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SURFACE-WATER CONSTRAINTS ON HERBIVORE FORAGING IN THE KRUGER NATIONAL PARK, SOUTH AFRICA

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Abstract. At a landscape scale, the combined influence of biotic and abiotic factors may determine the distribution patterns of large herbivores in African savanna ecosystems. Herbivores foraging in these ecosystems may become nutritionally stressed during an annual dry season when both forage quality and quantity are reduced. Additionally, the locations of water sources may impose a landscape-scale constraint on dry-season herbivore distributions. We used logistic regression to analyze 13 years of aerial census data collected in the Kruger National Park (KNP), South Africa, and evaluated hypotheses regarding the relative influences that surface water, forage quality, and forage quantity exert on the dry-season, landscape-scale distribution patterns of eight herbivore species. Hypotheses regarding the degree of correlation between species' distributions and distance to water were developed using previous observations of species' relative water dependence. We also developed hypotheses regarding species' responses to the trade-off that may occur between surface-water constraints and nutritional requirements when either forage quality or quantity is reduced. In general, we expect an increase in species' mean distance to water as a result of individuals mitigating limitations in nutritional requirements (i.e., intake quality or quantity) by foraging farther from water. Our analyses suggest that the trade-off between nutritional requirements and surface-water constraints that species face varies according to the species' water dependence, size, and gut morphology. Of the four grazers considered in our analyses, waterbuck distributions appear to be constrained primarily by surface-water availability. Distributions of buffalo, a large ruminant grazer, suggest that individuals face a trade-off between nutritional requirements and surface-water constraints when forage quantity is reduced. Alternatively, distributions of wildebeest, a smaller ruminant grazer, suggest that individuals face this trade-off when access to high-quality forage is limited. In comparison to buffalo and wildebeest, the strength of this trade-off is moderate for zebra, a nonruminant similar in size to wildebeest, when either forage quality or quantity is reduced. Distribution patterns for browsers are characterized by a weak relationship with distance to water, as expected for these relatively water-independent species. Population densities relative to forage quality confound exploration of this trade-off for mixed feeders.

Key words: abiotic constraints; biotic constraints; foraging; herbivore distribution; Kruger National Park, South Africa; landscape scale; logistic regression; resource trade-offs; savanna; South Africa; surface water.

INTRODUCTION

An important challenge facing wildlife managers is to identify landscape-scale determinants of the distribution of large herbivores. Mechanistic optimal foraging models of large herbivores have been applied to understand the determinants of aggregation (Fryxell 1991) and to predict habitat selection (Wilmshurst et al. 1999, 2000). Models based on the ideal free distribution, IFD (see Fretwell and Lucas 1970, Fretwell 1972), however, have not been successful at predicting animal distributions (Kennedy and Gray 1993), particularly when applied to large spatial areas (Tyler and Hargrove 1997). This failure may be caused by vio-

lations of IFD assumptions, specifically that individuals are free to move to any patch and that movement costs are negligible (Kennedy and Gray 1993, Tyler and Hargrove 1997). Additionally, the utility of many landscape-scale models of herbivore distributions may be limited because they focus primarily on the role of biotic factors. At a landscape scale, abiotic factors also act as constraints on large-herbivore distributions (Senft et al. 1987, Bailey et al. 1996), necessitating an evaluation of the influence of both biotic and abiotic factors (Senft 1989, Bailey et al. 1996).

The combined influence of biotic and abiotic factors may be particularly important in determining the distribution patterns of large herbivores in African savanna ecosystems. Herbivores foraging in these ecosystems may become nutritionally stressed during an annual dry season when both forage quality and quantity are reduced (Owen-Smith 1982, Prins 1996). Ad-
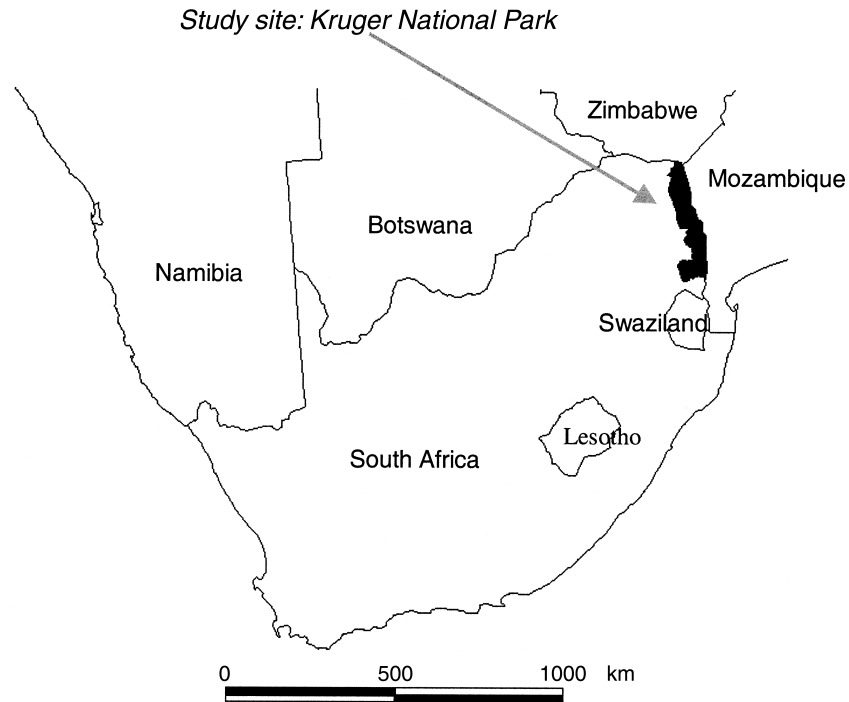
FIG. 1.   A map of southern Africa showing the study site, Kruger National Park, KNP (modified from Redfern et al. [2002]).

ditionally, previous studies suggest that the locations of water sources in these ecosystems impose a landscape-scale constraint on dry-season herbivore distributions (Young 1970, Western 1975, Owen-Smith 1996). For example, a study in Amboseli, Kenya, found that during the dry season, 99% of herbivore biomass occurred within 15 km of surface water, a region comprising 52% of the total ecosystem area (Western 1975). Hence, herbivores in African savanna ecosystems must meet their nutritional requirements within the constraints set by the location of water sources.

We used logistic regression to evaluate hypotheses regarding the relative influence exerted by surface water, forage quality, and forage quantity on the dry-season distribution patterns of eight herbivore species in the Kruger National Park (KNP), South Africa (Fig. 1). Herbivore species considered in these analyses were selected because of their relative abundance in the KNP (Fig. 2) and because they represent a spectrum of feeding types, sizes (as represented by female body mass estimates), and gut morphology (Table 1). Hypotheses were formulated in terms of the relative differences expected among species of the same feeding type, specifically grazers, browsers, and mixed feeders. In particular, species-specific hypotheses regarding the degree of correlation between species' distributions and distance to water in the KNP were developed using previous observations (Western 1975, Estes 1991, Owen-Smith 1996) of species' water dependence. We also developed hypotheses regarding each species' response to the trade-off that may occur between surface-

water constraints and nutritional requirements when either forage quality or quantity is reduced. In general, we expect an increase in a species' mean distance to water as a result of individuals mitigating limitations in nutritional requirements (i.e., intake quality or quantity) by foraging farther from water.

Hypotheses: distance-to-water correlations

If herbivore drinking requirements necessitate regular access to surface water, species' distributions relative to water sources should correspond to their water dependence. Specifically, herds of water-independent species should be distributed randomly with respect to distance to water, whereas herds of water-dependent species should occur close to water sources. Western (1975) found browsers to be more water independent than grazers. It can be hypothesized that the physiological barriers that species encounter in using forage low in water content when surface water is scarce place a greater restriction on grazer than on browser distributions because the water content of grass falls below that of browse during the dry season (Western 1975). Hence, we expect weaker correlations between distance to water and distributions of the two browsers considered in our analyses, giraffe and kudu, compared to correlations for grazers.

Additionally, Owen-Smith (1996) suggests that species with a high biomass density are the most affected by surface-water availability. In the KNP, three of the grazers considered in our analyses (buffalo, zebra, and wildebeest) occur at a high biomass density (Fig. 2)
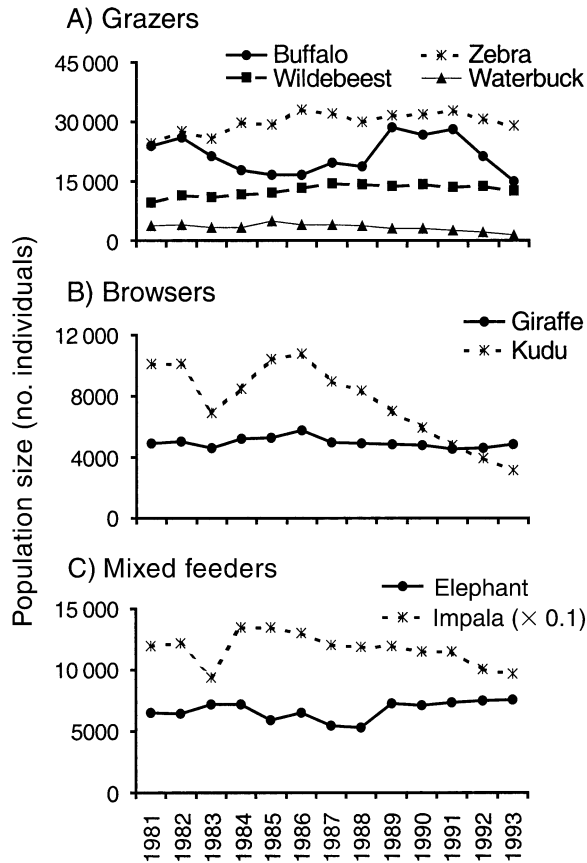
Fig. 2. Population size, estimated from the number of individuals recorded in the aerial census data during the study period (1981–1993), plotted annually. Note that depicted impala population sizes have been multiplied by 0.1; i.e., actual populations were 100 000–150 000.

and are considered water-dependent herbivores (Estes 1991). We expect, therefore, a strong correlation between distance to water and distributions of buffalo, zebra, and wildebeest. Among the four grazers, however, the strongest correlations are expected between

distance to water and waterbuck distributions because waterbuck are suggested to be the most water-dependent antelope (Estes 1991) (see Plate 1). Although the diets of the two mixed feeders considered in our analyses (elephant and impala) contain a high proportion of browse during the dry season (Estes 1991), both species occur at a high biomass density (Fig. 2) and are considered to be water-dependent herbivores (impala, Estes [1991]; elephant, Owen-Smith [1988]). Consequently, we expect strong correlations between distance to water and distributions of elephant and impala.

Hypotheses: response to reduced forage quality

No long-term, direct measures of forage quality are available for the KNP. Forage quality, however, is expected to differ between the eastern and western KNP landscapes (Fig. 3). The eastern KNP landscape occurs on soils rich in clay minerals derived mainly from basalts, whereas the more undulating western KNP landscape occurs on sandy soils derived mainly from granites (Venter 1986). We define the term "landscape" broadly, differentiating the eastern and western landscapes on the basis of the dominant soil substrate. Thus, our landscape definition subsumes smaller patches of differing soil types that increase variability at a finer level of resolution. For example, small patches created by gabbro intrusions are subsumed in the predominantly granite-derived western landscape. Aggregate soil mineral concentrations will be lower in the KNP western landscape than in the KNP eastern landscape; hence, forage quality may be lower in the western landscape (Bell 1982, Venter 1986, Scholes 1990). In particular, it is expected that patches of high-quality forage will form a smaller proportion of the landscape and, hence, will have a more dispersed distribution in the nutrient-poor western landscape than in the nutrient-rich eastern landscape (R. N. Owen-Smith, *personal communication*).

Previous studies suggest that critical forage quality thresholds are higher for small than large animals and

TABLE 1. Species' characteristics and hypotheses regarding species' responses to reductions in forage quality and quantity derived from species' feeding type, size, and gut morphology (see *Introduction* for references).

Species	Scientific name	Feeding type	Mass† (kg)	Gut morphology	Hypothesized increase in mean distance to water in response to forage differences‡	
					Forage quality	Forage quantity
Buffalo	*Syncerus caffer*	grazer	576	ruminant	weak	strong
Zebra	*Equus burchelli*	grazer	220	nonruminant	moderate	moderate
Wildebeest	*Connochaetes taurinus*	grazer	200	ruminant	strong	weak
Waterbuck	*Kobus ellipsiprymnus*	grazer	186	ruminant	strong	weak
Giraffe	*Giraffa camelopardalis*	browser	700	ruminant	weak	weak
Kudu	*Tragelaphus strepsiceros*	browser	170	ruminant	weak	weak
Elephant	*Loxodonta africana*	mixed	3000	nonruminant	weak	strong
Impala	*Aepyceros melampus*	mixed	45	ruminant	strong	weak

† Female body mass estimates (Estes 1991).
‡ Restricted access to high-quality forage in the KNP is expected in the nutrient-poor landscape compared to the nutrient-rich landscape. Lower forage quantities are expected in dry compared to wet years.

PLATE 1. A herd of waterbuck (*Kobus ellipsiprymnus*) at a water source in the Kruger National Park, South Africa. Photo by Jessica Veneris Redfern.

for ruminants than nonruminants (Jarman 1974, Owen-Smith 1982, Demment and Van Soest 1985, Prins 1996, Wilmshurst et al. 2000). Hence, among the four grazers considered in our analyses, we expect the smaller ruminants, wildebeest and waterbuck (Table 1), to occur farther from water in the nutrient-poor landscape if the dispersed distribution of high-quality forage, relative to the nutrient-rich landscape, forces individuals to travel farther to satisfy their forage quality requirements. Intermediate differences between distance-to-water distributions in the two landscapes are expected for zebra, a nonruminant grazer of similar size to wildebeest (Table 1), whereas smaller differences are expected for buffalo, a large ruminant grazer (Table 1).

We also expect size-based differences between distance-to-water distributions in the nutrient-rich and nutrient-poor landscapes for the two mixed feeders considered in our analyses. In particular, we expect impala, a small ruminant (Table 1), to occur farther from water in the nutrient-poor than in the nutrient-rich landscape, whereas smaller differences between landscapes are expected for elephant, a large nonruminant (Table 1). Finally, we expect distance-to-water distributions for giraffe and kudu to be comparatively unaffected by landscape because the suggested water independence of these browsers (Western 1975) implies that their ability to satisfy their forage quality requirements should be comparatively unconstrained by distance to water.

Hypotheses: response to reduced forage quantity

Long-term, direct measures of forage quantity are unavailable in the KNP. Forage quantity, however, is positively correlated with rainfall in semiarid regions (Coe et al. 1976, Rutherford 1980). Throughout our study period (1981–1993), daily rainfall data were collected at nine monitoring stations in the nutrient-rich landscape and 12 monitoring stations in the nutrient-poor landscape (Fig. 3); 17 stations recorded data throughout the entire study period, whereas four stations in the nutrient-poor landscape recorded data from July 1984 (i.e., the 1985 climate year) to the end of the study period. We used the data from these four stations to increase the accuracy of the average rainfall estimates. Analysis of long-term rainfall patterns in the KNP suggests an approximately 20-year oscillation, with 10 years of above-average annual rainfall and 10 years of below-average annual rainfall (Gertenbach 1980). Our study period corresponds to a below-average annual rainfall cycle, which included two years with the lowest recorded rainfall in the last century (Zambatis and Biggs 1995). Within each cycle of the long-term pattern, however, there is variation in average annual rainfall (Gertenbach 1980, Zambatis and Biggs 1995; see Fig. 4). Hence, during our study period, higher forage quantities should occur during years with higher average annual rainfall.

We analyzed distance-to-water distributions for KNP herbivores in wet vs. dry years, defining wet years as the six years with the highest average annual rainfall during our study period (1981–1993) and dry years as the six years with the lowest average annual rainfall (Fig. 4). Previous studies suggest that critical forage quantity thresholds are higher for large animals than small animals and for nonruminants than ruminants (Jarman 1974, Owen-Smith 1982, Demment and Van Soest 1985, Prins 1996, Wilmshurst et al. 2000). In the KNP, reduced forage production in dry years, relative to wet years, should result in a more rapid depletion of forage patches near water sources. Consequently, among the four grazers considered in our analyses, we
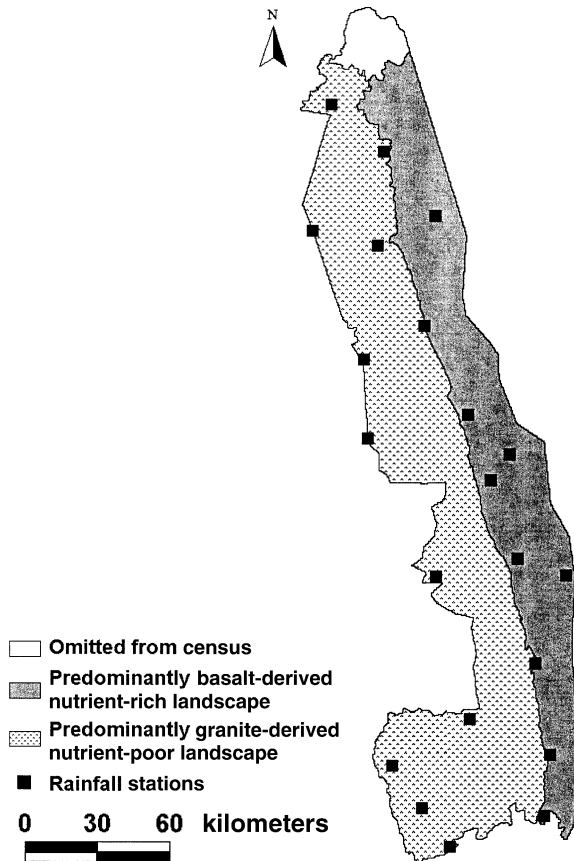
FIG. 3. The nutrient-rich eastern landscape (dark gray shading) occurs on clay soils derived mainly from basalt parent material, whereas the nutrient-poor western landscape (mottled shading) occurs on sandy soils derived mainly from granite parent material. Our landscape definition subsumes smaller patches of differing soil types that increase variability at a finer level of resolution. The northernmost section of the park (unshaded) is not included in the analyses because populations are not regularly counted in this area. Locations of the 21 rainfall stations are also indicated.

(i.e., wet vs. dry years) because the suggested water independence of these browsers (Western 1975) implies that their ability to satisfy their forage quantity requirements should be comparatively unconstrained by distance to water.

METHODS

Aerial census data

From 1981 to 1993, an aerial census using a total area count, strip-transect methodology was conducted during the dry season (May–August) over almost all of the KNP (see Fig. 3). The census recorded the location and herd size (where herd size is defined as one or more individuals) of the park's key herbivore species as well as a range of environmental variables, including the location of water sources (Viljoen 1996). From 1981 to 1984, the use of coarse data-recording procedures resulted in a range of spatial accuracy with an upper bound of ~1.5 km (P. C. Viljoen, *personal communication*). The implementation of improved recording procedures from 1985 to 1993 increased spatial accuracy to within ~800 m (P. C. Viljoen, *personal communication*). Although we acknowledge that the data contain unknown undercount bias (Redfern et al. 2002), a consistent methodology was applied to all surveys (Viljoen 1996). Thus, there is no reason to expect systematic error in the data relative to herbivore distance-to-water distributions.

Water recorded during the census represents the availability of dry-season natural, artificial, permanent, and temporary sources (Viljoen 1996). Temporary water sources result primarily from dry-season rainstorms that coincide with the timing of the census (P. C. Viljoen, *personal communication*). The minimum size of the temporary water sources included in the census data varies because all observed water sources were recorded regardless of size (P. C. Viljoen, *personal communication*). Some of these water sources, therefore,

expect buffalo, a large ruminant (Table 1), to occur farther from water in dry years if reduced forage production forces individuals to travel farther from water to satisfy their forage quantity requirements. Intermediate differences between distance-to-water distributions in wet vs. dry years are expected for zebra, a smaller nonruminant (Table 1), whereas smaller differences are expected for the smaller ruminants, specifically wildebeest and waterbuck (Table 1).

We also expect size-based differences between distance-to-water distributions in wet vs. dry years for the two mixed feeders considered in our analyses. In particular, we expect elephant, a large nonruminant (Table 1), to occur farther from water in dry than in wet years, but we expect smaller differences between dry and wet years for impala, a small ruminant (Table 1). Finally, we expect distance-to-water distributions for giraffe and kudu to be comparatively unaffected by rainfall
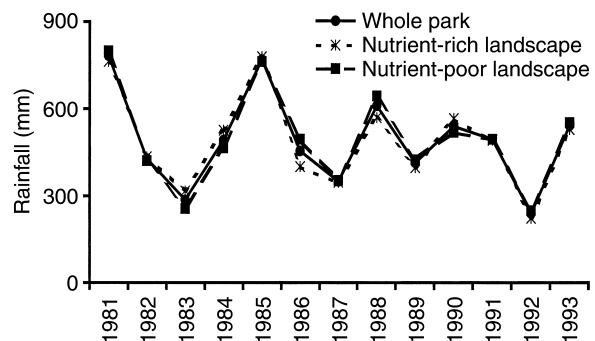

FIG. 4. Average annual rainfall, calculated over the entire KNP and in the nutrient-rich vs. nutrient-poor landscape, plotted for the study period. Annual rainfall, calculated for the whole KNP, was 623 ± 124 mm (mean ± 1 SD) in the six wettest years (1981, 1985, 1988, 1990, 1991, 1993) and 361 ± 86 mm in the six driest years (1982, 1983, 1986, 1987, 1989, 1992).
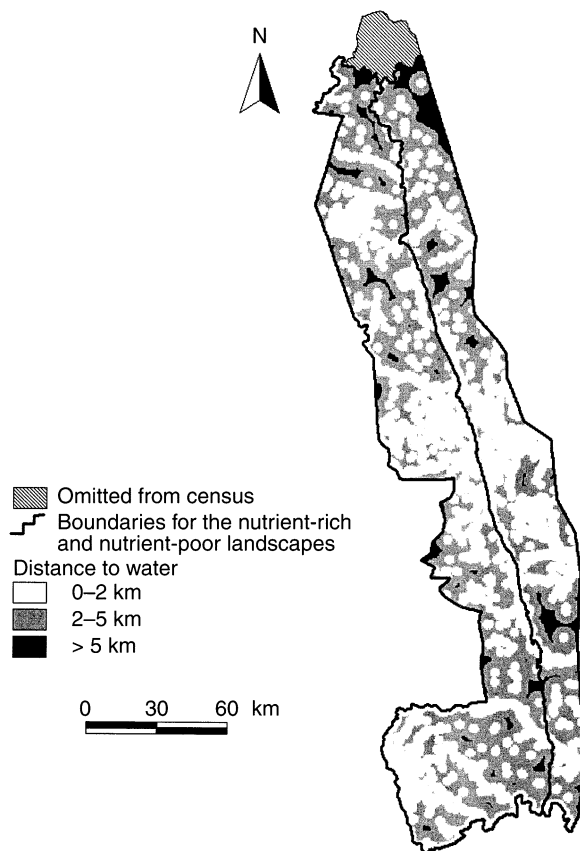
FIG. 5. The distribution of selected distance-to-water categories in the KNP, mapped using the 1990 aerial census data and locations of known permanent water sources. The occurrence of ephemeral water sources, resulting from the coincidence of dry-season rainstorms and the aerial census, can be seen in the central and southwestern regions. Average annual rainfall in 1990 was slightly above the median annual rainfall for the study period, 1981–1993 (Fig. 4); hence, 1990 was classified as a wet year in our analyses.

may represent small pans that are only available for a few days. However, it is expected that dry-season distribution patterns of large, mobile herbivores will be influenced, at least over the short term, by the location of temporary water sources (Western 1975, Thrash and Derry 1999). Temporary water sources were included in our analysis to obtain the most accurate representation of herbivore distance-to-water distributions, given the available data, because the data on water and herbivore locations were collected simultaneously.

Although temporary water sources may be overrepresented in the raw census data, permanent water sources are underrepresented. Visual inspection of maps produced using the census water data reveals that some permanent water sources, including perennial rivers and springs, dams, and boreholes, were not always recorded during surveys (for example, large breaks may occur in perennial rivers). These inspections also reveal that water locations were not recorded throughout the

entire park during some surveys. The absence of some permanent water sources in the raw census water data results from observer omission (P. C. Viljoen, *personal communication*) and leads to an underrepresentation of water availability. To compensate for this problem, final dry-season water availability maps were derived by adding permanent water sources to the census water data (Fig. 5).

Data analyses

The KNP landscape, herbivore, and water data were summarized and combined using the geographic information systems software ARC/Info version 8.0.2 (Environmental Systems Research Institute 2000). A map of the KNP landscapes, as defined by dominant soil substrate (Fig. 3), was converted into a grid of 1-km^2 cells that served as the base map for all analyses. This spatial resolution was chosen to balance the trade-off between computational time and information loss (as cell size increases, the precision in locating herds is reduced and the number of cells containing more than one herd increases). The distance from the center of each grid cell to the nearest water source was used as the explanatory variable for all analyses (Fig. 5). The distance-to-water measurements were categorized in 1-km increments such that all distances 0–1 km were assigned to the 1-km category, all distances 1–2 km were assigned to the 2-km category, etc. This categorization subsumes most of the location error in the census data.

The presence of herbivore herds in the 1-km^2 grid cells was the response variable in our analyses. All species considered in the analyses regularly occur in some form of social group, typically a herd (Estes 1991). Although single individuals are recorded as a herd, the KNP aerial census data are collected to represent cohesive social groups or herds (Viljoen 1996). Hence, it is more reasonable to assume independence among the locations of herds than among the locations of individuals. We did not explore differences in herd composition (e.g., herd size, sex ratio, or age distri-

TABLE 2. The proportion (mean and standard deviation) of occupied 1-km^2 cells that had exactly one herd is calculated over the period from 1981 to 1984, when data were recorded at a coarse spatial resolution; from 1985 to 1993, when data were recorded at a finer spatial resolution; and over the entire study period (i.e., 1981–1993).

Species	1981–1984		1985–1993		1981–1993	
	Mean	1 SD	Mean	1 SD	Mean	1 SD
Buffalo	0.74	0.02	0.94	0.02	0.88	0.10
Zebra	0.50	0.01	0.79	0.01	0.70	0.14
Wildebeest	0.60	0.02	0.82	0.02	0.75	0.11
Waterbuck	0.63	0.05	0.87	0.02	0.80	0.12
Giraffe	0.64	0.02	0.87	0.01	0.80	0.11
Kudu	0.65	0.05	0.91	0.01	0.83	0.13
Elephant	0.72	0.02	0.87	0.03	0.82	0.08
Impala	0.27	0.03	0.60	0.02	0.50	0.16

bution) with respect to distance to water because our analyses focus on herds rather than individuals. The particular method chosen to summarize herd presence determines the statistical analyses that can be performed. Herd presence can be defined as the number of herds in each cell, and Poisson regression can be used to assess herbivore distribution patterns (Neter et al. 1996). At smaller resolutions, however, Poisson regression may not be appropriate because a minimum distance is expected between herds. In particular, the use of Poisson regression appears to be inappropriate at the 1-km^2 grid cell resolution used in this study. From 1985 to 1993, when improved data-recording procedures increased spatial accuracy to within 800 m, a majority of occupied cells contained one herd for all species except impala (Table 2).

We therefore defined herd presence as a binary variable and used logistic regression to assess the distribution patterns of KNP herbivores. Specifically, in our analyses, herd presence was defined as those cells containing at least one herbivore herd (or at least one individual, because single individuals are treated as a herd). The number of herds uniquely represented at the 1-km^2 grid cell resolution is affected by the coarse data-recording procedures used from 1981 to 1984 (Table 2). However, we decided to include the 1981–1984 data in our analyses to obtain the best possible representation of the effect of rainfall (i.e., wet vs. dry years) on herbivore distributions. Inclusion of these coarse data results in a loss of information because cells containing multiple herds are treated as a single ''presence.'' We determined the effect of this information loss by running an alternative set of logistic regression analyses in which the number of ''presences'' was equal to the number of herds (i.e., if a cell contained two herds, two ''presences'' were assigned to that cell's characteristics in the logistic regression data set). Although we found relative differences among species' distance-to-water distributions in some cases, the major conclusions derived from our analyses were unaffected by our definition of herd presence. Note that in our analyses, the proportion of occupied cells provides a lower bound estimate of herd density (i.e., number of herds per square kilometer), because the area of each cell is 1 km^2 and cells containing multiple herds are treated as a single ''presence'' so that each cell is only counted once. When the number of cells containing multiple herds is small, as is the case for species like buffalo (Table 2), this estimated herd density closely approximates the actual herd density.

To assess differences between herbivore distance-to-water distributions in the nutrient-rich vs. nutrient-poor landscape and in wet vs. dry years, and hence to evaluate our forage quality and quantity hypotheses, we performed analyses on four discrete subsets of the KNP data set. First, we separated the data from the nutrient-rich and nutrient-poor landscapes. Within each landscape, we separated the data for wet and dry years on

TABLE 3. The number of presences in the logistic regression analyses of the four data subsets for each species.

Species	Nutrient-rich landscape		Nutrient-poor landscape	
	Wet	Dry	Wet	Dry
Buffalo	1271	1650	2181	2587
Zebra	7950	7810	10 169	9000
Wildebeest	5065	4619	3741	3407
Waterbuck	2010	1942	1851	1785
Giraffe	3428	3260	4974	4639
Kudu	3840	4025	6236	6250
Elephant	1665	1595	2744	2710
Impala	10 348	9126	23 151	20 147

Note: Presence is a lower bound estimate of the number of herds (see *Methods: Data analysis* and Table 2 for details).

the basis of average annual rainfall. We calculated average annual rainfall over the entire park because the average annual rainfall estimates obtained during the study period were similar in the nutrient-rich and nutrient-poor landscapes (Fig. 4). Specifically, we averaged the sum of the daily rainfall values recorded at each rainfall station over the climate year (July of the previous year to June of the current year; Zambatis and Biggs [1995]) in order to represent the total conditions influencing dry-season herbivore distributions. The wet-year data subset contains the six years (1981, 1985, 1988, 1990, 1991, and 1993) with average annual rainfall above the median for the study period. The dry-year data subset contains the six years (1982, 1983, 1986, 1987, 1989, and 1992) with average annual rainfall below the median for the study period. Data from the year with the median average annual rainfall (1984) were not included in the analyses.

The total sample size (i.e., the number of presences and absences) of each data subset is the same for all species and is determined by the number of cells in the landscape multiplied by the number of wet or dry years. The total sample size in the nutrient-rich landscape is 42 798 for both the wet- and dry-year data subsets, because the number of wet years is equal to the number of dry years. Likewise, the total sample size in the nutrient-poor landscape is 67 632 for both the wet- and dry-year data subsets. The number of herd presences (in our case, the number of cells with at least one herd) varies among species because of spatial and temporal differences in species' herd densities (Table 3).

For each of the four data subsets, we used logistic regression to assess the significance of the relationship between herd density and distance to water. Logistic regression fits a monotonic increasing or decreasing response to the observed data (Neter et al. 1996). Although the observed KNP data (Fig. 6) do not always conform to this shape (e.g., zebra and wildebeest herd densities are higher 1–2 km from water sources than within 1 km of water sources in some cases; waterbuck, giraffe, and kudu herd densities generally decrease as distance to water increases to 4 km, but may increase
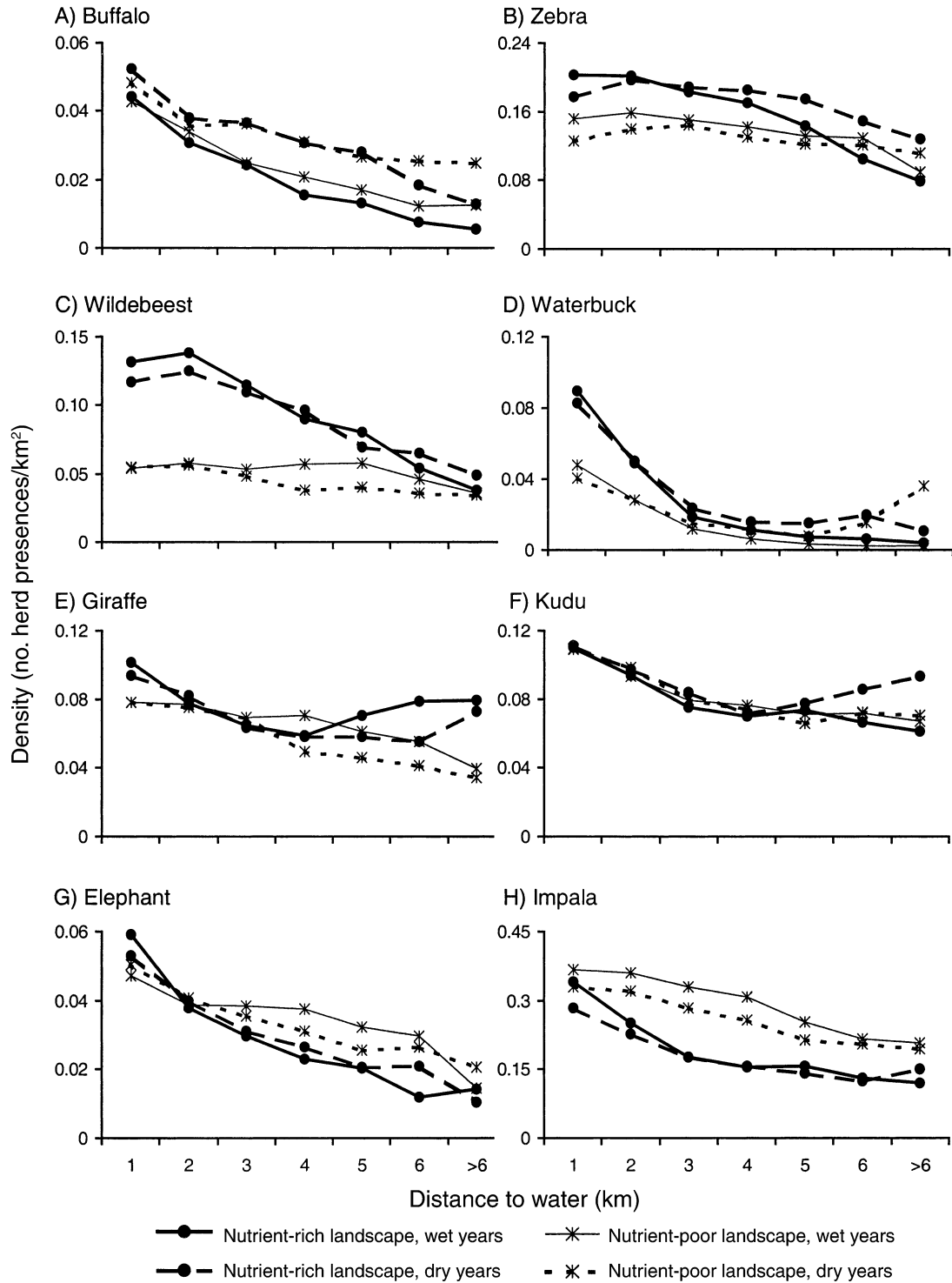
FIG. 6. Observed densities of herd presences (a lower bound estimate of actual herd density, because presences are defined as those 1-km² cells containing at least one herd for the logistic regression analyses), plotted to show differences between species' distance-to-water distributions in the nutrient-rich vs. nutrient-poor landscape and in wet vs. dry years. Because few areas >6 km from water exist in the KNP, distance-to-water categories >6 km have been combined.

4–6 km from water sources), the logistic regression models are representative of the relative differences among species' distance-to-water distributions. Additionally, logistic regression analyses were used because they account for the variability of the data within each distance-to-water category (whereas calculating the observed herd density yields a single point estimate for each distance category) and for differences in water-source distributions (as defined by the proportion of area in each distance-to-water category) among the four data subsets (Collett 1991).

In particular, for the ith data subset (i designates a particular species, landscape, and either wet or dry years), the coefficients a_{ki}, $k = 0$ and $k = 1$, were fit using the logistic regression model

$$\ln\left(\frac{\pi_i(X)}{1 - \pi_i(X)}\right) = a_{0i} + a_{1i}X$$

where X is distance to water calculated at 1-km intervals, and $\pi_i(X)$ is the proportion of cells occupied by a herd, or the herd density, at distance X (Collett 1991). The significance ($P < 0.05$) of the distance-to-water variable was determined using a likelihood ratio test (Collett 1991). The software package S-Plus (Windows Professional Version 4.5, Release 1; Mathsoft 1998) was used to fit the models and obtain variance estimates for the parameters.

Interpretation of the logistic regression parameter a_{1i} is more complex than the straightforward slope interpretation in a linear regression (Neter et al. 1996). For a unit increase in X, the estimated odds ratio ($\pi_i(X)/1 - \pi_i(X)$) changes from the value $e^{a_{0i}}e^{a_{1i}X}$ to the value $e^{a_{0i}}e^{a_{1i}(X+1)} = e^{a_{1i}}(e^{a_{0i}}e^{a_{1i}X})$. That is, the odds ratio increases by a factor $e^{a_{1i}}$, or, simply, the odds of finding a herd one unit (in our case 1 km) farther from water increase (decrease if $a_{1i} < 1$) by a factor $e^{a_{1i}}$. To test our hypotheses regarding species' responses to reduced forage quality and quantity, we quantified differences in species' distance-to-water distributions among the four data subsets using the odds ratio. Specifically, for any two data subsets k and l, we defined the following comparison parameter:

$$c_{kl} = e^{a_{1k} - a_{1l}}.$$

The comparison parameter measures the difference between the odds of finding a herd 1 km farther from water in the two data subsets. Estimates of the comparison parameter are the same as the odds ratio estimates obtained by combining the four equations for
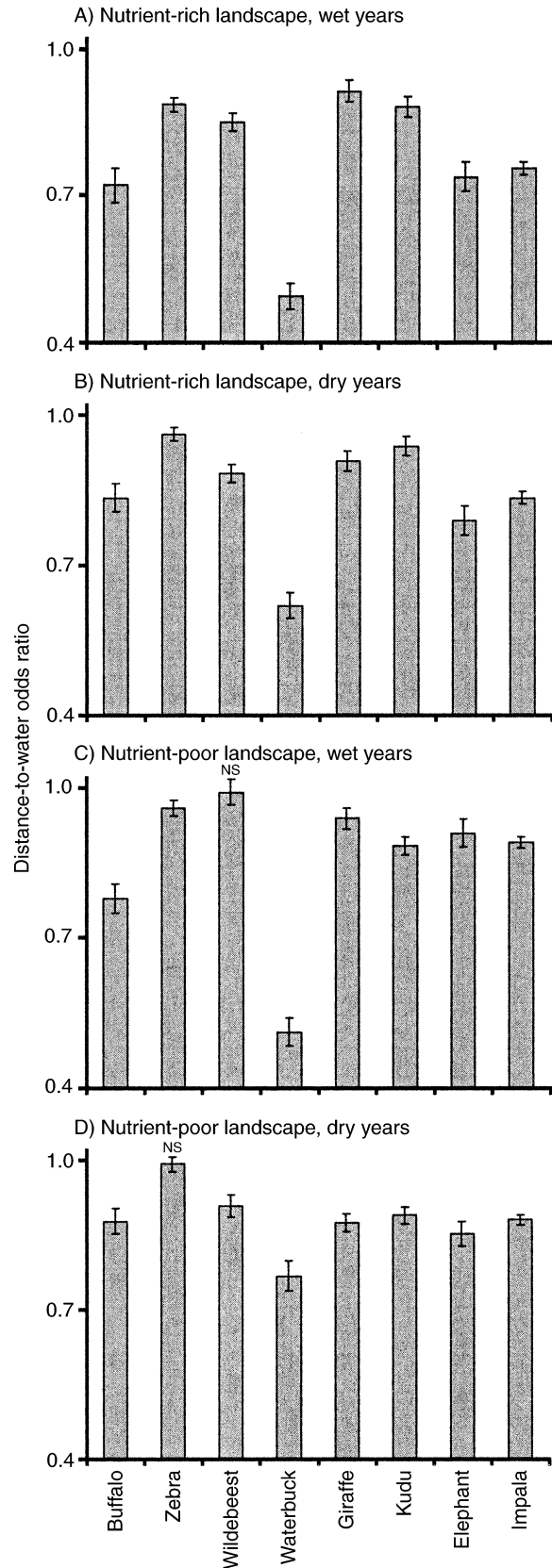
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FIG. 7. The odds ratio and its 95% confidence interval (NS indicates odds ratios that are not significantly different from 1.0), measuring the decreased odds of finding a herd 1 km farther from water, plotted using estimates of the parameter a_{1i} and its standard error obtained from the logistic regression analyses of the four data subsets (see *Methods: Data analyses* for further details).
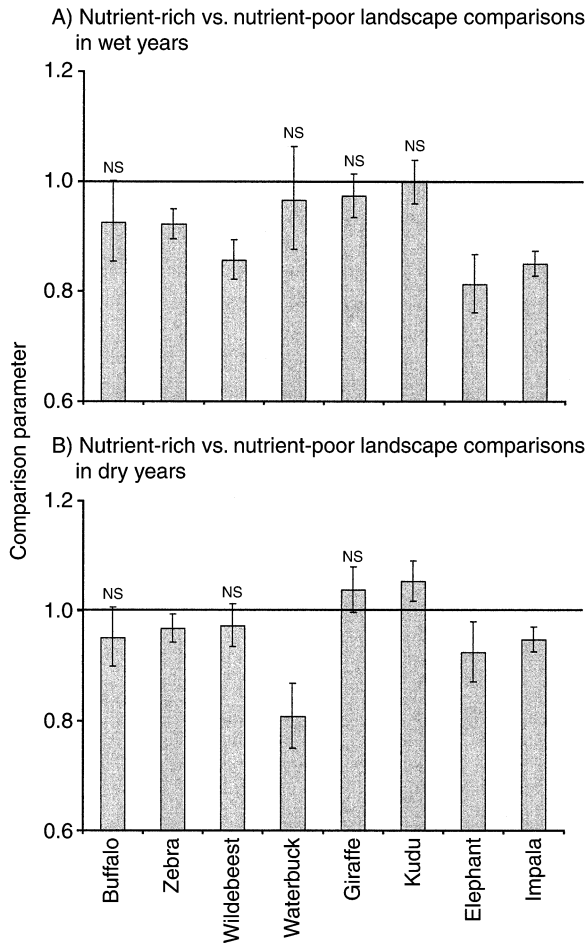

A) Nutrient-rich landscape, wet years

B) Nutrient-rich landscape, dry years

C) Nutrient-poor landscape, wet years

D) Nutrient-poor landscape, dry years

Distance-to-water odds ratio

Buffalo Zebra Wildebeest Waterbuck Giraffe Kudu Elephant Impala

A) Nutrient-rich vs. nutrient-poor landscape comparisons in wet years

B) Nutrient-rich vs. nutrient-poor landscape comparisons in dry years

FIG. 8. Comparison parameter estimates, c_{kl} (see *Methods: Data analyses* for details), are plotted to summarize differences between species' distance-to-water distributions in the nutrient-rich vs. nutrient-poor landscape; c_{kl} values are calculated for both the (A) wet-year and (B) dry-year data subsets (NS indicates comparisons that are not significant at a 95% family confidence level). Values of $c_{kl} < 1$ imply that the probability of a herd's presence falls more steeply as distance to water increases (i.e., herds are more likely to occur close to water sources) in the nutrient-rich compared to nutrient-poor landscape.

each species in a single regression analysis using indicator variables (for landscape and for wet vs. dry years) and the appropriate interaction terms. We have not, however, combined analyses of the four data subsets because we were interested in obtaining direct estimates of the significance of the distance-to-water coefficient in each data subset.

We calculated the parameter c_{kl} for the following four comparisons, representing two replicates addressing the forage quality hypotheses and two replicates addressing the forage quantity hypotheses:

1) nutrient-rich vs. nutrient-poor landscape in wet years (forage quality hypothesis);

2) nutrient-rich vs. nutrient-poor landscape in dry years (forage quality hypothesis);

3) wet vs. dry years in the nutrient-rich landscape (forage quantity hypothesis);

4) wet vs. dry years in the nutrient-poor landscape (forage quantity hypothesis).

For each comparison, we calculated the variance of c_{kl} assuming independence among the data subsets, i.e., using the relationship

$$\mathrm{var}[\ln(c_{kl})] = \mathrm{var}(a_{1k} - a_{1l}) = \mathrm{var}(a_{1k}) + \mathrm{var}(a_{1l}).$$

Variance estimates of a_{1i} were obtained during the logistic regression fitting procedure. From the calculated variance, we obtained a 95% confidence interval for c_{kl} ($e^{c_{kl} - z_{\alpha/2}\mathrm{SD}(\ln(c_{kl}))}$, $e^{c_{kl} + z_{\alpha/2}\mathrm{SD}(\ln(c_{kl}))}$). Multiple comparisons are evaluated for each species; hence, we used the Bonferroni procedure (Neter et al. 1996) to jointly estimate confidence intervals for c_{kl}. Specifically, for each species, we used $z_{\alpha/2g}$, where $g = 4$ is the number of comparisons and $z_{0.05/8} \cong 2.5$, to obtain the 95% confidence coefficient for all c_{kl} (Neter et al. 1996). If this confidence interval did not contain the value 1, c_{kl} was claimed to represent a significant difference between the distance-to-water distributions.

RESULTS

Distance-to-water correlations

The estimated odds ratio (Fig. 7), derived using estimates of the distance-to-water coefficient obtained from the logistic regression analyses, was significantly different from 1.0 in 30 out of 32 logistic regression models (i.e., for the eight species, separate logistic regression models were fit for the four cases: nutrient-rich landscape in wet years, nutrient-rich landscape in dry years, nutrient-poor landscape in wet years, and nutrient-poor landscape in dry years). The exceptions occurred for zebra in the nutrient-poor landscape during dry years and for wildebeest in the nutrient-poor landscape during wet years. In all significant models, the odds ratio was <1.0, indicating that species were closer to surface water than would be expected if individuals were randomly distributed throughout the landscape.

Among the four grazers considered in our analyses, waterbuck had the smallest odds ratio in all four cases (Fig. 7), indicating that waterbuck herd density showed the steepest decline as distance to water increased. Buffalo also had small odds ratios (Fig. 7), particularly in wet compared to dry years. In contrast, zebra and wildebeest had relatively large odds ratios in all four cases (Fig. 7), indicating a weaker relationship between herd density and distance to water. Giraffe and kudu, the two browsers considered in our analyses, also had relatively large odds ratios for all four cases (Fig. 7). Finally, the relative size of the odds ratios for elephant and impala, the two mixed feeders considered in our analyses, depended on landscape, with smaller values
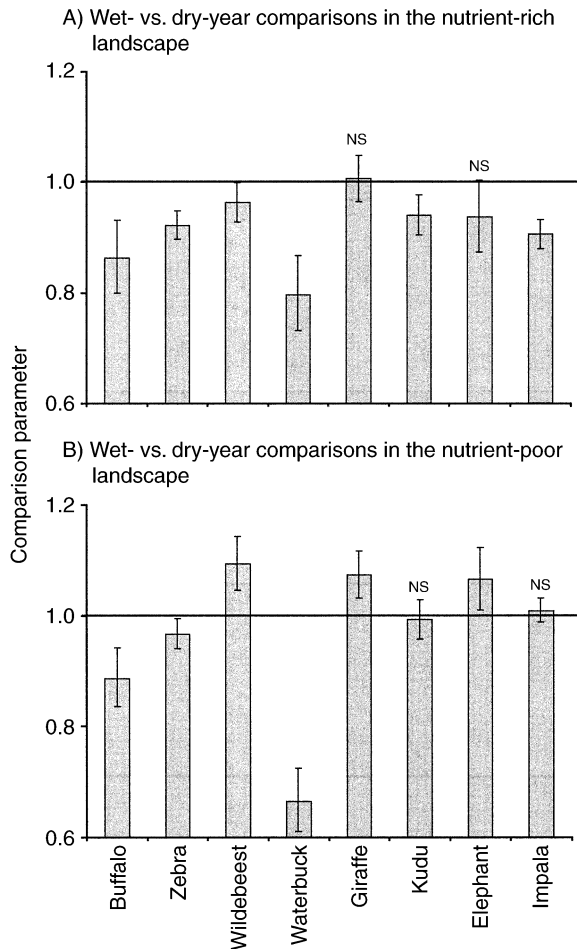
A) Wet- vs. dry-year comparisons in the nutrient-rich landscape

B) Wet- vs. dry-year comparisons in the nutrient-poor landscape

FIG. 9. Comparison parameter estimates, c_{kl} (see *Methods: Data analyses* for details), plotted to summarize differences between species' distance-to-water distributions in wet vs. dry years; c_{kl} values are calculated for both the (A) nutrient-rich and (B) nutrient-poor landscape data subsets (NS indicates comparisons that are not significant at a 95% family confidence level). Values of $c_{kl} < 1$ imply that the probability of a herd's presence falls more steeply as distance to water increases (i.e., herds are more likely to occur close to water sources) in wet than in dry years.

occurring in the nutrient-rich than in the nutrient-poor landscape (Fig. 7).

Response to reduced forage quality

For each species, the comparison parameter, c_{kl}, was used to measure the difference between distance-to-water distributions in the nutrient-rich and nutrient-poor KNP landscapes. In these forage quality comparisons, differences between the two landscapes were calculated for both wet (Fig. 8A) and dry (Fig. 8B) years. Among the grazers, species generally occurred farther from water in the nutrient-poor than in the nutrient-rich landscape (Figs. 6 and 8), and greater differences between distance-to-water distributions in the two landscapes were generally observed during wet com-

pared to dry years (Fig. 8). In particular, during wet years the greatest difference between the two landscapes was observed for wildebeest (Fig. 8A); differences for zebra were intermediate, whereas differences for buffalo and waterbuck were not significant (Fig. 8A). Waterbuck were the only grazers that had a larger difference between distance-to-water distributions in the two landscapes during dry compared to wet years (Fig. 8).

Distance-to-water distributions for the mixed feeders, specifically elephant and impala, were similar to those for grazers. In particular, both species occurred farther from water in the nutrient-poor than in the nutrient-rich landscape (Figs. 6 and 8), and greater differences between distance-to-water distributions in the two landscapes were observed in wet than in dry years (Fig. 8). In contrast to the pattern observed for grazers, values of the comparison parameter for mixed feeders did not vary according to the size of the species. Specifically, values of the comparison parameter were similar for elephant and impala (Fig. 8). Browsers, unlike grazers and mixed feeders, had similar distance-to-water distributions in the two landscapes. Specifically, differences between the two landscapes were insignificant for giraffe during wet and dry years (Fig. 8). Kudu occurred significantly farther from water in the nutrient-rich than in the nutrient-poor landscape during dry years, but the difference between landscapes was insignificant during wet years (Fig. 8).

Response to reduced forage quantity

For each species, the comparison parameter, c_{kl}, was also used to measure the difference between distance-to-water distributions in wet and dry years. In these forage quantity comparisons, differences between wet and dry years were calculated in both the nutrient-rich (Fig. 9A) and nutrient-poor (Fig. 9B) KNP landscapes. Three of the grazers (buffalo, zebra, and waterbuck) always occurred farther from water during dry than during wet years (Figs. 6 and 9). Buffalo and waterbuck had large differences between distance-to-water distributions in wet and dry years, whereas values for zebra were intermediate (Fig. 9). Wildebeest occurred farther from water during dry compared to wet years in the nutrient-rich landscape (Figs. 6 and 9), although the difference between wet and dry years was smaller than that observed for the other grazers (Fig. 9). In the nutrient-poor landscape, however, wildebeest occurred farther from water during wet compared to dry years (Figs. 6 and 9). This unexpected pattern may be the result of forage quality limitations in the nutrient-poor landscape.

Differences between distance-to-water distributions in wet vs. dry years for browsers and mixed feeders were small compared to the differences for buffalo and waterbuck (Fig. 9). Additionally, variability exists in whether species occurred farther from water in wet or dry years. Specifically, giraffe and elephant occurred

farther from water in wet than in dry years in the nutrient-poor landscape, whereas differences between wet and dry years for both species were insignificant in the nutrient-rich landscape (Figs. 6 and 9). Kudu and impala occurred farther from water in dry than in wet years in the nutrient-rich landscape, whereas differences between wet and dry years for both species were insignificant in the nutrient-poor landscape (Figs. 6 and 9).

DISCUSSION

Hypotheses: distance-to-water correlations

Our analyses of dry-season herbivore distributions in the Kruger National Park (KNP), South Africa, indicate some significant relationships between herd density and distance to water for all of the species considered. As expected, the smallest odds ratio estimates among grazers (Fig. 7) were obtained for waterbuck, indicating a strong relationship between waterbuck herd density and distance to water (see Plate 1). The relative estimates of the odds ratio obtained for the other species (Fig. 7), however, do not completely agree with our hypotheses that species' herd densities relative to distance to water should correspond to their water dependence.

Small odds ratios were predicted for the other grazers (buffalo, zebra, and wildebeest) and the mixed feeders (elephant and impala) because these species occur at a high biomass density and are considered water dependent. Small odds ratios were observed for buffalo, elephant, and impala, although the size of the odds ratio varied according to rainfall (i.e., wet vs. dry years) or landscape (Fig. 7). In contrast, large odds ratios (i.e., values closer to 1.0) were observed for zebra and wildebeest (Fig. 7). Hence, the odds ratios for grazers and mixed feeders do not support the hypothesis suggested by Owen-Smith's (1996) observation that species with a high biomass density should be the most affected by surface-water availability. Additionally, estimates of the odds ratio for zebra and wildebeest were similar or larger than those observed for the two browsers in our study, giraffe and kudu (Fig. 7). This result does not support the hypothesis that the relative water independence of browsers compared to grazers (Western 1975) should correspond to larger estimates of the odds ratio (i.e., values closer to 1.0) for browsers.

The lack of correspondence between species' water dependence and estimates of the odds ratio may arise from the relative abundance of surface water in the KNP. In particular, at most 8% of the area in the KNP occurred >5 km from surface water during our study period. The abundance of surface water in the KNP includes both temporary and permanent water sources. In particular, our analyses included the numerous temporary water sources created by dry-season rainstorms that occurred in random areas throughout the KNP during most of our study period (Redfern 2002). In ad-

dition, more than 300 artificial water sources have been constructed in the KNP, greatly increasing the amount of area within 5 km of permanent water sources (Redfern 2002). Therefore, disagreement between our observations of species' distance-to-water distributions and hypotheses based on species' water dependence may arise because no waterless areas exist in the KNP beyond the range of the large, mobile herbivores considered in our analyses. The disagreement, however, is also influenced by the relationship between species' distance-to-water distributions and forage quality or quantity, as represented by landscape or rainfall (i.e., wet vs. dry years).

Hypotheses: response to reduced forage quality

Large differences between distance-to-water distributions in the nutrient-rich vs. nutrient-poor landscape were predicted for the smaller ruminant grazers in our analyses, specifically wildebeest and waterbuck. Although large differences were observed for these species, the estimated difference varied according to rainfall (i.e., wet vs. dry years). Specifically, wildebeest occurred farther from water in the nutrient-poor landscape during wet years, whereas waterbuck occurred farther from water in the nutrient-poor landscape during dry years. In general, distance-to-water distributions for most species showed a larger difference between the two landscapes during wet years, with species occurring farther from water in the nutrient-poor landscape. With increasing rainfall, forage production may become limited by soil nutrients rather than soil water, resulting in an increase in forage quantity but a decrease in the proportion, or even the availability, of high-quality forage (Breman and de Wit 1983). Hence, the larger differences observed between species' distance-to-water distributions in the nutrient-rich vs. nutrient-poor landscape during wet years rather than dry years may be the result of increased forage quality constraints during wet years.

For waterbuck, the distance-to-water coefficient in the nutrient-poor landscape during dry years may have been underestimated. In particular, increasing herd densities of waterbuck were observed in distance-to-water categories >5 km. These increases are surprising because waterbuck are typically regarded as highly water dependent (Estes 1991). Consequently, further research is needed to explain the occurrence of waterbuck herds far from water in the nutrient-poor landscape during dry years. In our analyses, increases in waterbuck herd densities >5 km from water sources result in a smaller estimate of the distance-to-water coefficient than would be obtained using only the data from distance-to-water categories <5 km. If this distance-to-water coefficient was underestimated, comparison parameter estimates for waterbuck may be artificially high.

In agreement with our hypotheses for browsers, giraffe and kudu distance-to-water distributions were comparatively unaffected by landscape. For mixed
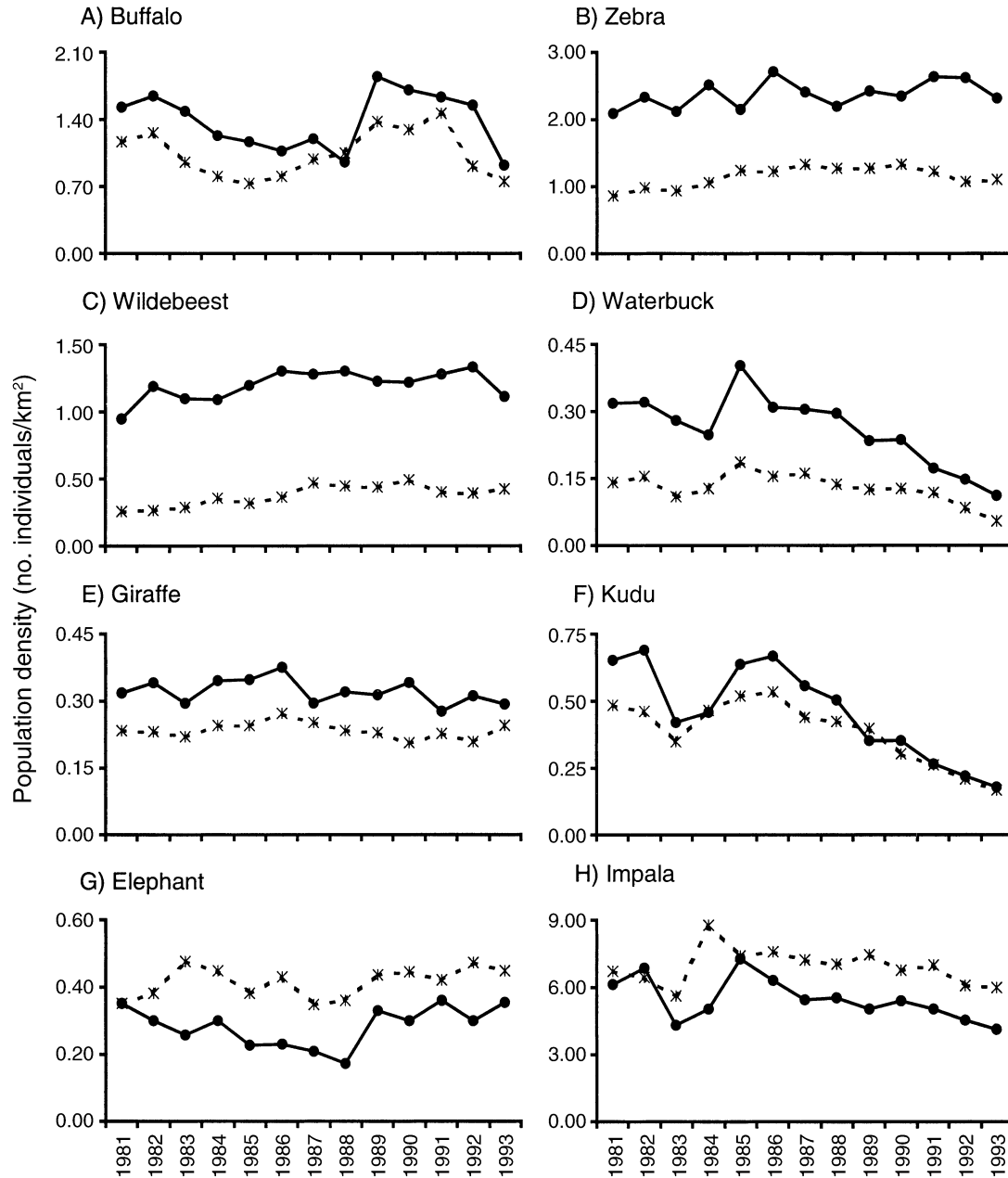
FIG. 10. Population density (number of individuals/km²) of eight herbivore species in the nutrient-rich (solid lines) and nutrient-poor (dashed lines) KNP landscapes, plotted annually.

feeders, the large difference between distance-to-water distributions in the nutrient-rich vs. nutrient-poor landscape predicted for impala was observed during wet years. Contrary to our hypotheses for mixed feeders, however, a large difference was also observed during wet years for elephant, the other mixed feeder considered in our analyses. Caution must be used in interpreting these results because both elephant and impala occur at higher densities in the nutrient-poor than in the nutrient-rich landscape (Fig. 10). An increase in intraspecific competition, caused by higher population

densities, could result in species searching larger areas to satisfy their nutritional requirements and, concomitantly, an increase in species' mean distance to water. Hence, although both species occur farther from water in the nutrient-poor landscape, the current data set cannot be used to determine whether these distribution differences signal a mitigation of reduced access to high-quality forage, a mitigation of increased intraspecific competition, or an association with some other factor not measured in our analyses. Analyses of distribution differences between the two landscapes for

the other six species are not confounded by density because these species occur at similar or higher densities in the nutrient-rich landscape (Fig. 10).

Hypotheses: response to reduced forage quantity

Among grazers, large differences between distance-to-water distributions in wet vs. dry years were predicted for buffalo because they are the largest species considered in our analyses (Table 1). Large differences were observed for buffalo in both the nutrient-rich and nutrient-poor landscape (Fig. 9). In particular, buffalo occurred farther from water during dry than wet years (Fig. 6), in agreement with the expectation that reduced forage quantities during dry years force individuals to travel farther from water sources to meet their nutritional requirements. Because our comparisons of buffalo distributions are based on the logistic regression distance-to-water coefficients, they are unaffected by the fact that observed buffalo herd densities are higher in dry than in wet years (Fig. 6). This difference in herd density may be caused by the fragmentation of herds during dry years and may also be an artifact of the data collection procedures; observers can detect small herds more easily during dry years because vegetation cover is reduced (P. C. Viljoen, *personal communication*).

In agreement with our hypotheses for browsers, giraffe and kudu distance-to-water distributions were comparatively unaffected by rainfall (i.e., wet vs. dry years; Fig. 9). Among mixed feeders, large differences between distance-to-water distributions in wet vs. dry years were predicted for elephant (Table 1). Contrary to our hypotheses, small differences were observed for elephant between distance-to-water distributions in wet vs. dry years (Fig. 9). As explained previously, a large difference was observed for elephant between distance-to-water distributions in the two landscapes during wet years.

Surface-water constraints on herbivore foraging

Previous studies have suggested that herbivores foraging in an African savanna ecosystem must satisfy their nutritional requirements within the constraints set by surface-water availability (Young 1970, Western 1975, Owen-Smith 1996). Analyses of distance-to-water distributions for eight herbivore species in the KNP suggest that the trade-off that species face between nutritional requirements and surface-water constraints varies according to the species' water dependence, size, and gut morphology. Higher observed densities in the nutrient-poor than in the nutrient-rich KNP landscape confound exploration of this trade-off for elephant and impala, the mixed feeders considered in our analyses. Interpretations of differences between distance-to-water distributions for grazers and browsers, however, are not confounded by density differences. In particular, these species occur closer to water in landscapes with

higher densities or show similar distribution patterns between landscapes with different densities.

Of the four grazers considered in our analyses, waterbuck distributions appear to be primarily constrained by surface-water availability. In particular, waterbuck distributions are generally characterized by an exponential decline in herd density as distance to water increases. Distance-to-water distributions for buffalo, the largest ruminant grazer considered in our analyses, suggest that individuals face a trade-off between nutritional requirements and surface-water constraints during dry years when forage quantity may be reduced. Alternatively, distance-to-water distributions for wildebeest, a smaller ruminant grazer, suggest that individuals face a trade-off between nutritional requirements and surface-water constraints in the nutrient-poor KNP landscape where access to high-quality forage may be limited. In comparison to buffalo and wildebeest, distance-to-water distributions for zebra, a nonruminant similar in size to wildebeest, suggest that individuals face a moderate trade-off between nutritional requirements and surface-water constraints during dry years and in the nutrient-poor landscape. The agreement between our grazer results and the general relationship expected between species' size, gut morphology, and the relative importance of forage quality vs. quantity, suggests that the landscape and rainfall dichotomies, respectively, are viable forage quality and quantity surrogates for KNP grazers at a landscape scale.

Distribution patterns for giraffe and kudu, the two browsers considered in our analyses, were characterized by a weak relationship between herd density and distance to water, as expected for these relatively water-independent species (Western 1975). Additionally, differences between distance-to-water distributions for giraffe and kudu in the nutrient-rich vs. nutrient-poor landscape and in wet vs. dry years were small and contained no discernible pattern relative to those observed for grazers. The lack of response to landscape and rainfall (i.e., wet vs. dry years) observed for giraffe and kudu may arise because the relative water independence of browsers (Western 1975) implies that these species do not face a trade-off between nutritional requirements and surface-water constraints. At least two additional hypotheses, however, may also explain the observed lack of response. First, it is possible that critical forage thresholds have not been reached for browsers in the KNP; hence, they can satisfy their nutritional requirements with relatively little difficulty. Second, it is possible that the landscape and rainfall dichotomies are not good indicators of browse quality and quantity. This possibility is particularly likely for browse quantity. Although it appears reasonable to accept average annual rainfall as a surrogate for grass quantity, browse quantity may be less directly related to average annual rainfall because trees have greater nutrient storage ca-

pacities and access to deeper water sources than do grasses (Walker and Noy-Meir 1982, Rutherford 1984).

Future research

We have presented an analysis of data that were not collected to address the hypotheses considered here. Developing hypothesis-specific data collection methods through the use of an experimental design would strengthen our ability to evaluate the potential trade-off between nutritional requirements and surface-water constraints facing herbivores in African savanna ecosystems during the dry season. For example, measurement of actual browse quantities in the KNP would increase our ability to determine whether forage quantity is limiting for browsers, understand the observed differences in giraffe and kudu distributions, and evaluate the relationship between rainfall and browse quantity. Through the use of an appropriate experimental design, we also may be able to separate the effects of population density and forage quality on mixed feeder distributions.

Conclusion

Identifying landscape-scale determinants of large-herbivore distributions can benefit wildlife management and conservation because an understanding of these determinants allows the prediction of herbivore species aggregations, impacts, and range overlap. Bailey et al. (1996) suggest that herbivore distribution patterns at a landscape scale are determined by the operation of biotic mechanisms within the constraints set by abiotic factors, such as slope and distance to water. Our analyses reveal that distance to water is significantly correlated with the distributions of eight herbivore species in the Kruger National Park (KNP), South Africa, during the dry season. Hence, our results suggest that water sources can be viewed as domains of attraction (Senft 1989) at a landscape scale, although the strength of the attraction varies among species. Because of this attraction, herbivore aggregations can be expected at water sources during the dry season. Herbivore aggregation at water sources may affect local soil characteristics (Andrews 1988, Thrash and Derry 1999), species composition and biomass of both woody and herbaceous vegetation (Andrews 1988, Thrash and Derry 1999), and the dynamics of the herbivore community (Smuts 1978, Walker et al. 1987, Owen-Smith 1996).

In order to assess the interaction of biotic and abiotic factors on landscape-scale herbivore distributions, we evaluated hypotheses regarding the relative influences that surface water, forage quality, and forage quantity exert on herbivore distributions during the dry season. Our analyses suggest that species may face a trade-off between surface-water constraints and nutritional requirements when either forage quality or quantity is reduced. Among grazers, we found that larger species tend to occur farther from water when forage quantity is reduced, whereas smaller species tend to occur farther from water when forage quality is reduced. These results suggest that species mitigate limitations in nutritional requirements (i.e., intake quality or quantity) by foraging farther from water. Specifically, species incur an increased cost traveling to water sources in order to satisfy their nutritional requirements.

Hence, surface-water constraints on KNP herbivores appear to have some elasticity that can be used to mitigate limitations in forage requirements. In the KNP, however, permanent and temporary water sources are relatively abundant during the dry season (Redfern 2002). For example, during our study period, a minimum of 92% of the area in the KNP occurred within 5 km of some type of water source during the dry season. We cannot, therefore, determine the effects of surface-water constraints under conditions in which surface water is scarce. It is possible that species can no longer mitigate forage limitations via elasticity in surface-water constraints when water sources are less abundant and, hence, farther apart. However, the potential for elasticity in abiotic constraints demonstrated by our analyses supports assertions by Bailey et al. (1996) that evaluation of landscape-scale determinants of herbivore distributions must take into account the influence of abiotic and biotic factors.

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