D. Zhao, W. A. Phillips, and S. W. Coleman. 2006. Herbage mass, nutritive value and canopy spectral reflectance of bermudagrass pastures. Grass and Forage Science 61:101–111.

Underwood, R. 1982. Vigilance behaviour in grazing African antelopes. Behaviour 79:81–107.

Ungar, E. D., and I. Noy-Meir. 1988. Herbage intake in relation to availability and sward structure: grazing processes and optimal foraging. Journal of Applied Ecology 25(3): 1045–1062.

van Wildgen, B. W., W. S. W. Trollope, H. C. Biggs, A. L. F. Potgieter, and B. H. Brockett. 2003. Fire as a driver of ecosystem variability. Pages 149–170 *in* J. T. Du Toit, K. H. Rogers, and H. C. Biggs, editors. The Kruger experience: ecology and management of savanna heterogeneity. Island Press, Washington, D.C., USA.

Venter, F. J., R. J. Scholes, and H. C. Eckhardt. 2003. The abiotic template and its associated vegetation pattern. Pages 83–129 *in* J. T. Du Toit, K. H. Rogers, and H. C. Biggs, editors. The Kruger experience: ecology and management of savanna heterogeneity. Island Press, Washington, D.C., USA.

Winnie, J., Jr., and S. Creel. 2007. Sex-specific behavioural response to spatial and temporal variation in the threat of wolf predation. Animal Behaviour 73:215–225.

Wittemyer, G., H. B. Rasmussen, and I. Douglas-Hamilton. 2007. Breeding phenology in relation to NDVI variability in free-ranging African elephant. Ecography 30:42–50.

Zar, J. H. 1999. Biostatistical analysis. Prentice Hall, Upper Saddle River, New Jersey, USA.