Manipulating Surface Water Availability to Manage Herbivore Distributions in the Kruger National Park, South Africa

by

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Professor Wayne M. Getz, Chair
Professor Tracy Benning
Professor Bin Yu

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Abstract

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A prevalent hypothesis in the management of African savanna ecosystems is that surface water availability can be manipulated to influence herbivore distributions. This hypothesis rests on two assumptions: 1) surface water availability is a primary determinant of herbivore distributions; and 2) surface water availability can be manipulated at scales that impact herbivore distributions. My research uses data collected from 1981-1993 in the Kruger National Park (KNP), South Africa, to analyze these two assumptions.

To evaluate determinants of KNP herbivore distributions, logistic regression is used to model dry season distance-to-water distributions for eight herbivore species in soil substrate-defined landscapes and in wet versus dry years. The soil substrate-defined landscapes represent a potential surrogate for forage quality and wet versus dry years represent a potential surrogate for forage quantity. The results indicate that although significant relationships exist between species' distribution patterns and distance-to-water, variability occurs between landscapes and years. This variability is interpreted using an optimal foraging approach designated "limiting factor mitigation" (LFM). Application of LFM analysis to the distance-to-water distributions of KNP herbivores suggests that grazers may be limited by forage quality and/or quantity and suggests future research programs that can expand our understanding of relationships between forage characteristics and distance-to-water distributions for browsers and mixed feeders.

To determine whether surface water availability in the KNP can be manipulated at scales that impact herbivore distributions, rainfall-related heterogeneity in the location of dry season water sources is analyzed. These analyses suggest that our capacity to manipulate surface water availability over large scales is limited if water sources are characterized by high temporal and spatial heterogeneity and if the area of interest is characterized by high rainfall. In general, this research suggests that distance-to-water and forage characteristics may influence the distribution patterns of KNP herbivores. Additionally, this research suggests the importance of determining how herbivores respond to ephemeral water sources created by dry season rainstorms. If forage or dry season rainstorms exert a substantial influence on herbivore distributions, it is not likely that we can manage distribution patterns of large, mobile herbivores by manipulating surface water availability in the KNP.

I dedicate this dissertation to Christopher Flint Redfern,

the love of my life and my best friend,

without whom this dissertation would not have

come into being and would never have reached fruition.

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DISSERTATION SUMMARY

An important aspect of the management of African savanna ecosystems is understanding the relationship between surface water availability and herbivore distributions. For example, Owen-Smith (1996) states that water provision ranks with fire and culling policies as one of the main interventions available to managers. Previous studies have documented that herbivore distributions are influenced by the location of water sources, particularly during the dry season (Western 1975, Fryxell and Sinclair 1988, Bergstrom and Skarpe 1999). Additionally, piosphere studies have documented increased herbivore impacts on a range of forage and soil variables close to natural and artificial water sources (Thrash et al. 1991a and 1991b, Thrash et al. 1993, Thrash 1997, 1998a, 1998b, Parker and Witkowski 1999, Thrash and Derry 1999). Studies exploring how herbivore populations are affected by the addition of artificial water sources to an ecosystem suggest that water provision may increase herbivore drought mortality (Walker et al. 1987), increase the predation levels experienced by different herbivore species (Smuts 1978, Harrington et al. 1999), and contribute to the decline of rare antelope species (Harrington et al. 1999).

Underlying many of these previous studies is the hypothesis that surface water availability can be manipulated to manage the distribution and size of herbivore populations in African savanna ecosystems. This hypothesis rests on two assumptions: 1) surface water availability is a primary determinant of herbivore distributions and consequently population size; and 2) surface water availability can be manipulated at scales that impact how herbivores are distributed throughout the landscape. An uncritical

acceptance of this hypothesis can be problematic because these assumptions fail to address the potential influence other factors, such as controlled burning and forage condition, exert on herbivore distributions. For example, herbivores in African savanna ecosystems may struggle to meet water and foraging requirements during the dry season when access to surface water is restricted and forage quality and quantity are reduced (Owen-Smith 1982, Prins 1996).

In my dissertation, data collected from 1981-1993 in the Kruger National Park (KNP), South Africa (Fig. 1), is used to analyze the two assumptions inherent in the hypothesis that surface water availability can be manipulated to manage herbivore distributions. The first and second chapters of my dissertation present an analysis of the relationship between herbivore distributions, surface water availability, and landscape-scale forage surrogates. In the third chapter, the KNP data is used to infer temporal and spatial scales at which surface water can be manipulated.

CASE STUDY MOTIVATIONS

In the KNP, the hypothesis that surface water availability can be manipulated to manage the distribution and size of herbivore populations underlies the original motivations for constructing artificial water sources as well as current justifications for removing artificial water sources. The KNP water provision program began in the 1930's and has resulted in the establishment of over 300 artificial water sources in the KNP, predominately boreholes (Pienaar et al. 1997). Reasons for implementing this program include the desire to homogenize the spatial distribution of herbivore populations and to increase the size of herbivore populations (Pienaar et al. 1997). Currently, the artificial

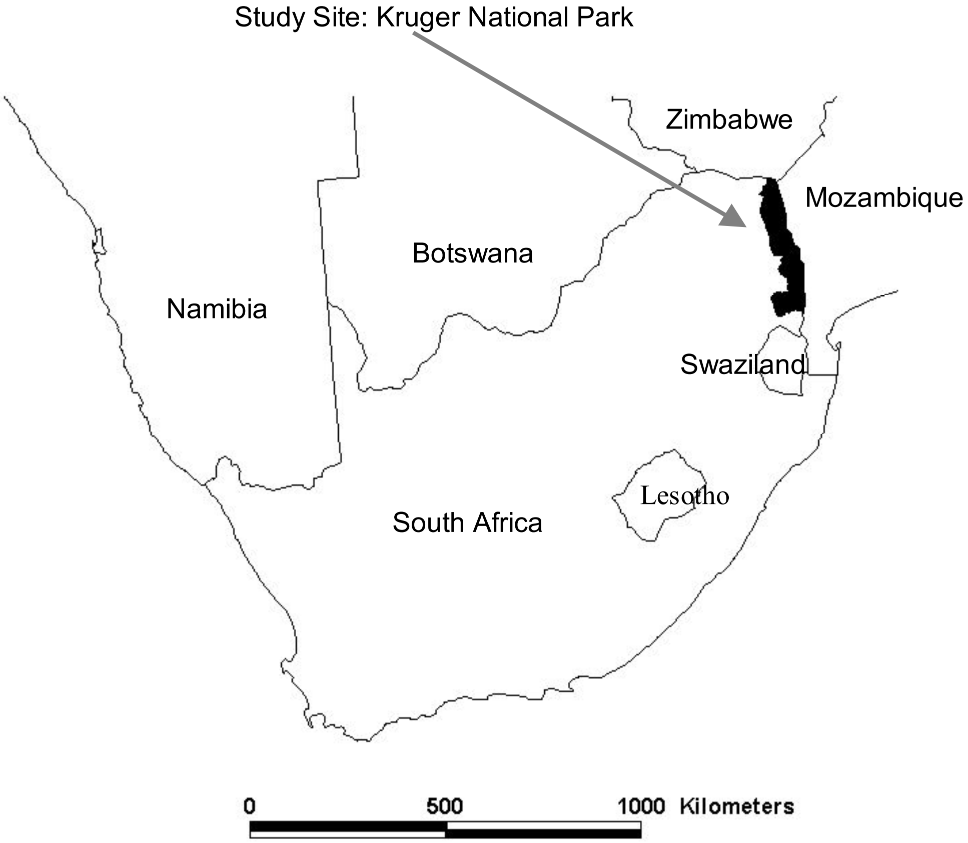

Figure 1. A map of southern Africa showing the study site, Kruger National Park.

water sources constructed under this program are viewed as incompatible with KNP management objectives, which emphasize the heterogeneity of ecosystem processes, and plans to remove a substantial number of boreholes are underway (Pienaar et al. 1997). It has been assumed that the removal of artificial water sources will increase heterogeneity in the spatial distribution of herbivore populations by creating waterless areas during the dry season that occur beyond the range of water-dependent herbivores.

The KNP provides a natural setting for analyzing the relationship between herbivore distributions and surface water availability because comparatively long-term data sets on dry season herbivore and water distributions are available, the KNP’s major soil substrates are well documented and mapped, and long-term rainfall monitoring has occurred throughout the park. Specifically, from 1981 to 1993 an aerial census using a total area count, strip transect methodology was conducted during the dry season over almost all of the KNP. The census recorded the location and herd size of the park's key herbivore species as well as a range of environmental variables, including the location of water sources (Viljoen 1996). Water recorded during the census represents the availability of dry season natural, artificial, permanent, and ephemeral sources (Viljoen 1996). Ephemeral water sources result primarily from dry season rainstorms that coincide with the timing of the census (P. C. Viljoen, *personal communication*--cf. Viljoen, 1996).

From 1981-1984, the use of coarse data recording procedures resulted in a spatial accuracy of 1.5 km (P. C. Viljoen, *personal communication*). The implementation of improved recording procedures from 1985-1993 increased spatial accuracy to approximately 800 m (P. C. Viljoen, *personal communication*). While it is acknowledged that the data contain unknown undercount bias, 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.

CHAPTER ONE: DISTANCE-TO-WATER DISTRIBUTIONS FOR KNP HERBIVORES

In this chapter, logistic regression is used to model dry season herbivore distributions relative to water sources in the KNP. Specifically, herbivore distance-to-water distributions are analyzed in soil substrate-defined landscapes and in wet versus dry years using 12 years of aerial census data. Herbivore species considered in these analyses include four grazers (buffalo, *Syncerus caffer*; zebra, *Equus burchelli*; wildebeest, *Connochaetes taurinus*; and waterbuck, *Kobus ellipsiprymnus*), two browsers (giraffe, *Giraffa camelopardalis*, and kudu, *Tragelaphus strepsiceros*), and two mixed feeders (elephant, *Loxodonta africana*, and impala, *Aepyceros melampus*). These eight herbivore species were selected because of their relative abundance in the KNP and because they represent a spectrum of feeding guilds and body sizes.

Analyses of dry season herbivore distributions in the KNP indicate some significant relationships between herd density and distance-to-water for all of the species considered. If herbivore drinking requirements necessitate regular access to surface water, a species' water dependence may be inferred from the size of the distance-to-water coefficient in our analyses. Specifically, herds of water-independent species should be distributed evenly with respect to distance-to-water, while herds of water-dependent species should occur close to water sources. Hence, our analyses suggest that waterbuck are the most water-dependent of the eight species analyzed, having distributions strongly related to the proximity of water sources. Buffalo and elephant distributions also showed strong water dependence, although for both species the strength of the dependence varied temporally with buffalo distributions occurring close to water in wet years while elephant distributions occurred close to water in dry years. Zebra were the most water-independent species, having relatively similar herd densities across distance categories compared to the other species. Wildebeest, giraffe, and kudu were also relatively water-independent. Impala distributions were intermediate between the strong water dependence shown by waterbuck, buffalo, and elephant, and the more water-independent distribution patterns shown by zebra, wildebeest, giraffe, and kudu.

These analyses also reveal that distance-to-water distributions for some KNP herbivores differ between the soil substrate-defined landscapes and between wet versus dry years. In particular, distance-to-water distributions for grazers and mixed feeders are characterized by strong responses to either landscape or rainfall. Distribution patterns for browsers, however, are comparatively similar between landscapes and in wet versus dry years.

CHAPTER TWO: FORAGE QUALITY AND QUANTITY LIMITATIONS ON KNP HERBIVORE DISTRIBUTIONS

In this chapter, an optimal foraging approach designated "limiting factor mitigation" (LFM) is developed to identify factors that limit population distributions. LFM focuses on how a population's distribution, defined with respect to an independent landscape variable, changes in response to a perturbation in a putative limiting factor.

Specifically, if a factor is limiting, perturbation of the factor alters the population's distribution as an implicit mitigation of the trade-off between the limiting factor and the independent landscape variable. LFM also incorporates a threshold effect in which factors above some critical level do not influence distributions. LFM differs from mechanistic optimal foraging models because it does not explicitly include a fitness function and from ideal free distribution models because the proposed relationship between the independent landscape variable and putative limiting factors is not static.

LFM analysis is applied to determine whether distance-to-water distributions for seven of the KNP herbivore species described in chapter one indicate that potential surrogates for forage quality and quantity represent limiting factors. No long-term, direct measures of forage quality and quantity are available for the KNP, but forage quantity is positively correlated with rainfall (Rutherford 1980) and forage quality is expected to differ between the nutrient-rich clay soils of the basalt-dominated eastern KNP landscape and the nutrient-poor sandy soils of the granite-dominated western KNP landscape (Bell 1982, Venter 1986, Scholes 1990) (Fig. 2). In particular, it is expected that patches of high quality forage will form a smaller proportion of the landscape and hence have a more dispersed distribution in the nutrient-poor western landscape, compared to the nutrient-rich eastern landscape (Owen-Smith, *personal communication*). Therefore, the soil substrate-defined landscapes are a potential surrogate for forage quality and wet versus dry years are a potential surrogate for forage quantity.

Application of LFM analysis provides useful insights into KNP herbivore distributions. The results obtained for KNP grazers are concordant with current

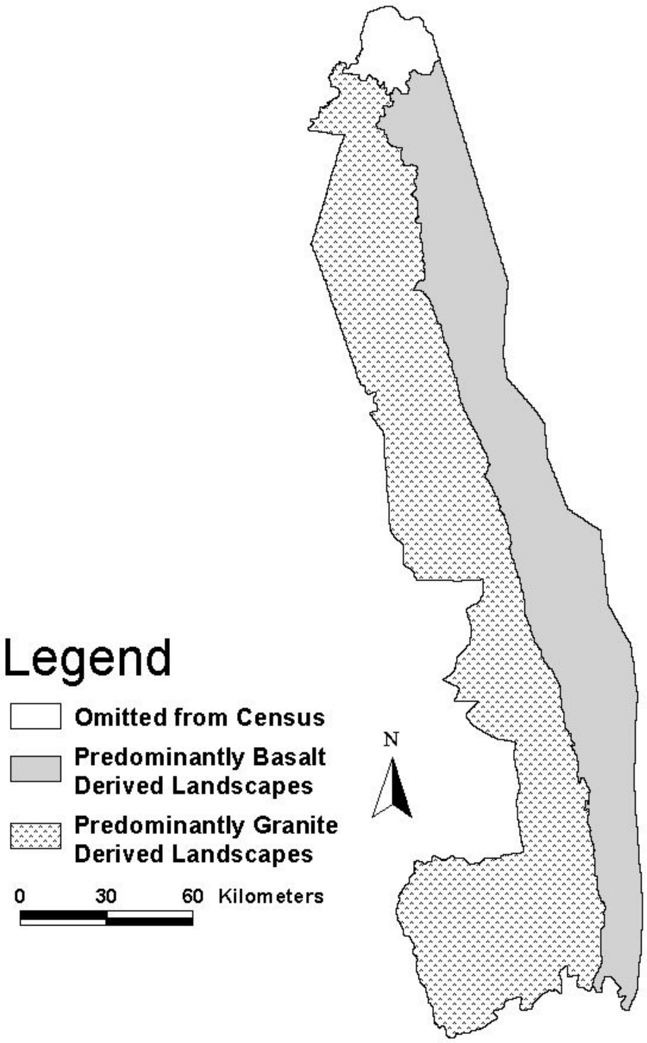

Figure 2. The eastern landscape (gray shading) occurs on soils rich in clay minerals derived mainly from basalt parent material while the western landscape (checked shading) occurs on sandy soils derived mainly from granite parent material. The northernmost section of the park (unshaded) is not included in analyses because censuses occur infrequently in this area.

expectations of the factors that should be limiting for these three species, at least in a comparative sense considering their relative size and gut morphology. This concordance suggests that for KNP grazers the east-west landscape and wet-dry rainfall dichotomies, respectively, are viable surrogates for forage quality and quantity. Further, these analyses reveal that KNP forage quality and quantity are at levels that limit distance-to-water distributions for some grazers but not others. Specifically, distance-to-water distributions for buffalo are limited by forage quantity while distance-to-water distributions for wildebeest are limited by forage quality. Distance-to-water distributions for zebra are limited by both forage quantity and forage quality, although they are less limited by forage quantity than buffalo and less limited by forage quality than wildebeest. This application of LFM analysis also suggests future research programs that can expand our understanding of the influence of forage quantity on browser distributions and determine whether increased intraspecific competition due to higher mixed feeder densities in the western versus eastern KNP landscape has resulted in these species searching larger areas to obtain needed resources.

CHAPTER THREE: MANIPULATING SURFACE WATER AVAILABILITY IN THE KNP

In this chapter, the KNP census water data is used to infer temporal and spatial scales at which surface water availability can be manipulated. Specifically, patterns of surface water availability are described for two water source assemblages: 1) a total water source assemblage containing ephemeral water sources that vary over a range of temporal scales and perennial water sources; and 2) a persistent water source assemblage representing relatively permanent water locations. Examining changes in surface water availability following the removal of all KNP boreholes reveals radically different outcomes in the two assemblages.

Analyses of the total water source assemblage suggest that our capacity to create large-scale changes in surface water availability decreases with increasing rainfall and increasing temporal and spatial heterogeneity in natural water sources. Following the removal of all boreholes, at most 6% of the area in the KNP occurs more than 10 km from water sources during dry years. Additionally, removing boreholes from the total water source assemblage creates few areas that are consistently more than 10 km from water sources because the locations of the ephemeral water sources contained in this assemblage vary temporally and spatially according to dry season rainstorms. Some herbivore species may disperse to patches in which a dry season rainstorm has occurred to obtain access to forage that would otherwise occur too far from water sources or to obtain access to higher quality forage if the rainfall produces a green flush of vegetation. Hence, results from the total water source assemblage suggest that large, mobile herbivores, which disperse to areas experiencing dry season rainstorms, will continue to have access to a majority of the KNP's area after borehole closure.

In the KNP, the availability of persistent water sources should influence the distribution patterns of herbivore species that remain in areas that regularly contain water sources. In contrast to the total water source assemblage, removing boreholes from the persistent water source assemblage considerably increases the percentage of area more than 10 km from persistent water sources, particularly during dry years. This result is a direct consequence of the fact that the persistent water source assemblage is composed primarily of boreholes and perennial rivers. In the KNP, perennial rivers may occur as far as 175 km apart. Removing boreholes, therefore, creates large tracts of area that are more than 10 km from persistent water sources. Consequently, herbivore populations that depend on persistent water sources may be concentrated in smaller areas and face barriers to movement during the dry season. The degree of range contraction will depend on the species' habitat preference. For example, some species may be concentrated near perennial rivers because riparian habitat satisfies both their forage and water requirements. It is unlikely that borehole removal will directly affect such species. These populations may, however, be indirectly affected by increased competition and predation if borehole removal increases the number of species that concentrate in riparian habitat.

In contrast to perennial rivers, the impact of boreholes on habitat characteristics is limited to a local area. While further research is needed to determine the generality of previous piosphere studies in the KNP, these studies suggest that alteration of forage characteristics may only occur within several hundred meters of a borehole (Thrash 1998a, Thrash and Derry 1999). Thus, it is unlikely that these habitat changes explain the relationship between boreholes and herbivore distributions. Rather, boreholes may be an important determinant of herbivore distributions because they provide access to regions that would otherwise be unavailable to less mobile, water-dependent herbivores. Therefore, removing all of the KNP boreholes significantly decreases the potential distribution range for such species. This range contraction may result in a reduction of population sizes.

CONCLUSIONS

Underlying many previous studies of the relationship between water provision programs and herbivore distributions in African savanna ecosystems is the hypothesis that surface water availability can be manipulated to manage herbivore distributions. This hypothesis assumes that surface water availability is a primary determinant of herbivore distributions and that surface water availability can be manipulated at scales that impact how herbivores distribute themselves throughout the landscape. Further research is needed to determine the applicability of these assumptions.

The KNP case study presented here suggests that forage quality and quantity limitations may impact herbivore distributions. These relationships, however, were derived from a post-hoc analysis of data that was not collected to address this particular question. Hence, these analyses would be stronger if an experimental design, motivated by the questions of interest, guided data collection. For example, measurement of actual browse quantities would allow us to determine whether KNP forage quantities limit distance-to-water distributions for browsers and increase our understanding of the relationship between rainfall and browse quantity. Through the use of an appropriate experimental design, we may also be able to separate the effect of population density and forage quality on mixed feeder distributions.

Furthermore, patterns of surface water availability in the KNP reveal the paramount necessity of conducting future research to determine how herbivore populations respond to temporal and spatial heterogeneity in water sources. In particular, a better understanding of how herbivore distributions are influenced by the location of dry season rainstorms is needed. Specific issues that future research should address include:

- Identification of species that disperse to patches where dry season rainstorms have occurred;
- Determination of the rate of dispersal to these patches;
- Measurement of the total time spent in these patches;
- Determination of the amount of rainfall required to cause dispersal.

In addition, this research should incorporate a multi-scale perspective as an explicit acknowledgment that herbivores may respond to temporal and spatial heterogeneity in water sources at multiple scales. For example, it is possible that large-scale distribution patterns, such as the location of herbivore home ranges, are influenced by perennial water sources. Local distribution patterns, however, may be influenced by ephemeral water sources at a range of temporal scales.

Until we obtain a better understanding of how herbivore distributions are influenced by temporal and spatial heterogeneity in water sources, caution should be used in generalizing conclusions about the relationship between herbivore populations and water sources. Specifically, the KNP case study suggests that relationships between herbivore populations and water sources documented in a particular location may not be applicable to an area with different rainfall patterns. Such applications have been made among studies conducted in South Africa, Botswana, Kenya, and Australia. Conclusions derived from these studies need to be re-evaluated within a context that specifically accounts for rainfall derived differences in water source heterogeneity.

The hypothesis that surface water availability can be manipulated to manage the distribution and size of herbivore populations in African savanna ecosystems pervades the literature, influencing the interpretations and generalizations of studies dealing with the relationship between surface water availability and the characteristics of herbivore populations. Additionally, the influence of this hypothesis can be seen in the dearth of studies that rigorously evaluate the relative and potentially synergistic influences that water sources and other factors, such as forage conditions and culling, exert on herbivore populations. To progress in our understanding of the ecology and management of African savanna herbivores, we must move beyond an uncritical acceptance of these assumptions. This viewpoint encourages the development of broad questions about the role multiple interacting factors play in determining the distribution and size of herbivore populations.

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Chapter One

Water availability constraints on herbivore distributions in the Kruger National Park, South Africa

J. V. Redfern, C. C. Grant, H. C. Biggs & W. M. Getz

ABSTRACT

African savannas are characterized by high herbivore diversity that is heterogeneously distributed in space and time. At a landscape scale, the relationship between herbivore diversity and heterogeneity can only be understood by considering the constraints non-foraging factors place on herbivore distributions. In semi-arid ecosystems, the location of water sources has been identified as an important factor influencing the distribution patterns of large herbivores, particularly during the dry season. We use logistic regression to model dry season herbivore distributions relative to water sources in the Kruger National Park (KNP), South Africa. Specifically, we analyze herbivore distance-to-water distributions in soil substrate-defined landscapes and in wet versus dry years using 12 years of aerial census data. Herbivore species considered in these analyses include four grazers (buffalo, zebra, wildebeest, and waterbuck), two browsers (giraffe and kudu), and two mixed feeders (elephant and impala). In general, waterbuck, buffalo, elephant, and impala were characterized by distributions in which herd density declined steeply as distance-to-water increased, while distributions for wildebeest, giraffe, kudu, and zebra were characterized by a weaker relationship between herd density and distance-to-water. Additionally our results suggest that herbivore distance-to-water distributions differ in the soil substrate-defined landscapes and in wet versus dry years. For KNP grazers, distance-to-water distributions for larger species differed between wet and dry years while distance-to-water distributions for smaller species differed between the soil substrate-defined landscapes. Distance-to-water

distributions for KNP browsers were similar between landscapes and in wet versus dry years, while distance-to-water distributions for KNP mixed feeders were characterized by differences between landscapes.

INTRODUCTION

African savannas contain the earth's greatest diversity and density of large herbivore species (du Toit and Cumming 1999). Conservation of this biodiversity is an increasingly important issue for managers of protected areas. For example, the mission statement of the Kruger National Park (KNP) explicitly includes the maintenance of biodiversity in all of its facets and fluxes (Braack 1997 a and b). To conserve biodiversity, we must understand the processes that determine the attributes of biodiversity–composition, structure, and function–for at least four levels of ecological organization including landscape, ecosystem-community, population-species, and genetic (Noss 1990).

In African savannas, spatial and temporal heterogeneity influence the attributes of biodiversity at all levels of ecological organization (du Toit and Cumming 1999). At a landscape scale, the relationship between herbivore diversity and heterogeneity must be examined in the context of the non-foraging factors that constrain herbivore distributions. In semi-arid ecosystems, the location of water sources has been identified as an important factor influencing the distribution patterns of large herbivores, particularly during the dry season (Owen-Smith, 1996, Western 1975, Young 1970). 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).

The water availability constraints imposed on herbivore distributions have been shown to vary between feeding guilds. Western (1975) found that browsers tend to occur farther from water than grazers. During the dry season, the water content of grass falls below that of browse (Western 1975). Thus the physiological barrier species face in utilizing low water content forage when surface water is scarce can be hypothesized to place a greater restriction on grazer distributions (Western, 1975). Within the grazer community, the species most impacted by water availability tend to have the highest biomass density, such as buffalo, zebra, and wildebeest (Owen-Smith, 1996).

Although the potential importance of water availability in driving herbivore distribution patterns is clearly suggested by previous studies, no work exploring herbivore distribution patterns relative to water sources has been conducted at a landscape scale since the 1970's. In this paper we use logistic regression to model dry season herbivore distributions relative to water sources in the Kruger National Park (KNP), South Africa. Specifically, we analyze herbivore distance-to-water distributions in soil substrate-defined landscapes and in wet versus dry years using 12 years of aerial census data. Herbivore species considered in these analyses include four grazers (buffalo, *Syncerus caffer*; zebra, *Equus burchelli*; wildebeest, *Connochaetes taurinus*; and waterbuck, *Kobus ellipsiprymnus*), two browsers (giraffe, *Giraffa camelopardalis*, and kudu, *Tragelaphus strepsiceros*), and two mixed feeders (elephant, *Loxodonta africana*, and impala, *Aepyceros melampus*).

Study Site

The KNP (Fig. 1) provides a natural setting for analyzing variation in the distribution of herbivores relative to water sources because comparatively long-term data sets on dry season herbivore and water distributions are available, the KNP's major soil substrates are well documented and mapped, and long-term rainfall monitoring has occurred throughout the park. Data on the dry season distribution of herbivores and water have been collected on an annual basis since 1977. However, censuses covering the majority of the park (Fig. 2) were only conducted during the 13 year period spanning 1981-1993. The eight herbivore species considered here were selected because of their relative abundance in the KNP (Fig. 3) and because they represent a spectrum of feeding guilds and body sizes.

The eastern KNP landscape (Fig. 2) occurs on soils rich in clay minerals derived mainly from basalts while the more undulating western KNP landscape (Fig. 2) occurs on sandy soils derived mainly from granites (Venter 1986). Soil mineral concentrations will be lower in the west on granite derived soils (Scholes 1990). We define the term landscape broadly, differentiating the eastern and western landscapes on the basis of the dominant soil substrate. Our landscape definition subsumes smaller patches of differing soil types that increase variability at a finer level of resolution. For example, at our scale of analysis, small patches created by gabbro intrusions are subsumed in the predominantly granite derived western landscape. We conducted separate analyses in each landscape (Fig. 2) to determine the influence of the dominant soil substrate on herbivore distance-to-water distributions.

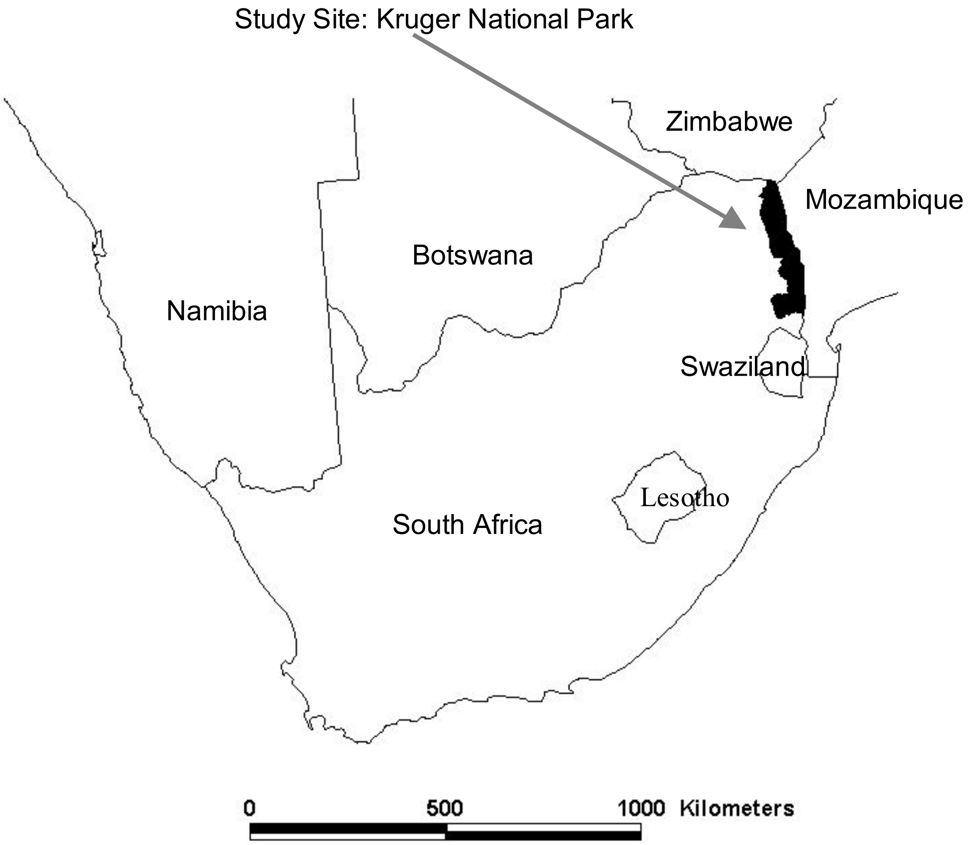

Figure 1. A map of southern Africa showing the study site, Kruger National Park.

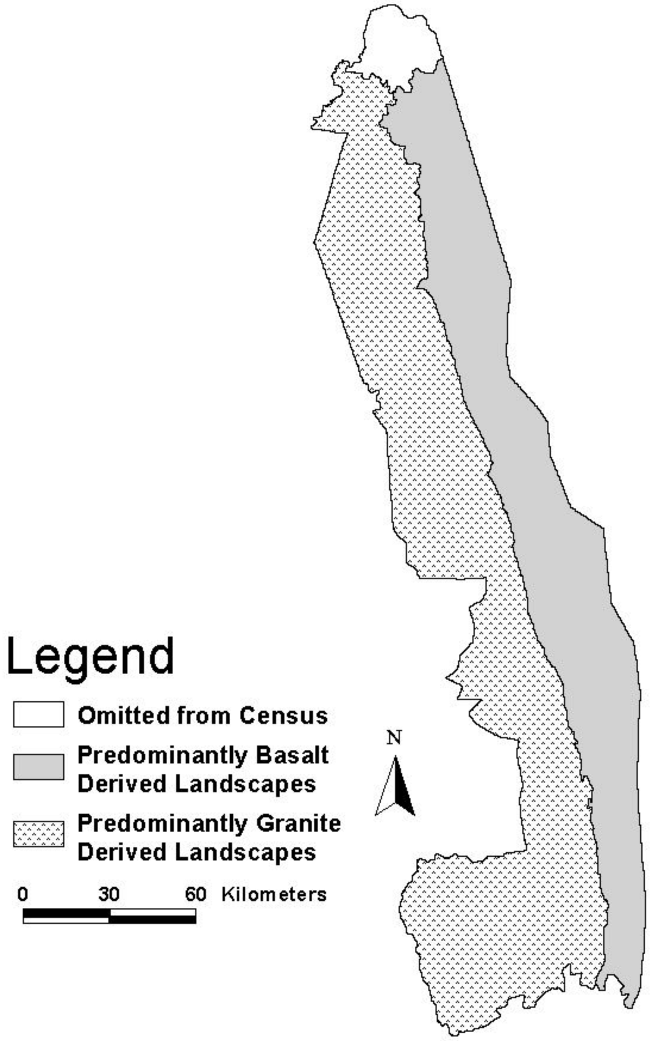

Figure 2. The eastern landscape (gray shading) occurs on soils rich in clay minerals derived mainly from basalt parent material while the western landscape (checked shading) occurs on sandy soils derived mainly from granite parent material. The northernmost section of the park (unshaded) is not included in analyses because populations are not regularly counted in this area.

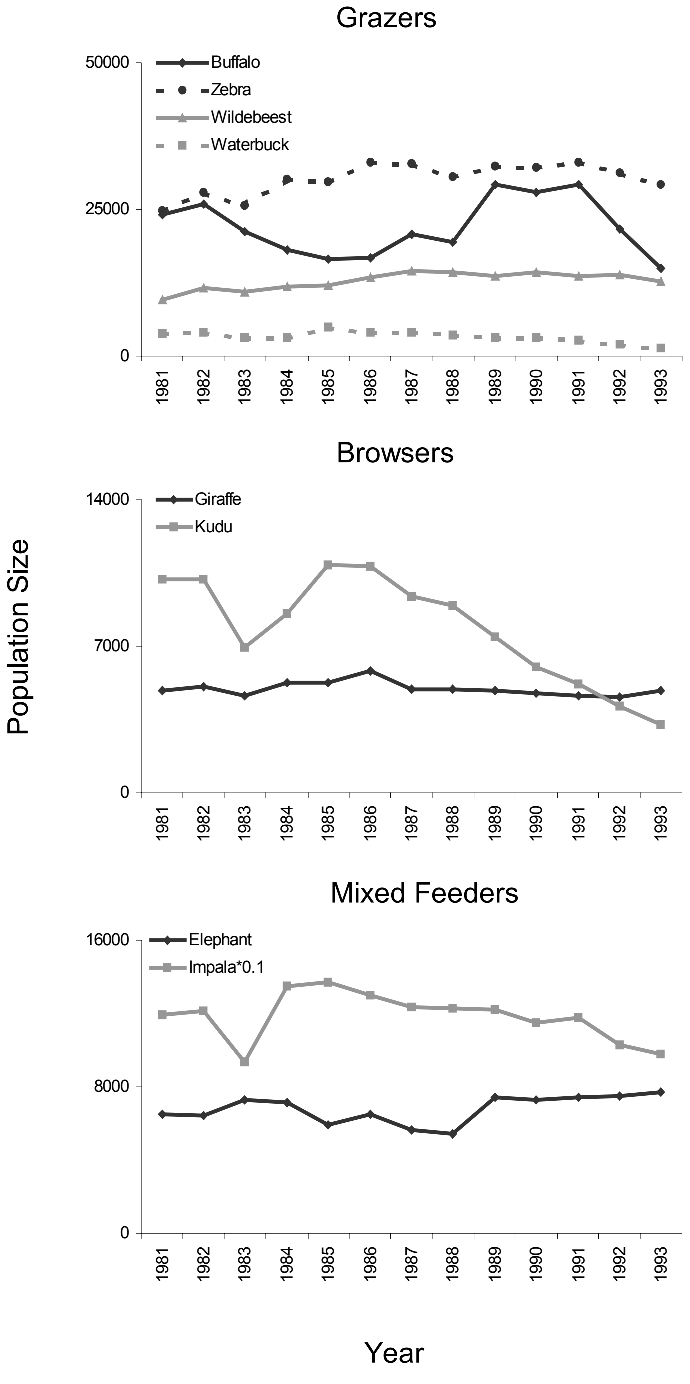

Figure 3. Population size, estimated from the aerial census data collected during the study period (1981-1993), is plotted annually. (Note that impala population sizes are multiplied by 0.1).

Throughout the study period (1981-1993), daily rainfall data was collected at 9 monitoring stations in the eastern landscape and 12 monitoring stations in the western landscape; 17 stations recorded data throughout the entire study period while four stations in the western 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 values. 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 the average annual rainfall (Gertenbach 1980, Zambatis and Biggs 1995, and see Fig. 4). To examine the influence of the rainfall variation during our study period on herbivore distributions, separate analyses were conducting using data from the six wettest and the six driest years (Fig. 4) in both the eastern and western landscapes.

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. 2). The census recorded the location and herd size of the park's key herbivore species as well as a range of environmental variables, including the location of water sources (Viljoen 1996). From 1981-1984, the use of coarse data recording

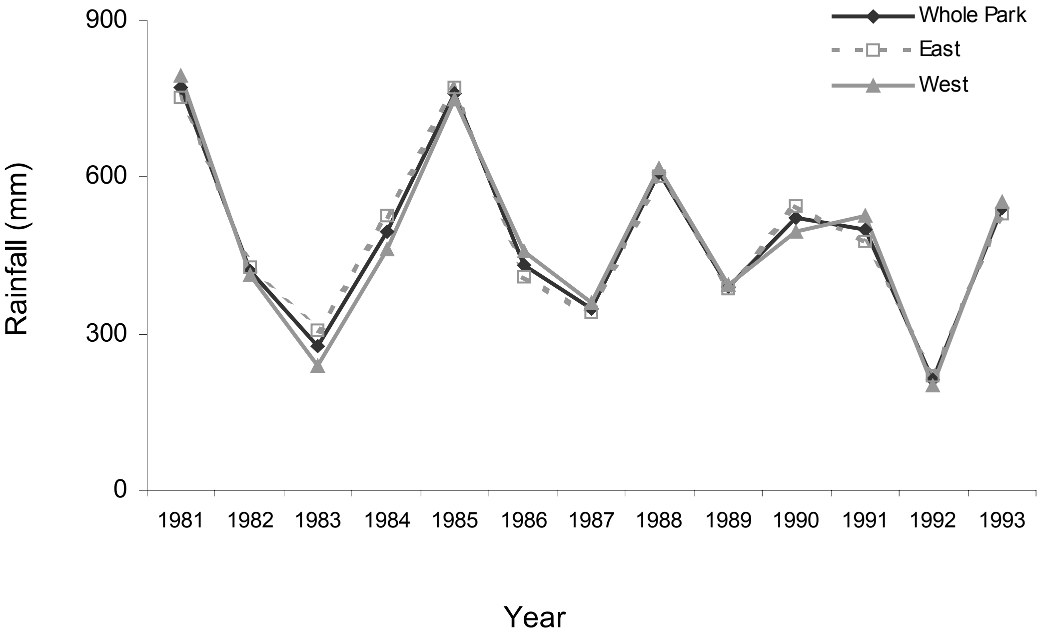

Figure 4. Average annual rainfall, calculated over the entire KNP and in the eastern versus western landscape, is plotted for the study period. The mean annual rainfall, calculated for the whole KNP, was 617 (standard error = 50) in the six wettest years (1981, 1985, 1988, 1990, 1991, 1993) and 346 (standard error = 36) in the six driest years (1982, 1983, 1986, 1987, 1989, 1992).

procedures resulted in a spatial accuracy of 1.5 km (P. C. Viljoen, *personal communication*). The implementation of improved recording procedures from 1985-1993 increased spatial accuracy to approximately 800 m (P. C. Viljoen, *personal communication*). While it is acknowledged that the data contain unknown undercount bias, 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 ephemeral sources (Viljoen 1996). Ephemeral water sources result primarily from dry season rainstorms that coincide with the timing of the census (P. C. Viljoen, *personal communication*). Variability exists in the size of the ephemeral water sources recorded because of the subjective classification used by observers (P. C. Viljoen, *personal communication*). This subjectivity may result in an over-representation of the availability of ephemeral water sources. 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 these ephemeral water sources (Western 1975, Thrash and Derry 1999). Ephemeral 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 was collected simultaneously.

While ephemeral water sources may be over-represented in the raw census data, permanent water sources are under-represented. Visual inspection of maps produced using the census water data reveals that permanent water sources, including perennial rivers and springs, dams, and boreholes, were not always recorded during surveys (for example, large breaks may occur in the perennial rivers). These inspections also reveal that water locations were not recorded throughout the entire park during some surveys. The absence of permanent water sources in the raw census water data results from observer omission (P. C. Viljoen, *personal communication*) and leads to an under-representation 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 (GIS) software ARC/INFO (version 8.0.2, Environmental Systems Research Institute, Inc.). A map of the KNP landscapes, as defined by dominant soil substrate (Fig. 2), 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 discretized to 1 km units, a spatial resolution that subsumes most of the location error in the census data.

The presence of herbivore herds in the GIS grid 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). The KNP aerial census data is collected so that each

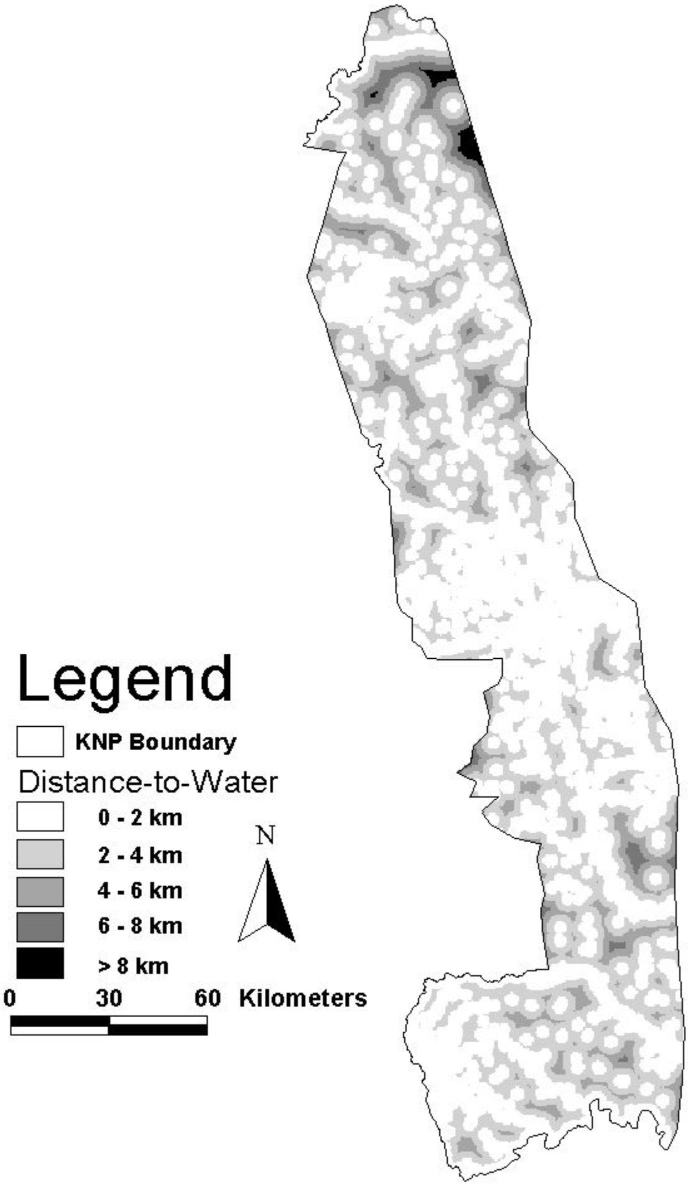

Figure 5. The distribution of 2 km distance-to-water categories in the KNP is mapped using the 1990 aerial census data and locations of known permanent water sources. The occurrence of ephemeral water sources, resulting from the coincidence of winter rainstorms and the aerial census, can be seen in the central and southwestern regions. Average annual rainfall in 1990 is slightly above the median annual rainfall for the study period 1981-1993 (Fig. 4); hence 1990 is classified as a wet year in our analyses.

record represents a cohesive social group or herd (Viljoen 1996). Hence, it is more reasonable to assume independence among the locations of herds than among the locations of individuals. We do not address differences in herd composition (e.g. herd size, sex ratio, or age distribution) 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 model distribution patterns (Neter et al. 1996). However, this method was not used to analyze the KNP census data because, for all species considered, few cells contain more than two herds. Rather, we defined herd presence as a binary variable and used logistic regression to describe the relationship between the binary response variable and corresponding explanatory variables and provide an assessment of the significance of each explanatory variable (Collett 1991). Specifically, in our analyses, herd presence was defined as those cells containing at least one herbivore herd.

The number of herds uniquely represented at the 1 km^2 cell resolution is affected by the coarse data recording procedures used from 1981-1984 (Table 1). However, we decided to include the 1981-1984 data in our analyses to obtain the best possible representation of the effect of rainfall on herbivore distributions. Inclusion of this 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 three herds, three “presences” were

Table 1. The average proportion of occupied 1 km^2 cells that had exactly one herd is calculated over the entire study period (i.e. 1981-1993) and over the period from 1985-1993 in which the data were recorded at a finer spatial resolution.

	1981 – 1993		1985 – 1993	
	Mean	Std. Dev.	Mean	Std. Dev.
Buffalo	0.88	0.10	0.94	0.02
Zebra	0.70	0.14	0.79	0.02
Wildebeest	0.71	0.15	0.81	0.02
Waterbuck	0.79	0.12	0.86	0.02
Giraffe	0.79	0.12	0.87	0.01
Kudu	0.83	0.12	0.90	0.01
Elephant	0.82	0.08	0.87	0.03
Impala	0.50	0.17	0.62	0.02

assigned to that cell's characteristics in the logistic regression data set). The results from the two logistic regression analyses were similar. Although in some cases we found relative differences among species' distance-to-water distributions, the major conclusions derived from the analyses were unaffected by our definition of herd presence. Note that in the analyses presented here (i.e. 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) the proportion of occupied cells can be interpreted as the herd density. When the number of cells containing multiple herds is small, as is the case for species like buffalo (Table 1), this estimated herd density closely approximates actual herd density.

To assess differences between herbivore distance-to-water distributions in the soil substrate-defined landscapes and in wet versus dry years, logistic regression analyses were performed on four discrete subsets of the KNP data set. First, we separated the data from the eastern and western landscapes (Fig. 2). Within each landscape, we separated the data for wet and dry years on the basis of average annual rainfall. We calculated average annual rainfall over the entire park since the average annual rainfall values collected during the study period were similar in the eastern and western 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, 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, 1992) with average annual rainfall below the median for the study period. Data from the year with the median average annual rainfall (1984) was not included in the logistic regression analyses.

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

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

where X is distance-to-water calculated at 1 km intervals and π_i is the proportion of cells occupied by a herd or the herd density (Collett 1991). (Technically, the equations for each species can be combined into a single regression analysis using discrete landscape and rainfall variables, but presentation of the results in this form is unnecessarily complicated.) 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, Inc.) was used to fit the models and obtain variance estimates for the parameters.

The total sample size (i.e. the number of presences and absences) of the i^{th} 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 eastern 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 western landscape is 67,632 for both the wet and dry year data subsets. The number of presences in the logistic regression analyses varies among species because of spatial and temporal differences in species' herd densities (Table 2).

Table 2. The number of herds, and hence the number of presences in the logistic regression analyses, varies among species because of spatial and temporal differences in species' herd densities.

	East		West	
	Wet	Dry	Wet	Dry
Buffalo	1271	1650	2181	2587
Zebra	7950	7810	10169	9000
Wildebeest	5065	4619	3741	3407
Waterbuck	2010	1942	1851	1785
Giraffe	3428	3260	4974	4639
Kudu	3840	4025	6236	6250
Elephant	1664	1595	2744	2710
Impala	10348	9126	23151	20147

In the logistic regression equation, a_{1i} represents the slope of herd density in the distance-to-water distribution. Differences between the four data subsets were quantified using this slope parameter. Specifically, for any two cases k and l we defined the following comparison parameter

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

We calculated the variance of c_{kl} assuming independence among the data subsets, i.e. using the relationship

$$Var(c_{kl}) = Var(a_{1k} - a_{1l}) = Var(a_{1k}) + Var(a_{1l}).$$

Variance estimates of a_{1i} were obtained during the logistic regression fitting procedure. From the calculated variance, we obtained a 95% confidence interval $c_{kl} \pm z_{\alpha/2}\sqrt{Var(c_{kl})}$. 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 obtain a 95% confidence coefficient for all c_{kl} using $c_{kl} \pm z_{\alpha/2g}\sqrt{Var(c_{kl})}$, where g is the number of comparisons (Neter et al. 1996). If this confidence interval did not contain zero, c_{kl} was claimed to represent a significant difference between the distance-to-water distributions. We calculated the parameter c_{kl} for the following four comparisons:

1) eastern versus western landscape in wet years;
2) eastern versus western landscape in dry years;
3) wet versus dry years in the eastern landscape;
4) wet versus dry years in the western landscape.

The logistic regression models were used in all comparative analyses since they account for the variability of the data within each distance category (calculating the observed herd density yields a single point estimate for each distance category) and can be used to determine whether the relationship between herd density and distance-to-water is significant (Collett 1991). Logistic regression fits a monotonic increasing or decreasing response to the observed data (Neter et al. 1996). Where the KNP data does not conform to this shape, the logistic regression results in a best-fit, monotonic approximation of the observed pattern. We used a 6 x 2 contingency test (Sachs 1982) to determine where deviations between the observed and fitted logistic curves are significant. Only the first six distance-to-water classes were analyzed in the contingency test because there is little area more than 6 km from water in the KNP.

RESULTS

In figures 6, 7, and 8, the observed and fitted logistic relationship between herd density and distance-to-water is plotted for grazers, browsers, and mixed feeders, respectively. The contingency tests (Table 3) reveal that the logistic regression models provide a very good fit for buffalo and elephant distributions. The models also provide a good fit for kudu distributions in three of the four cases considered (Table 3). For the other five species, the logistic regression provided a better fit to distribution patterns in the western landscape (Table 3). In general, deviations between the observed and fitted logistic herd densities occur at the ends of the distributions. For zebra and wildebeest, herd density within one kilometer of water is lower than predicted by the logistic regression model (Fig. 6) indicating that other factors, such as intraspecific competition, interspecific competition, or predator densities, may be causing these species to avoid areas within one kilometer of water sources.

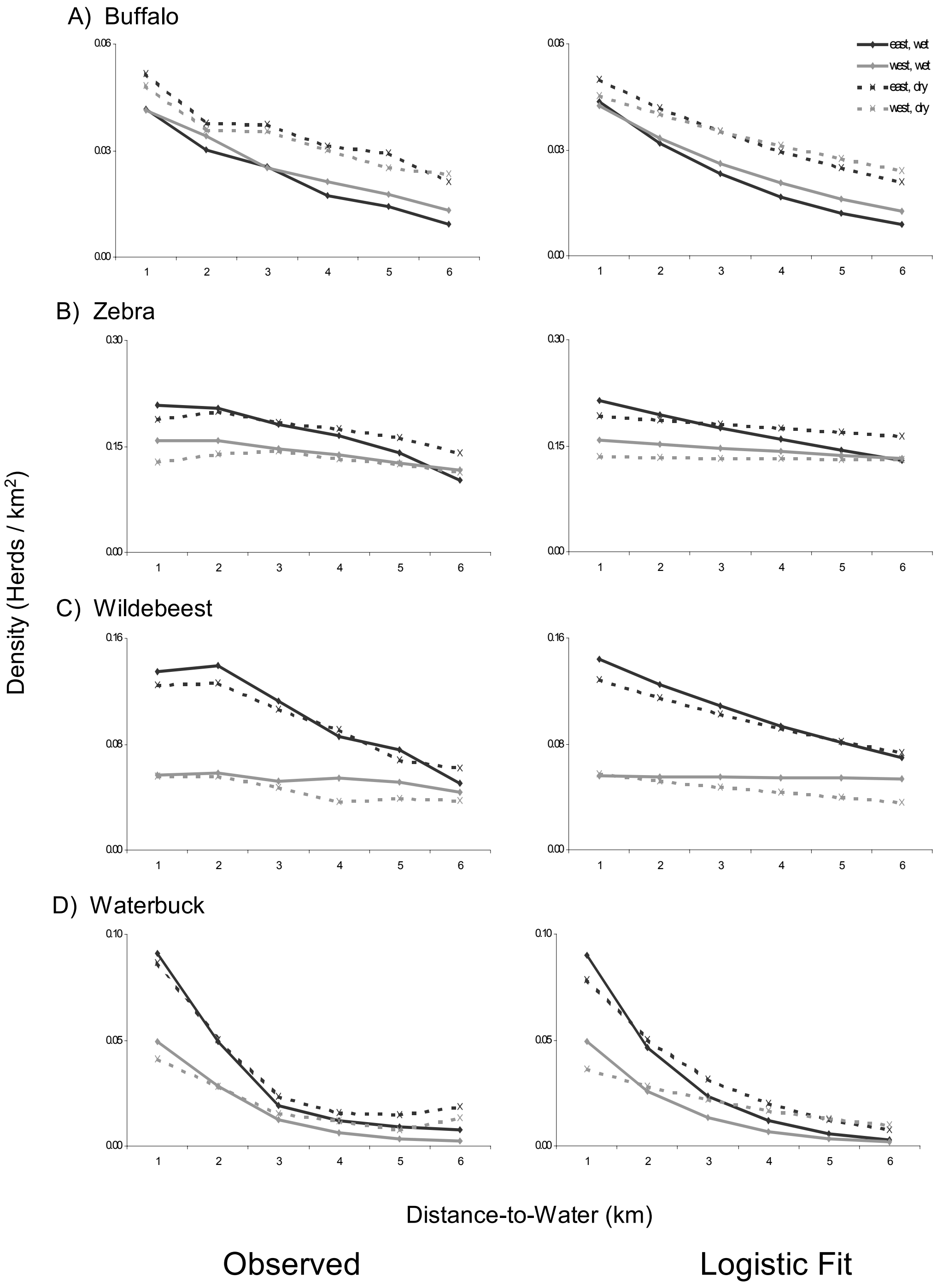

Figure 6. Observed and fitted logistic herd densities are plotted to show landscape and rainfall differences in grazer distance-to-water distributions. Because few areas more than 6 km from water exist in the KNP, only distance-to-water categories 1-6 km are shown.

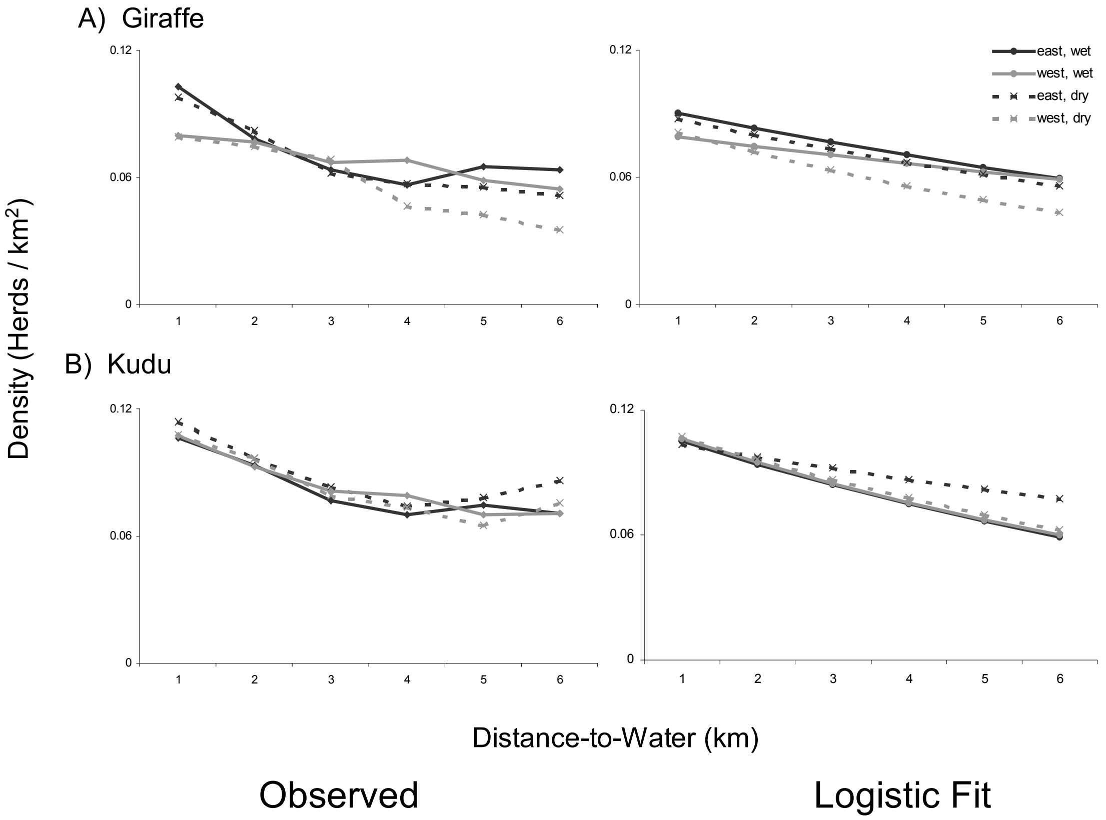

Figure 7. Observed and fitted logistic herd densities are plotted to show landscape and rainfall differences in browser distance-to-water distributions. Because few areas more than 6 km from water exist in the KNP, only distance-to-water categories 1-6 km are shown.

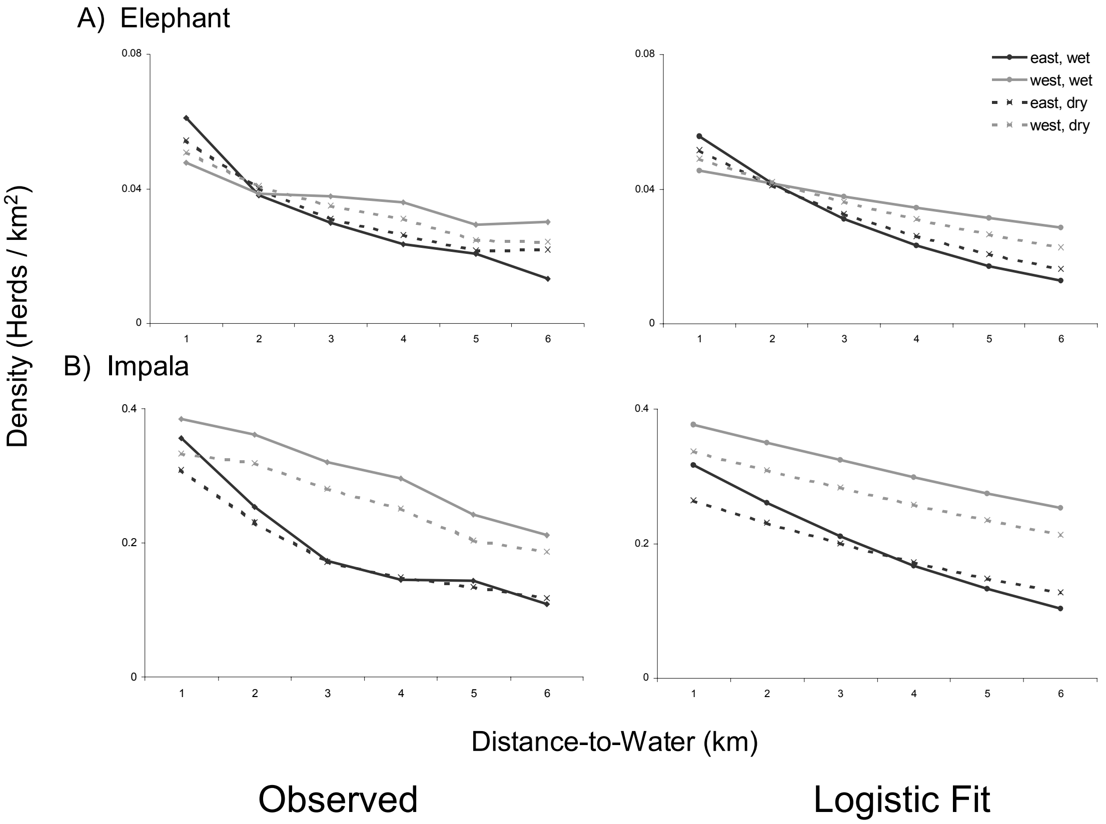

Figure 8. Observed and fitted logistic herd densities are plotted to show landscape and rainfall differences in mixed feeder distance-to-water distributions. Because few areas more than 6 km from water exist in the KNP, only distance-to-water categories 1-6 km are shown.

Table 3. Using a 6 x 2 contingency test, chi-square p-values were calculated to determine the significance of deviations between observed and fitted logistic herd densities. Values less than 0.05 imply a particularly poor fit (see Figures 6, 7, and 8).

	Eastern Landscape		Western Landscape	
	Wet	Dry	Wet	Dry
Buffalo	0.969	0.519	0.982	0.239
Zebra	0.034	0.010	0.369	0.006
Wildebeest	0.002	0.005	0.652	0.224
Waterbuck	0.197	0.0005	0.604	4E-06
Giraffe	0.00006	0.043	0.869	0.100
Kudu	0.197	0.013	0.399	0.216
Elephant	0.446	0.885	0.574	0.912
Impala	2E-09	0.0002	0.016	0.068

In contrast, herd density for waterbuck, giraffe, and impala is higher than predicted by the logistic regression model close to and far from water sources (Fig. 6, 7, and 8). In particular, higher than predicted herd densities are noticeable more than five kilometers from water for waterbuck during dry years and for giraffe in the eastern landscape during wet years (Fig. 6 and 7). The data from these distance classes is highly variable because they occupy a relatively small proportion of the KNP's area, suggesting the need to further examine the reliability of these patterns. In general, the slope of the logistic regression models for these three species is flatter than the slope of the data for the first several distance classes (Fig. 6, 7, and 8), and hence the models may underestimate the distance-to-water coefficient. For all species except buffalo and elephant, the contingency tests reveal significant deviations between observed and fitted logistic herd densities in at least one of the four cases considered, suggesting that herd density does not decline monotonically with distance-to-water. However, in spite of these deviations, the logistic regression models are representative of the relative differences among species' distance-to-water distributions (Fig. 6, 7, and 8).

The logistic regression models show that distance-to-water, or some variable correlated with distance-to-water, affects KNP herbivore distributions. The distance-to-water coefficient (Table 4) was significantly different from zero in 30 out of 32 cases (the exceptions occurred for zebra in western landscape in dry years and for wildebeest in the western landscape in wet years). In all cases this coefficient was negative, indicating that species were closer to water than would be expected if individuals were randomly distributed throughout the landscape. In all four of the cases considered (i.e. the eastern versus western landscape and wet versus dry years), waterbuck had the largest distance-

Table 4. The parameter a_{1i}, the slope of the curve between herd density and distance-to-water (see text), and its standard error (*se*) obtained from logistic regression.

	Eastern Landscape				Western Landscape			
	Wet		Dry		Wet		Dry	
	a_{11}	*se*	a_{12}	*se*	a_{13}	*se*	a_{14}	*se*
Buffalo	-0.328	0.025	-0.180	0.017	-0.250	0.019	-0.130	0.014
Zebra	-0.121	0.008	-0.040	0.007	-0.040	0.008	-0.007*	0.007
Wildebeest	-0.162	0.011	-0.125	0.010	-0.008*	0.013	-0.097	0.012
Waterbuck	-0.706	0.027	-0.478	0.022	-0.670	0.028	-0.263	0.020
Giraffe	-0.090	0.012	-0.096	0.011	-0.063	0.011	-0.134	0.011
Kudu	-0.126	0.012	-0.064	0.010	-0.124	0.011	-0.117	0.009
Elephant	-0.303	0.021	-0.237	0.019	-0.096	0.016	-0.159	0.015
Impala	-0.279	0.009	-0.180	0.008	-0.117	0.006	-0.126	0.006

* These parameters are not significantly different from zero at the p=0.05 level.

to-water coefficient (Table 4), indicating that waterbuck herd density showed the steepest decline as distance-to-water increased. Buffalo and elephant also had large distance-to-water coefficients (Table 4), although buffalo coefficients were larger during wet years and elephant coefficients were larger during dry years. Values of the distance-to-water coefficients for impala (Table 4) typically occurred in the middle of the range. Zebra, wildebeest, giraffe, and kudu generally had the smallest distance-to-water coefficients (Table 4), indicating a weaker relationship between herd density and distance-to-water.

For each species, the comparison parameter, c_{kl}, measures the difference between distance-to-water coefficients for the eastern versus western landscape and wet versus dry years. In the KNP, grazer distributions were characterized either by landscape or rainfall differences (Table 5). Comparison parameter values for waterbuck and buffalo show that the largest differences occur between distance-to-water coefficients for wet and dry years (Table 5). In particular, both species occur farther from water in dry years (Fig. 6). Waterbuck distributions also showed some evidence of landscape differences (Table 5). However, the distance-to-water coefficient for waterbuck in the western landscape during dry years was potentially underestimated due to the variability of the data collected more than five kilometers from water. Therefore, comparison parameter values for waterbuck may be artificially high.

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 versus wet years (Fig. 6). This density difference 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

Table 5. The comparison parameter, c_{kl}, and 95% confidence interval (see text for details) obtained from the logistic regression distance-to-water coefficients. For the eastern versus western landscape, a negative c_{kl} value indicates that herds occur farther from water in the west. This analysis was performed separately for wet and dry years. For wet versus dry years, a negative c_{kl} value indicates that herds occur farther from water in dry years. This analysis was performed separately for the eastern and western landscapes.

	Eastern vs. Western Landscape		Wet vs. Dry Years	
	Wet	Dry	East	West
Buffalo	-0.078 ± 0.080*	-0.050 ± 0.058*	-0.148 ± 0.078	-0.120 ± 0.062
Zebra	-0.081 ± 0.030	-0.032 ± 0.027	-0.082 ± 0.029	-0.033 ± 0.029
Wildebeest	-0.154 ± 0.043	-0.028 ± 0.041*	-0.037 ± 0.038*	0.089 ± 0.046
Waterbuck	-0.035 ± 0.099*	-0.215 ± 0.075	-0.228 ± 0.088	-0.407 ± 0.088
Giraffe	-0.027 ± 0.043*	0.037 ± 0.041*	0.006 ± 0.043*	0.071 ± 0.041
Kudu	-0.002 ± 0.041*	0.052 ± 0.035	-0.062 ± 0.040	-0.007 ± 0.037*
Elephant	-0.207 ± 0.067	-0.078 ± 0.061	-0.066 ± 0.072*	0.063 ± 0.055
Impala	-0.162 ± 0.028	-0.054 ± 0.025	-0.099 ± 0.030	0.009 ± 0.022*

* Indicates that the comparison parameter is not significantly different from zero at the $p=0.05$ level.

dry years because vegetation cover is reduced (P. C. Viljoen, *personal communication*). Comparison parameter values for wildebeest show that the largest difference occurs between distance-to-water coefficients for the eastern and western landscapes during wet years (Table 5). In particular, wildebeest occurred farther from water in the western landscape than the eastern landscape (Fig. 6). Comparison parameter values for zebra indicate both landscape and rainfall differences in their distance-to-water distributions, although the differences were not as large as those observed for buffalo or wildebeest (Table 5).

Distance-to-water distributions for browsers were characterized by small changes in response to landscape and rainfall (Table 5). Comparison parameter values for both giraffe and kudu were never greater than 0.071 (Table 5). In contrast, the comparison parameter values indicating large landscape and rainfall differences for grazers ranged from 0.12 to 0.15 (Table 5). Additionally, there was no discernible pattern in giraffe and kudu comparison parameter values (Table 5). In particular, the greatest differences in both species' distribution patterns occur in wet versus dry years. However, giraffe occur farther from water in the western landscape during wet years, while kudu occur farther from water in the eastern landscape during dry years (Fig. 7). Alternatively, the largest differences, excluding waterbuck, were obtained when comparing distributions in the eastern versus western landscape for mixed feeders (Table 5). In particular, both elephant and impala occur farther from water in the western landscape, particularly during wet years (Fig. 8).

DISCUSSION

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. If herbivore drinking requirements necessitate regular access to surface water, a species' water dependence may be inferred from the size of the distance-to-water coefficient in our analyses. Specifically, herds of water-independent species should be distributed evenly with respect to distance-to-water, while herds of water-dependent species should occur close to water sources. Hence, our analyses suggest that waterbuck are the most water-dependent of the eight species analyzed, having distributions strongly related to the proximity of water sources. Buffalo and elephant distributions also showed strong water dependence, although for both species the strength of the dependence varied temporally with buffalo distributions occurring close to water in wet years while elephant distributions occurred close to water in dry years. Zebra were the most water-independent species, having relatively similar herd densities across distance categories compared to the other species. Wildebeest, giraffe, and kudu were also relatively water-independent. Impala distributions were intermediate between the strong water dependence shown by waterbuck, buffalo, and elephant, and the more water-independent distribution patterns shown by zebra, wildebeest, giraffe, and kudu.

The results of our analyses do not agree with the findings of previous studies and reviews (Western 1975, Owen-Smith 1996). Western (1975) found that grazers were more water-dependent than browsers. Owen-Smith (1996) notes that among grazers, species having the highest biomass density are typically the most affected by surface water availability. Two of the grazers consider in our analyses, waterbuck and buffalo, showed strong water dependence, although the strength of buffalo water dependence varied with rainfall. Distribution patterns for the other two grazers, zebra and wildebeest, were relatively water-independent. In at least two of the four cases considered (i.e. eastern versus western landscape and wet versus dry years) zebra and wildebeest distributions were more water-independent than browser distributions. Of the four grazers, waterbuck have the lowest biomass density followed by wildebeest, zebra, and buffalo (Fig. 3).

The differences between our results and those of previous studies may arise from the relative abundance of surface water in the KNP. For example, in Western's study area, water distribution was highly localized as evidenced by the fact that 48% of the area occurred more than 15 km from water sources (Western 1975). Alternatively, during our study period, at most 8% of the area in the KNP occurred more than 5 km from water. The low percentage obtained for the KNP can be partially attributed to the fact that our analyses included ephemeral water sources resulting from dry season rainstorms. Therefore, species water dependence may not be fully expressed in the KNP because no waterless areas exist beyond the range of the large, mobile herbivores considered in our analyses.

Although our analyses address distribution patterns at the smaller scale imposed by the close spacing of the KNP water sources, our results suggest that distance-to-water distributions for KNP herbivores can be differentiated on the basis of landscape and rainfall comparisons. For buffalo, the largest grazer considered in our analyses, the greatest difference occurred between distance-to-water distributions in wet and dry years.

Alternatively, for wildebeest, the smallest grazer considered in our analyses, the greatest difference occurred between distance-to-water distributions in the eastern and western landscapes. For zebra, whose body size falls between buffalo and wildebeest, changes in distributions occurred in response to both landscape and rainfall. However, the changes were not as large as those observed for buffalo or wildebeest.

Distribution patterns for waterbuck, the fourth grazer considered in our analyses, were generally characterized by an exponential decline in herd density as distance-to-water increased. Exceptions occurred during dry years, particularly in the western landscape, when increases in herd density were observed more than five kilometers from water instead of the decreases suggested by the general pattern of exponential decline. These exceptions are surprising because waterbuck are typically regarded as a highly water-dependent species (Estes 1991). The reliability of the data collected more than five kilometers from water needs further investigation since these distance classes form a small proportion of the total KNP area. If the data is reliable, further research is needed to develop an ecological explanation for the elevated number of waterbuck herds occurring far from water in the western landscape during dry years.

Distribution patterns for giraffe and kudu, the two browsers considered in our analyses, were comparatively similar between landscapes and in wet versus dry years. In general, their distributions were characterized by a weak relationship between herd density and distance-to-water. Alternatively, the largest differences in distance-to-water distributions were observed between the eastern and western landscapes for elephant and impala, both mixed feeders whose diets contain a large proportion of browse during the dry season. In contrast to the other six species, both elephant and impala occur at higher population densities in the western versus eastern landscape (Fig. 9). If higher densities result in an increase in intraspecific competition, we would expect a flattening in distance-to-water distributions. Hence the large differences between distance-to-water distributions in the eastern and western landscapes, observed for both elephant and impala, may in part be attributed to a response to intraspecific competition. However, distribution patterns for browsers and grazers cannot be explained by density differences because these species occur closer to water in landscapes with higher densities or show similar distribution patterns between landscapes with different densities. For these species, an alternative hypothesis must be derived to explain the observed differences in distance-to-water distributions.

Herbivore distributions define the template in which they influence and are influenced by the attributes of biodiversity (i.e. composition, structure, and function) at all levels of ecological organization. Previous studies have shown that herbivore congregations can affect the structure and dynamics of the vegetation community (Pellew 1983, Owen-Smith 1988, Dublin et al. 1990) as well as ecosystem processes, namely nutrient cycling and energy flow (McNaughton 1976, 1979, Botkin et al. 1981, McNaughton et al. 1988). Specific studies of herbivore congregation at water sources have shown an effect on 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), the dynamics of the herbivore community (Smuts 1978, Walker et al. 1987, Fryxell et al. 1988), and the maintenance of diversity within the herbivore community (Owen-Smith 1996, Harrington et al. 1999).

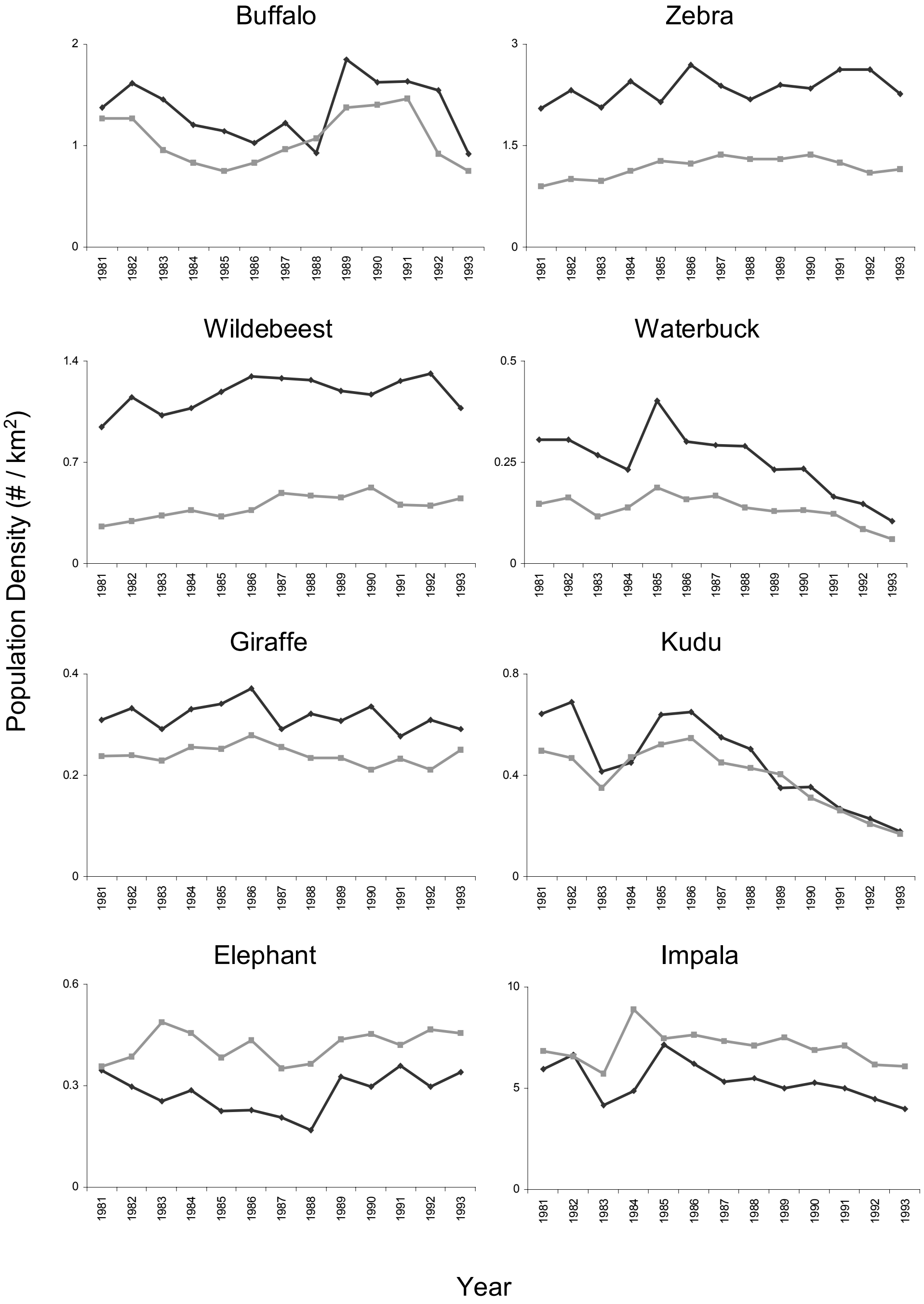

Figure 9. The population density (# of individuals / km^2) of eight herbivore species in the eastern (black lines) and western (gray lines) KNP landscapes is plotted annually.

Manipulation of artificial water sources provides a potential tool for managing herbivore congregations at water sources (Owen-Smith 1996). Strategic placement of artificial water sources can increase the economic potential of protected areas since the resulting herbivore congregations can serve as a focal point for tourists (Owen-Smith 1996). However, these artificial water sources may also have a negative impact on biodiversity and hence they may compromise the conservation goals of protected areas (Owen-Smith 1996). For example, placing artificial water sources in areas previously devoid of water during the dry season may increase competition between abundant water-dependent species and rare water-independent species (Owen-Smith 1996). In order to develop water management plans that successfully address these issues, we must continue to refine our understanding of the ecological factors determining the shape of herbivore distance-to-water distributions and the relationship between variation in these factors and distribution changes.

Our analyses of the distance-to-water distributions of eight herbivore species in the KNP reveal that herbivore congregation around water sources can be expected during the dry season. The analyses also reveal that patterns of herbivore congregation will differ between soil substrate-defined landscapes and in wet versus dry years. In particular, we found large differences between distance-to-water distributions in soil substrate-defined landscapes for wildebeest, elephant, and impala and large differences between distance-to-water distributions in wet and dry years for buffalo. Because of the large impact herbivore congregations can have on the attributes of biodiversity at all levels of ecological organization, it is important to identify the factors associated with rainfall and the soil substrate-defined landscapes that influence the distance-to-water distributions of KNP herbivores.

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Chapter Two

Limiting factor mitigation: evaluating determinants of herbivore distributions in an African savanna

J. V. Redfern & W. M. Getz

ABSTRACT

The identification of factors that limit population distributions is an essential component of wildlife management and conservation. We develop an optimal foraging approach we designate “limiting factor mitigation” (LFM) to analyze the influence of putative limiting factors on population distributions. LFM focuses on how a population’s distribution, defined with respect to an independent landscape variable, changes in response to a perturbation in a putative limiting factor. Specifically, if a factor is limiting, perturbation of the factor alters the population’s distribution as an implicit mitigation of the trade-off between the limiting factor and the independent landscape variable. LFM also incorporates a threshold effect in which factors above some critical level do not influence distributions. We use LFM analysis to interpret distribution changes for seven herbivore species in Kruger National Park (KNP), South Africa. This application of LFM analysis suggests that distance-to-water distributions for KNP grazers may be limited by forage quality and/or quantity and suggests future research programs that can expand our understanding of relationships between distance-to-water distributions for browsers and forage quantity and distance-to-water distributions for mixed feeders and forage quality.

INTRODUCTION

The distribution of a population with respect to an independent landscape variable, such as distance to the nearest water source, is influenced by a host of environmental and ecological factors. A list of all possible factors influencing the shape of a population's distribution can be divided into two categories: factors that cause distribution changes when perturbed and factors that do not cause a distribution change when perturbed. The former we refer to as "limiting factors". This definition contrasts with the more traditional concept of the existence of a single limiting factor for any given set of circumstances (e.g. Liebig's law of the minimum), although it does not exclude the possibility that some factors may be more limiting than others. For example, if multiple factors are perturbed by an equal percentage, the factor producing the greatest distribution change can be regarded as the most limiting.

Implicit in our definition of limiting factors is a relationship between the factors and the independent landscape variable. Specifically, limiting factors are defined in the context of the landscape variable, implying that the statement "factor Z is limiting" must be accompanied by the qualifying clause "for population distributions defined with respect to landscape variable X". A factor that is limiting in the context of one landscape variable may not be limiting in the context of another landscape variable. For example, forage quality may limit a particular species' distribution when the distribution is defined with respect to distance-to-water (i.e. perturbations in forage quality cause a change in the distance-to-water distribution of the species) but not when the distribution is defined with respect to distance-to-roads. Thus it is important to select an independent landscape variable that is influential in determining population distributions and that has a potential interaction with the limiting factors.

Although the identification of limiting factors is of great practical importance to wildlife managers and conservation biologists, it can be difficult to accomplish. Recent studies suggest that traditional statistical techniques such as correlation and regression analyses do not adequately characterize or test for the relationship between population abundance and putative limiting factors (Thomson et al. 1996, Cade et al. 1999). While alternative methods of statistical analysis have been developed (Thomson et al. 1996, Cade et al. 1999), they do not specifically address the issues involved in identifying factors that limit population distributions.

In the context of herbivore foraging, bottom-up or mechanistic optimal foraging models have been used to analyze consumer-resource relationships (for example see Owen-Smith and Novellie 1982, Belovsky 1984). Mathematical formulations of these mechanistic models generally involve the specification of a fitness function, which will be maximized by the behavior of individuals. These mechanistic optimal foraging models have been applied to understand large herbivore aggregation (Fryxell 1991) and to predict habitat selection for large herbivores (Wilmshurst et al. 1999, Wilmshurst et al. 2000). Models based on the ideal free distribution (IFD, see Fretwell and Lucas 1970, Fretwell 1972) have also been used to analyze herbivore-resource relationships (reviewed in Kennedy and Gray 1993, Farnsworth and Beecham 1999). On the basis of resource-derived fitness per individual, IFD models predict that the distribution of herbivores should correspond to the distribution of resources.

We present an optimal foraging approach we designate "limiting factor mitigation" (LFM) for identifying factors that limit population distributions. LFM differs from mechanistic optimal foraging models because it does not explicitly include a fitness function and from IFD models because the proposed relationship between the independent landscape variable and putative limiting factors is not static. LFM analysis can be applied to understand consumer-resource systems; here we develop the analysis in the context of herbivory. We use LFM analysis to interpret distribution changes, described in Chapter 1, for seven herbivore species in Kruger National Park (KNP), South Africa. These species represent a spectrum of sizes, feeding types, and gut morphology (Table 1). In Chapter 1, we used logistic regression to characterize distance-to-water distributions for these seven species and found that distribution patterns for some species differed in soil substrate-defined landscapes and in wet versus dry years. Here we propose that the soil substrate-defined landscapes are a potential surrogate for forage quality and that wet versus dry years are a potential surrogate for forage quantity. We use LFM analysis to determine whether these potential surrogates for forage quality and quantity represent limiting factors for the herbivore species considered.

LIMITING FACTOR MITIGATION

LFM analysis rests on two basic tenets. The first tenet postulates the existence of a characteristic population distribution with respect to an independent landscape variable while the second tenet defines the relationship between the landscape variable and factors that limit the population's distribution. Specifically, LFM's first tenet is that various ecological processes including both interspecific interactions (competitive, exploitative,

Table 1. Characteristics of the species considered in the analyses.

Species	Scientific Name	Feeding Type	Weight* (kg)	Gut Morphology
Buffalo	*Syncerus caffer*	Grazer	576	Ruminant
Zebra	*Equus burchelli*	Grazer	220	Non-Ruminant
Wildebeest	*Connochaetes taurinus*	Grazer	186	Ruminant
Giraffe	*Giraffa camelopardalis*	Browser	700	Ruminant
Kudu	*Tragelaphus strepsiceros*	Browser	170	Ruminant
Elephant	*Loxodonta africana*	Mixed	3000	Non-Ruminant
Impala	*Aepyceros melampus*	Mixed	45	Ruminant

*Female weight estimates (Estes 1991).

or mutualistic) and biotic-abiotic interactions (nutrient flows, temperature effects, etc.) result in the establishment of a characteristic population distribution with respect to an independent landscape variable. For example, we use distance-to-water as our landscape variable in the KNP data analysis presented below. Previous studies have suggested that water availability places a large-scale constraint on herbivore distributions (Bailey et al. 1996), particularly in semi-arid ecosystems such as the KNP (Western 1975, Owen-Smith 1996). Other possible landscape variables include distance-to-cover, home range size, or an independent environmental variable such as soil nitrogen level. Population distributions defined with respect to the landscape variable may correspond to an ideal free distribution (Fretwell and Lucas 1970, Fretwell 1972), although they may also represent average distributions in populations that are not inherently stable or distributions that are influenced by anthropogenic factors.

The second tenet is that limiting factors determine the shape of the characteristic population distribution. A limiting factor is identified when perturbation of the factor results in measurable changes to the characteristic population distribution. Therefore, the second tenet implies that population distributions change in response to limiting factor perturbations as an implicit mitigation of the trade-off between the limiting factor and the independent landscape variable. One can associate a “level of tension” with the landscape variable that keeps the population in a particular distribution pattern. If the population becomes stressed by reduced accessibility to a limiting factor, the tension associated with the landscape variable increases as animals search larger areas to mitigate the reduced accessibility of the limiting factor.

Limiting factors are, of course, highly context dependent. A factor may be limiting under one set of ecological conditions but not another (e.g. a factor may be limiting for a species only in the absence of a mutualist or in the presence of a predator or competitor). The distributions of different species should also be affected by different limiting factors. For example, a perturbation in forage quantity may have no measurable effect on how one species is distributed across a landscape but may have a strong effect on a second species. In this case, forage quantity would be identified as a limiting factor for the distribution of the second species but not the first.

The two basic tenets of LFM analysis can be formalized in various mathematical models. We begin by letting $f(x;\alpha)$ represent some measure of a population distribution with respect to an independent landscape variable x and a putative limiting factor that has a value α. The integral $F_{[x_1,x_2]}(\alpha) = \int_{x_1}^{x_2} f(x;\alpha)dx$ may simply be a measure of the numbers or biomass of the population in a unit of area that is within the range $[x_1,x_2]$ specified by the independent landscape variable or it may represent the probability of finding at least one individual (solitary species) or one herd (gregarious species) in the unit area. LFM analysis posits that if the two distributions $f(x;\alpha)$ and $f(x;\alpha+\Delta\alpha)$ are different whenever $\Delta\alpha \neq 0$, then α is a limiting factor. In practice, we must interpret this statement in the context of the statistical variability associated with empirical data and the degree to which $f(x;\alpha)$ is perturbed for a unit perturbation of α (i.e. the relative strength of the limitation can be compared among several limiting variables).

A threshold value may also exist with regard to the putative limiting factor in the sense that $f(x;\alpha) = f^0(x)$ for all $\alpha > \alpha^0$, and $f(x;\alpha) \neq f^0(x)$ for all $\alpha \leq \alpha^0$. In this case the factor may only become limiting when its value falls below the threshold value, α^0, in an ecological context in which all other factors remain fixed. For example, studies based on feeding trials suggest that a saturating relationship exists between forage quality and herbivore consumption (Jones 1972, Baile and Forbes 1974, Spalinger et al. 1986). A similar relationship has been proposed between forage quantity and herbivore consumption (Wickstrom et al. 1984, Renecker and Hudson 1985, Short 1985).

LIMITING FACTOR MITIGATION APPLIED: HERBIVORE DISTRIBUTIONS IN KRUGER NATIONAL PARK, SOUTH AFRICA

The study described in Chapter 1, analyzing distance-to-water distributions for herbivore species in the Kruger National Park (KNP), South Africa, provides a natural context in which to apply LFM analysis. Herbivores foraging in an African savanna ecosystem may become nutritionally stressed during an annual dry season when both forage quality and quantity are reduced (Owen-Smith 1982, Prins 1996). In addition to meeting nutritional requirements, herbivores must satisfy non-foraging needs including water requirements. In particular, previous studies suggest that, in semi-arid ecosystems such as the KNP, the locations of water sources impose a large-scale constraint on dry season herbivore distributions (Western 1975, Owen-Smith 1996).

We apply LFM analysis to determine whether distance-to-water distributions for seven KNP herbivore species indicate that potential surrogates for forage quality and quantity represent limiting factors. No long-term, direct measures of forage quality and quantity are available for the KNP, but forage quantity is positively correlated with rainfall (Rutherford 1980) and forage quality is expected to differ between the nutrient-rich clay soils of the basalt-dominated eastern KNP landscape and the nutrient-poor sandy soils of the granite-dominated western KNP landscape (Fig. 1) (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 have a more dispersed distribution in the nutrient-poor western landscape, compared to the nutrient-rich eastern landscape (Owen-Smith, *personal communication*).

In Chapter 1, we analyzed herbivore distributions in the eastern and western KNP landscapes and in wet versus dry years. We defined wet years as the six years with the highest average annual rainfall during the study period (1981-1993) and dry years as the six years with the lowest average annual rainfall (see Chapter 1). We propose that the eastern versus western landscape represents a potential surrogate for forage quality in the KNP and that rainfall represents a potential surrogate for forage quantity.

We hypothesize that critical species-specific forage quality and quantity thresholds exist, above which a species' distance-to-water distribution can be characterized as an "unstressed foraging" distribution. (Note that we expect actual critical thresholds to differ between species because of variations in foraging behavior. The shape of the "unstressed foraging" distribution is also expected to vary between species, reflecting differences in water dependence). Below these thresholds, LFM analysis predicts an increase in a species' mean distance-to-water as a result of individuals mitigating limitations in nutritional requirements (e.g. intake quality or quantity) by foraging farther from water.

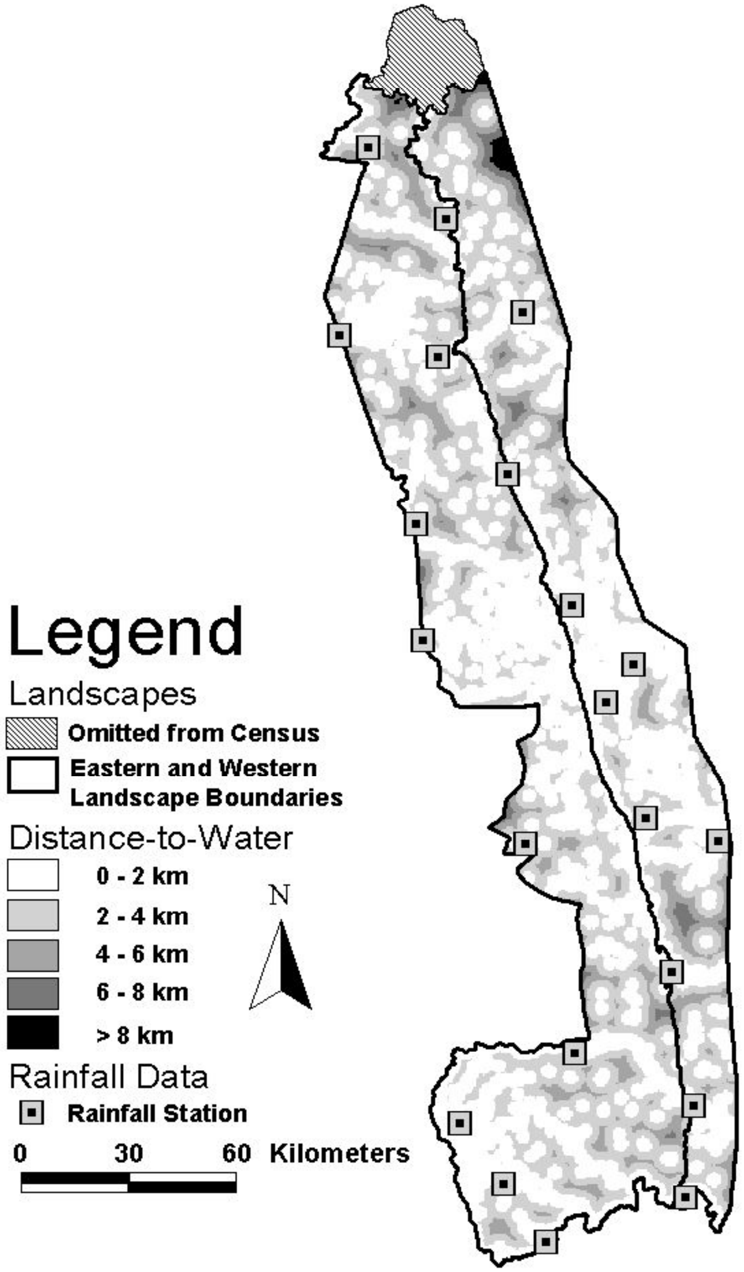


Figure 1. This Geographic Information System representation of our landscape variable, distance-to-water, was produced using the 1990 KNP aerial census data. The boundaries of the eastern and western landscapes and the sites of the 21 rainfall stations are also indicated.

In the KNP ecosystem, the hypothesis that the forage quality surrogate represents a limiting factor for herbivore species is supported if herbivore distributions differ significantly in the eastern and western landscapes. Species should occur farther from water in the western landscape if the dispersed distribution of high quality forage, relative to the eastern landscape, forces individuals to travel farther to satisfy their forage quality requirements. With increasing rainfall, forage production becomes nutrient rather than water limited, resulting in a high biomass of low quality forage (Breman and de Wit 1983). Hence, we expect greater distribution differences between the eastern and western landscapes in wet years, rather than dry years, for species limited by forage quality. The hypothesis that the forage quantity surrogate represents a limiting factor for herbivore species is supported if herbivore distributions differ significantly in wet and dry years. Reduced forage production in dry years, relative to wet years, should result in a more rapid depletion of forage patches near water sources. Consequently, species should occur farther from water in dry years if reduced forage production forces individuals to travel farther from water to satisfy their forage quantity requirements.

In Chapter 1, we characterized distance-to-water distributions for each species in the eastern and western KNP landscapes during wet and dry years using the logistic regression model

$$f(x;i) = \ln\left(\frac{\pi_i}{1-\pi_i}\right) = a_{0i} + a_{1i}x\,,$$

where the index i designates data for a particular species aggregated according to one of the four cases defined by the landscape and rainfall dichotomies; x is the distance-to-water calculated at 1 km intervals; and π_i is the proportion of cells occupied by at least one herd. If landscape is a viable surrogate for forage quality, comparing distribution patterns in the eastern and western landscapes is tantamount to comparing distributions in which a putative limiting factor, α_1 – representing forage quality, is perturbed to a new value, $\alpha_1+\delta_1$. Likewise, if rainfall is a viable surrogate for forage quantity, comparing distribution patterns in wet versus dry years is tantamount to comparing distributions in which a putative limiting factor, α_2 – representing forage quantity, is perturbed to a new value, $\alpha_2+\delta_2$.

In Chapter 1, we used the logistic regression slope parameter, a_{1i}, to analyze differences in the distance-to-water distributions for each species. Specifically, for the following four cases, we calculated a comparison parameter, $c_{kl} = a_{1k} - a_{1l}$ where k and l signify the particular distributions under comparison in each case:

1) eastern versus western landscape in wet years
   (a putative forage quality comparison);
2) eastern versus western landscape in dry years
   (a putative forage quality comparison);
3) wet versus dry years in the eastern landscape
   (a putative forage quantity comparison);
4) wet versus dry years in the western landscape
   (a putative forage quantity comparison).

Note that forage quality limitations should be stronger in wet rather than dry years, as explained above, and hence we expect comparison parameter values to be larger for case 1 than case 2. The comparison parameter was assumed to represent a significant difference between the two distributions if the 95% confidence interval, calculated using the Bonferroni procedure for joint estimation (see Chapter 1), did not include zero. Comparison parameter values that are significantly different from zero suggest that the forage quality and quantity surrogates represent limiting factors.

The conditions under which the three grazers occurred farther from water can be explained on the basis of each species' size and gut morphology. Buffalo distance-to-water distributions substantially flatten or stretch out in dry versus wet years in both the eastern and western landscapes (Fig. 2). In response to rainfall, zebra and wildebeest distributions exhibit a smaller change (Fig. 2). On the other hand, wildebeest wet year distributions show a strong flattening response in the western versus eastern landscape (Fig. 2). Buffalo and zebra distributions exhibit a smaller change in response to landscape. For all three species, the difference between distribution patterns in the eastern and western landscapes is larger for wet years in accordance with the expectation that increased rainfall results in a high biomass of low quality forage (Breman and de Wit 1983).

If landscape and rainfall are viable forage quality and quantity surrogates, respectively, for KNP grazers, our LFM analysis indicates that distance-to-water distributions for buffalo are more limited by forage quantity than forage quality while distance-to-water distributions for wildebeest are more limited by forage quality than forage quantity. These results are concordant with our understanding of buffalo and wildebeest feeding requirements. Specifically, buffalo are the largest ruminant grazers considered in the analyses, with average adult females weighing close to 600 kg (Estes, 1991). In contrast, wildebeest are a much smaller ruminant with an average adult female weighing approximately 200 kg (Estes 1991). Previous studies have shown a relationship

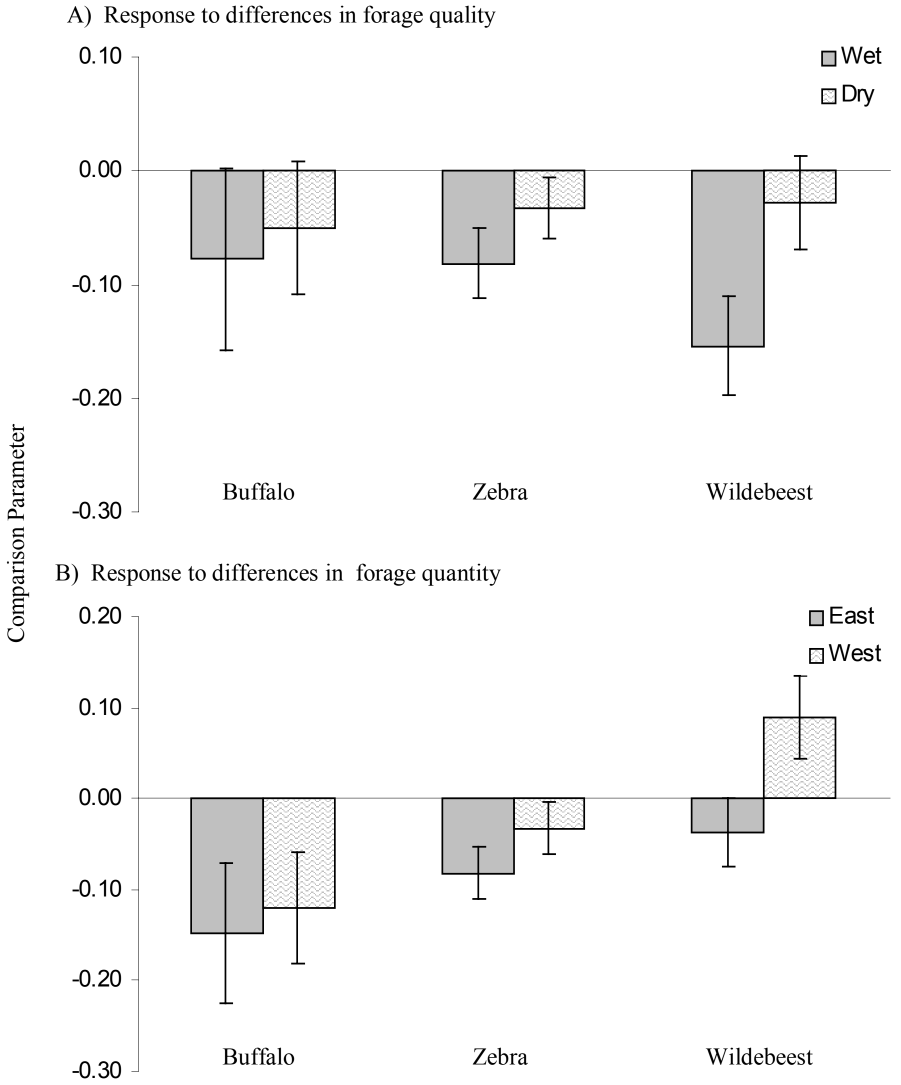


Figure 2. The comparison parameter values, c_{kl} (see text for details), reported in Chapter 1 are plotted to summarize changes in distance-to-water distributions for buffalo, zebra, and wildebeest. In plot A), distribution change is measured in response to forage quality in wet and dry years (negative values of c_{kl} imply that the probability of a herd's presence falls more steeply as distance-to-water increases in the eastern versus western landscape). In plot B), distribution change is measured in response to forage quantity in the eastern and western KNP landscapes (negative values of c_{kl} imply that the probability of a herd's presence falls more steeply as distance-to-water increases in wet versus dry years).

between species' body size and the relative emphasis placed on forage quality versus quantity maximization (Jarman 1974, Owen-Smith 1982, Demment and Van Soest 1985, Prins 1996). In particular, larger species such as buffalo are expected to emphasize forage quantity maximization while smaller species, such as wildebeest, are expected to emphasize forage quality maximization.

LFM analysis also indicates that distance-to-water distributions for zebra are limited by both putative forage quantity and putative forage quality perturbations, although they are less limited by forage quantity than buffalo and less limited by forage quality than wildebeest. This result is concordant with our understanding of zebra feeding requirements, as determined by gut morphology and size. Zebra are a non-ruminant grazer with adult females weighing approximately 220 kg (Estes 1991). Their gut morphology suggests that zebra distributions should change in response to forage quantity limitations, although this response should be smaller than that observed for larger species (Jarman 1974, Owen-Smith 1982, Demment and Van Soest 1985, Prins 1996). Their size suggests that zebra distributions should change in response to forage quality limitations, although the response should be smaller than that observed for a ruminant of similar size (Jarman 1974, Owen-Smith 1982, Demment and Van Soest 1985, Prins 1996). The agreement between our grazer results and the general relationship between body size, gut morphology, and the relative importance of forage quality versus quantity, suggests that the east-west landscape and wet-dry rainfall dichotomies are viable forage quality and quantity surrogates, respectively, for KNP grazers.

The parameters measuring the change in distance-to-water distributions were much smaller for browsers relative to grazers and there is no discernible pattern to these parameter values (Fig. 3). LFM analysis suggests that the browser results can be interpreted in at least three ways. First, it is possible that critical forage thresholds have not been reached for browsers in the KNP. Second, it is possible that the east-west and wet-dry dichotomies are not good indicators of browse quality and quantity. This possibility is particularly likely for browse quantity. While 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 since trees have greater nutrient storage capacities and access to deeper water sources than grasses (Rutherford 1984, Walker and Noy-Meir 1982). Third, browsers are expected to be more water-independent than grazers or mixed feeders (Western 1975, Owen-Smith 1996). Hence, it is possible that the small distribution changes observed for browsers are representative of a weaker relationship between the landscape variable, distance-to-water, and the forage surrogates.

For all seven species, the largest difference was observed between mixed feeder distance-to-water distributions in the eastern and western landscapes during wet years (Fig. 4). However, caution must be used in interpreting these results because both elephant and impala occur at higher densities in the nutrient-poor western landscape compared to the nutrient-rich eastern landscape (see Chapter 1). Hence, although both species occur farther from water in the western landscape, the degree to which this distribution change can be attributed to a mitigation of decreased forage quality versus a mitigation of increased intraspecific competition cannot be determined using the current data set. Application of LFM analysis for the other five species is not confounded by density because these species occur at similar or higher densities in the nutrient-rich eastern landscape (see Chapter 1).

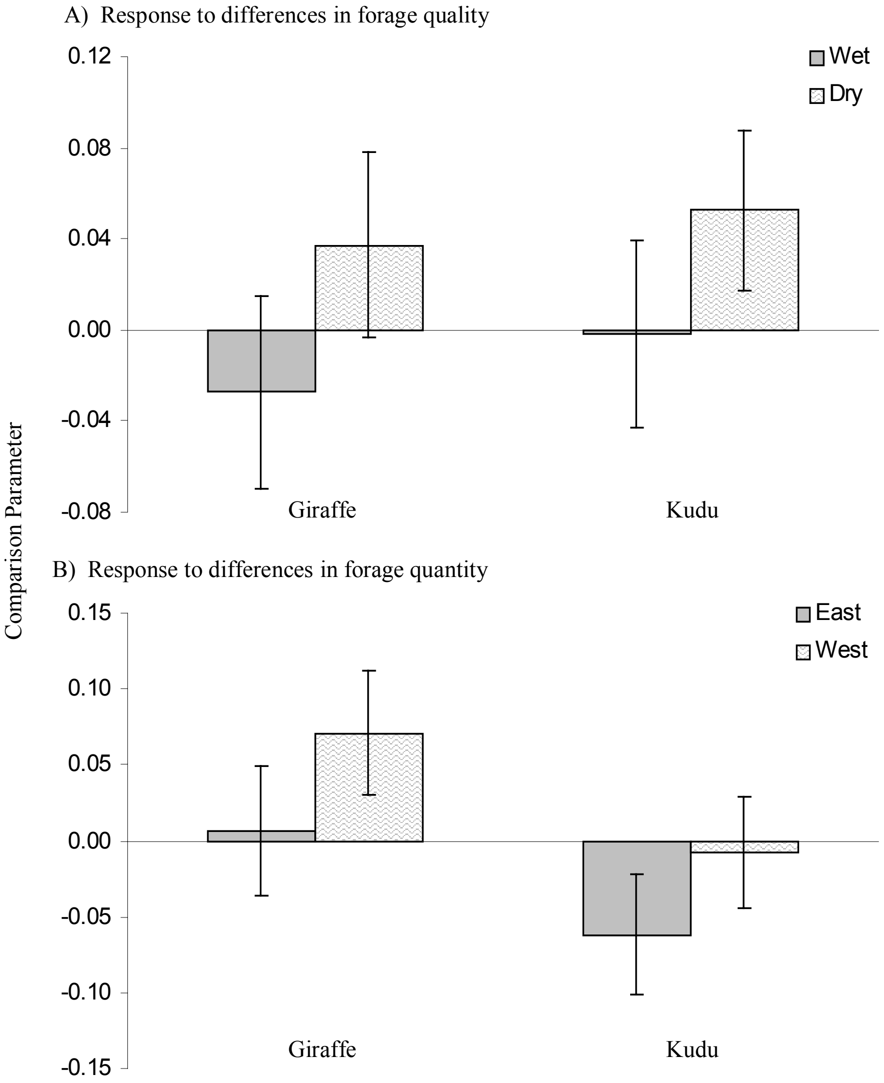
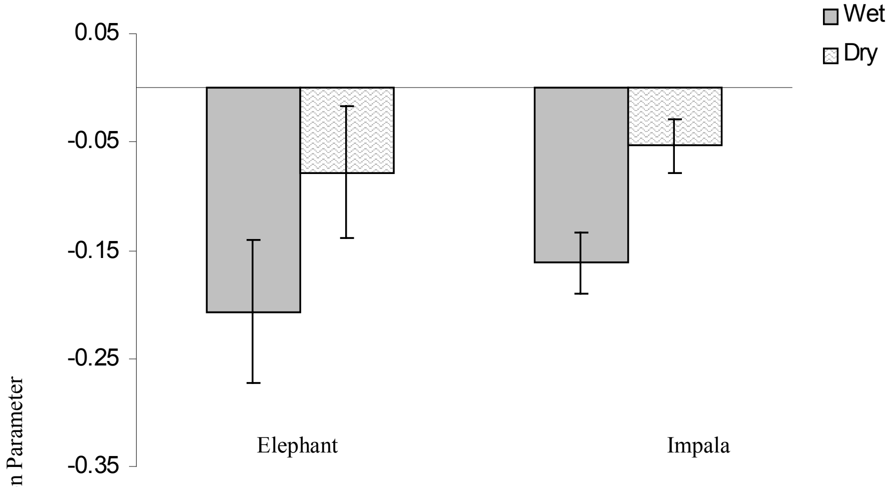


Figure 3. The comparison parameter values, c_{kl} (see text and Fig. 2 for details), reported in Chapter 1 are plotted to summarize changes in distance-to-water distributions for giraffe and kudu.

A) Response to differences in forage quality



B) Response to differences in forage quantity

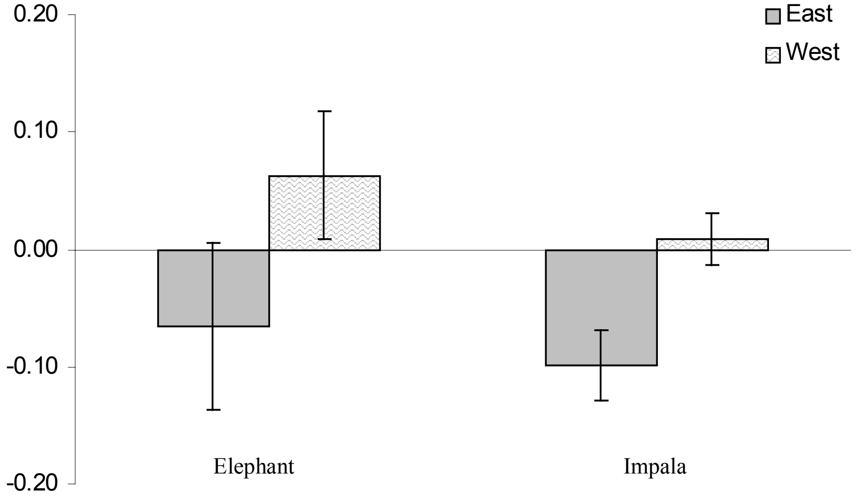


Figure 4. The comparison parameter values, c_{kl} (see text and Fig. 2 for details), reported in Chapter 1 are plotted to summarize changes in distance-to-water distributions for elephant and impala.

In an LFM context, however, it is interesting to note that the difference between distributions in the eastern versus western landscape, observed for both elephant and impala, is in the expected direction (i.e. populations occur farther from water in the western landscape during wet years in agreement with an implicit mitigation of the trade-off between limited forage quality and distance-to-water). For both species, this difference is larger than the differences observed for species that must only mitigate forage quality limitations. Hence, the combined effect of intraspecific competition and forage quality limitations may cause elephant and impala populations to occur much farther from water in the western versus eastern landscape. Both elephant and impala distributions also changed in response to rainfall (Fig. 4). Although this result is not confounded by density, it is hard to interpret the relative strength of this response since distribution change in response to landscape is confounded.

DISCUSSION

We have conducted a post-hoc analysis of data that was not collected to address the questions considered here. Our application of LFM analysis would be stronger if an experimental design, motivated by the questions of interest, guided data collection. For example, measurement of actual browse quantities would allow us to determine whether KNP forage quantities limit distance-to-water distributions for browsers, understand the observed difference in giraffe and kudu distribution changes (Fig. 3), and increase our understanding of the relationship between rainfall and browse quantity. Through the use of an appropriate experimental design, we may also be able to separate the effect of population density and forage quality on mixed feeder distributions.

In spite of the limitations in the data set, our application of LFM analysis provides useful insights into KNP herbivore distributions. The results obtained for KNP grazers are concordant with current expectations of the factors that should be limiting for these three species, at least in a comparative sense considering their relative size and gut morphology. This concordance suggests that for KNP grazers the east-west landscape and wet-dry rainfall dichotomies, respectively, are viable surrogates for forage quality and quantity. Further, these analyses reveal that KNP forage quality and quantity are at levels that limit distance-to-water distributions for some grazers but not others (e.g. quantity is limiting for buffalo but not wildebeest). This application of LFM analysis also suggests future research programs that can expand our understanding of the influence of forage quantity on browser distributions and determine whether increased intraspecific competition due to higher mixed feeder densities in the western versus eastern KNP landscape has resulted in these species searching larger areas to obtain needed resources.

LFM analysis represents a simple, powerful tool that is directly relevant to the issues facing ecosystem managers, conservation biologists, and wildlife ecologists. For a wide range of consumer-resource systems, LFM analysis provides a framework for the collection of data needed to evaluate whether resources are limiting to particular populations. In addition, influential factors identified by LFM analysis can form the basis of environmental monitoring programs. Perturbations in these factors signal shifts in population distributions and early detection of these trends would allow ecosystem managers to evaluate and respond to consequences of the new distribution patterns.

Long-term changes in the relative influence exerted by the limiting factors may signal changes in the environment due to climatic trends or anthropogenic disturbance.

ACKNOWLEDGEMENTS

We wish to thank Chris Redfern, Norman Owen-Smith, and Phil Starks for stimulating discussions that helped shape the ideas presented. Harry Biggs and Rina Grant provided invaluable insights into GIS techniques, the multiple constraints on herbivore distributions, and the potential importance of herbivore body size and gut morphology. We are also grateful to Allison Bidlack and Chris Wilmers for helpful comments on the manuscript. NSF Grant INT-9731202 to WMG supported this research.

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Chapter Three

Surface water availability and the management of herbivore distributions in an African savanna

J. V. Redfern & W. M. Getz

ABSTRACT

A prevalent hypothesis in the management of African savanna ecosystems is that surface water availability can be manipulated to manage herbivore distributions. This hypothesis rests on two assumptions: 1) surface water availability is a primary determinant of herbivore distributions; and 2) surface water availability can be manipulated at scales that impact herbivore distributions. An uncritical acceptance of this hypothesis can be problematic because these assumptions fail to address the potential influence other factors exert on herbivore distributions and surface water availability. As a first step in exploring this hypothesis we use data from the Kruger National Park (KNP), South Africa, to infer temporal and spatial scales at which surface water availability can be manipulated. Our analysis explicitly accounts for differences between ephemeral water sources, which vary over a range of temporal scales, and persistent water sources, which are comparatively permanent. Our results suggest that our capacity to create large-scale changes in surface water availability decreases with increasing rainfall and increasing temporal and spatial heterogeneity in natural water sources. In particular, our results suggest that large, mobile herbivores, which disperse to areas experiencing dry season rainstorms, will continue to have access to a majority of the KNP's area following the removal of all boreholes. Alternatively, herbivore populations that depend solely on persistent water sources may be concentrated in smaller areas and face barriers to movement during the dry season following the removal of all KNP boreholes. Our results, therefore, reveal the necessity of determining how herbivores respond to heterogeneity in water sources.

INTRODUCTION

An important aspect of the management of African savanna ecosystems is understanding the relationship between surface water availability and herbivore distributions. For example, Owen-Smith (1996) states that water provision ranks with fire and culling policies as one of the main interventions available to managers. Previous studies have documented that herbivore distributions are influenced by the location of water sources, particularly during the dry season (Western 1975, Fryxell and Sinclair 1988, Bergstrom and Skarpe 1999, see also Chapter 1). Additionally, piosphere studies have documented increased herbivore impacts on a range of forage and soil variables close to natural and artificial water sources (Thrash et al. 1991a and 1991b, Thrash et al. 1993, Thrash 1997, 1998a, 1998b, Parker and Witkowski 1999, Thrash and Derry 1999). Studies exploring how herbivore populations are affected by the addition of artificial water sources to an ecosystem suggest that water provision may increase herbivore drought mortality (Walker et al. 1987), increase the predation levels experienced by different herbivore species (Smuts 1978, Harrington et al. 1999), and contribute to the decline of rare antelope species (Harrington et al. 1999).

Underlying many of these previous studies is the hypothesis that surface water availability can be manipulated to manage the distribution and size of herbivore populations in African savanna ecosystems. This hypothesis rests on two assumptions: 1) surface water availability is a primary determinant of herbivore distributions and consequently population size; and 2) surface water availability can be manipulated at scales that impact how herbivores are distributed throughout the landscape. An uncritical acceptance of this hypothesis can be problematic because these assumptions fail to address the potential influence other factors exert on herbivore populations and surface water availability. Specifically, factors such as forage condition, controlled burning, fence construction, disease, predator culling, and herbivore culling may affect the distribution and size of herbivore populations, while the temporal and spatial heterogeneity of natural water sources may affect our capacity to manipulate surface water availability at meaningful scales. For example, in Chapter 2 we suggest that changes in grazer distributions relative to water sources in the Kruger National Park, South Africa, may be related to variations in forage quality and/or quantity.

The effects of these factors frequently operate in concert with the effects of water provision programs, making it difficult to isolate the relative influence of any particular factor. Without an analysis of the relative contribution of multiple factors, it is difficult to conclude that water provision is primarily responsible for the changes observed in herbivore populations. In particular, previous studies of the relationship between herbivore populations and the consequences of water provision programs have rarely taken into account the potential influence of these other factors. They may, therefore, incorrectly attribute changes in herbivore populations to water provision programs.

Direct evaluation of the hypothesis that surface water availability can be manipulated to manage herbivore distributions is difficult because the large data sets needed to analyze the effects of multiple factors rarely exist. However, as a first step in exploring this hypothesis we use data from the Kruger National Park (KNP), South Africa, to infer temporal and spatial scales at which surface water availability can be manipulated. In the KNP, the hypothesis that surface water availability can be manipulated to manage the distribution and size of herbivore populations underlies the original motivations for constructing artificial water sources as well as current justifications for removing artificial water sources. The KNP water provision program began in the 1930's and has resulted in the establishment of over 300 artificial water sources in the KNP, predominately boreholes (Pienaar et al. 1997). Reasons for implementing this program include the desire to homogenize the spatial distribution of herbivore populations and to increase the size of herbivore populations (Pienaar et al. 1997).

Currently, the artificial water sources constructed under this program are viewed as incompatible with KNP management objectives, which emphasize the heterogeneity of ecosystem processes, and plans to remove a substantial number of boreholes are underway (Pienaar et al. 1997). It has been assumed that the removal of artificial water sources will increase heterogeneity in the spatial distribution of herbivore populations by creating waterless areas during the dry season that occur beyond the range of water-dependent herbivores. We argue that the relationship between surface water availability and the management of herbivore distributions requires further research before the effects of borehole removals can be predicted. As a first step in this investigation, we analyze the distribution of area in categories defined by distance-to-water before and after borehole removal to infer the temporal and spatial scales at which surface water availability can be manipulated in the KNP. Our analysis explicitly accounts for differences between ephemeral water sources, which vary over a range of temporal scales, and persistent water sources, which are comparatively permanent. We use the results of our analyses to outline the future research needed to determine whether the scale at which surface water availability can be manipulated is meaningful in the context of herbivore distributions.

METHODS

Study Site and Data Sources

The dry season (May-August) distribution of water sources in the KNP was recorded from 1981-1993 during an annual aerial census. In particular, the locations of natural perennial, artificial, and ephemeral water sources were documented over almost all of the KNP using a total area count, strip transect methodology (Viljoen 1996). A large proportion of the ephemeral water sources recorded during the census result from dry season rainstorms (P. C. Viljoen, *personal communication*--cf. Viljoen, 1996). The minimum size of the ephemeral water sources included in the census data varies because of subjectivity in the classification system used by observers (P. C. Viljoen, *personal communication*). The locations of census water points are recorded with an accuracy of approximately 800 m (P. C. Viljoen, *personal communication*). We believe that no systematic errors occur in the census water data because a consistent methodology was applied to all surveys (Viljoen 1996).

Gertenbach (1980) analyzed rainfall patterns in the KNP using data collected at rainfall stations from varying starting dates, some as early as the 1920's and 1930's, to 1979. His analyses suggest that KNP rainfall oscillates between approximately 10 years of above average annual rainfall and 10 years of below average annual rainfall. Our study period (1981-1993) corresponds to a below average rainfall cycle and includes two years with the lowest recorded rainfall in the last century (Zambatis and Biggs 1995). Gertenbach (1980) also described an increasing rainfall gradient from north to south.

The KNP can be subdivided into a northern region and a southern region along the Olifants river (Fig. 1), which is a barrier to large-scale migration for many herbivore species (Smuts 1974). Using data collected during our study period (1981-1993), we determined the average annual and dry season (May-August) rainfall in the northern and southern regions (Fig. 2). Specifically, average annual rainfall was calculated by averaging the sum of the daily rainfall values recorded at selected rainfall stations over the climate year (i.e. July of the previous year to June of the current year – Zambatis and Biggs 1995). A total of 10 northern and 11 southern rainfall stations were included in the analyses; 17 stations recorded data throughout the entire study period while four stations (VLA and WOO in the north, HOU and STO in the south – see Fig. 1) 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 values. These analyses suggest that the northern region experiences lower annual and dry season rainfall than the southern region (Fig. 2).

In all analyses, data from the northern and southern regions are treated separately because of the broad relevance of these regions to general herbivore management issues. Additionally, the rainfall differences between the two regions can provide an understanding of the relationship between rainfall and surface water availability. Conclusions about the relationship between surface water availability and rainfall derived from analyses conducted in the two regions do not take into account smaller patches that may deviate from the overall rainfall patterns. The significance of these deviations will increase as the scale of interest decreases. Therefore, it may be important to consider

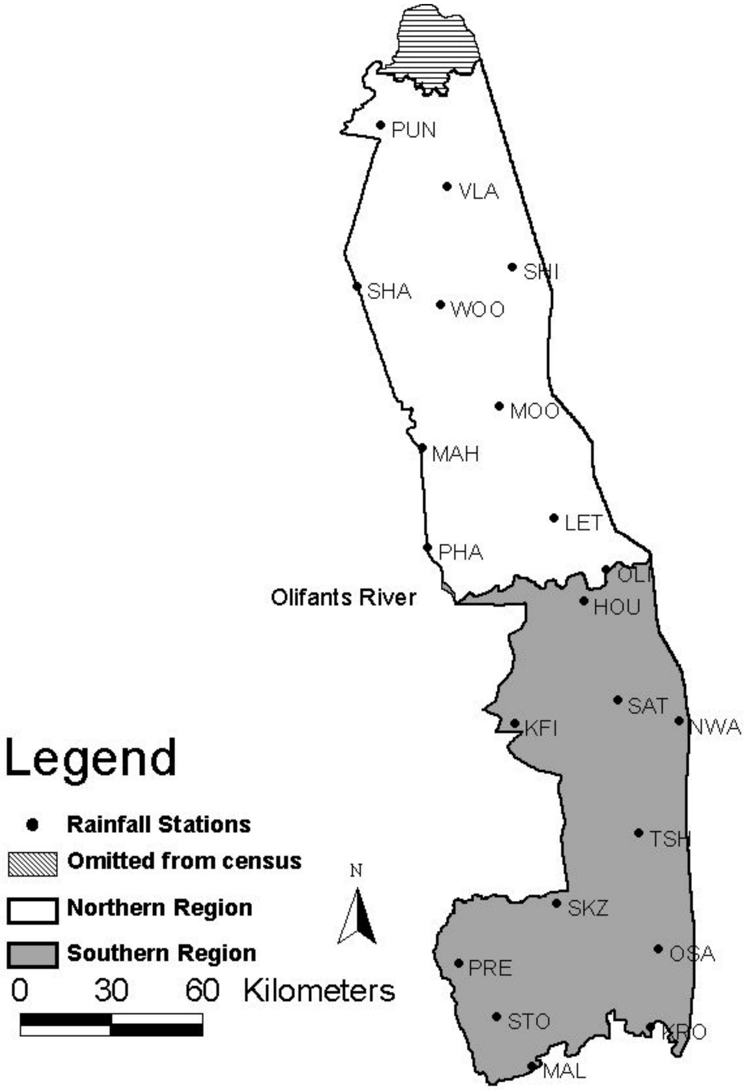


Figure 1. The KNP is naturally divided into a northern region and a southern region by the Olifants river. Surveys of the northern-most region of the park occur infrequently; therefore this region is excluded from analyses. Locations of the 21 rainfall stations that provided data for analyses are also shown.

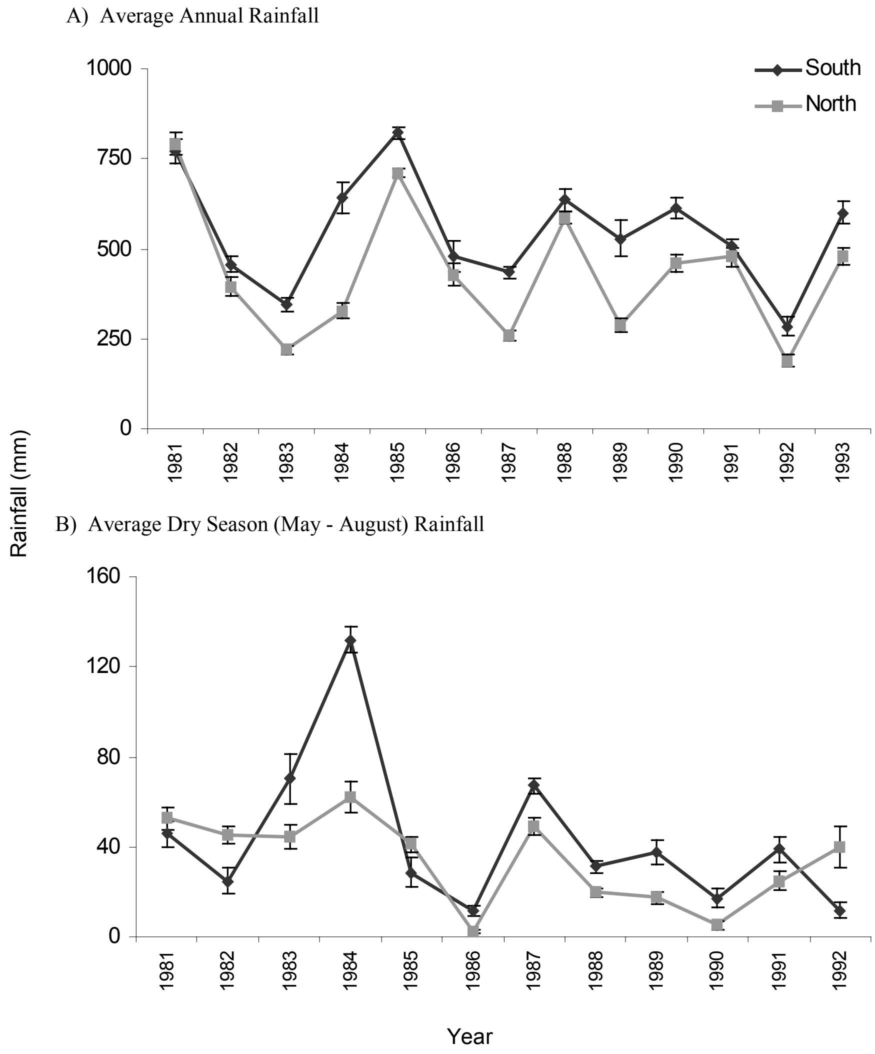


Figure 2. Average annual and dry season rainfall, calculated in the northern and southern regions, are plotted for the study period. Data from the northern or southern rainfall stations (see Fig. 1) are averaged and the standard error is shown.

these patches separately when analyzing local rather than landscape scale patterns of surface water availability.

Quantifying Patterns of Surface Water Availability

Patterns of surface water availability can be meaningfully described, at a range of scales, by the percentage of area occurring at different distances from the nearest water source. At a landscape scale, areas at varying distances from water may support different herbivore densities. At a more local scale, ecological variables, such as shrub density, forage quality, forage quantity, and soil compaction, may change along a distance-to-water gradient. We calculated the percentage of area in categories defined by distance-to-water for two water source assemblages in the KNP, which are composed of different classes of water sources.

For the purposes of this study, we differentiate among three classes of water sources: perennial, ephemeral, and persistent. Perennial water sources represent continuously extant water sources of known location, specifically rivers, springs, dams, and boreholes. We use the term ephemeral water sources to refer to all of the water sources recorded in the census water data. These water sources are expected to vary over a range of temporal scales, from pools in seasonal rivers that are available throughout the dry season to small pans formed by dry season rainstorms that are only available for a few weeks. We use the term persistent water sources to refer to the subset of ephemeral water sources that are comparatively permanent. Specifically, persistent water sources represent locations that regularly contain a water source according to the census water data (this definition is developed more fully below).

Total Water Source Assemblage

The first water source assemblage, hereafter referred to as the total water source assemblage, combines ephemeral water sources (i.e. the census water data) with perennial water sources. Perennial water sources were not always recorded in the census data; hence, they are added to this assemblage to obtain a more complete record of the total water available each year. Boreholes are considered a perennial water source and analyses of the consequences of borehole removal are conducted by eliminating boreholes from the data set of perennial water sources. Boreholes, however, may also be represented in the census water data. To determine census water points that may represent boreholes, we created a circular buffer of 1.5 km radius around each borehole. Among the census water points contained in the buffer, the point closest to the borehole was removed from each year of the census water data. The chosen buffer radius is larger than may be needed to account for potential location errors in the census water data (estimated as approximately 800 m) to ensure that the consequences removing boreholes are not underestimated due to the inclusion of census water points that represent boreholes in analyses.

Using 1 km distance-to-water categories, the percentage of area at different distances from the nearest water source was calculated for each year of data using the Geographic Information Systems (GIS) software ARC/INFO (version 8.0.2, Environmental Systems Research Institute, Inc.). This resolution was chosen as the smallest convenient distance compatible with the approximately 800 m spatial accuracy of the census water data. The percentage of area in each distance-to-water category was averaged to describe surface water availability patterns according to our definitions of wet and dry years. Wet and dry years are defined separately for the northern and southern regions, in accordance with our rainfall analyses and the increasing rainfall gradient from north to south described by Gertenbach (1980). Specifically, wet years are defined as the six years with the highest average annual rainfall values (1981, 1985, 1988, 1990, 1991, and 1993 in the northern region and 1981, 1984, 1985, 1988, 1990, and 1993 in the southern region) and dry years are defined as the six years with the lowest average annual rainfall values (1982, 1983, 1984, 1987, 1989, and 1992 in the northern region and 1982, 1983, 1986, 1987, 1991, and 1992 in the southern region). For both the northern and southern regions, the year with the median annual rainfall value was omitted from analyses.

Persistent Water Source Assemblage

The second water source assemblage, hereafter referred to as the persistent assemblage, combines persistent water sources with perennial water sources. We refer to the water sources in this data set as persistent because they represent locations in which surface water occurs continuously throughout the year or repeatedly each dry season. We determined the persistence of water sources by summarizing the presence and absence of census water points in wet and dry years, where definitions of wet and dry years are the same as those used for the total water source assemblage. Specifically, we used the GIS to grid each year of the census water data, adding perennial water sources with known locations for the reasons mentioned above, at a 1 km x 1 km resolution. As stated previously, this resolution was chosen to subsume the potential location error in the census water data.

In both the northern and southern regions, wet year persistent water sources were defined as those cells containing at least one water source in all six wet years. Dry year persistent water sources were defined as those cells containing at least one water source in all six wet years and all six dry years. According to these definitions, dry year persistent water sources are equal to or a subset of wet year persistent water sources. Hence, variation in the location of water sources in the persistent assemblage only occurs between wet and dry years. In contrast, the location of water sources in the total assemblage may vary each year. The persistent assemblage, therefore, represents relatively permanent water sources while the total assemblage represents temporally and spatially heterogeneous water sources. The GIS was used to calculate the percentage of area in 1 km distance-to-water categories for the wet and dry year persistent water sources.

Borehole Removal

Having documented surface water availability patterns in the KNP using both the total and persistent water source assemblages, we evaluated our capacity to manipulate surface water availability by analyzing the changes produced by removing all of the KNP boreholes. Specifically, after removing all boreholes from both water source assemblages, the analyses described above were repeated. The effects of borehole removal on both water source assemblages in wet and dry years and in the northern and southern regions were compared on the basis of the percentage of area in the 1 km distance-to-water categories.

Statistical Comparisons

Several comparisons are made among the patterns of surface water availability, as described by the percentage of area in each distance-to-water category, documented by our analyses. These comparisons include differences between the northern versus southern region, wet versus dry years, and total versus persistent water source assemblage. The significance of these comparisons can be determined by an $R \times C$ contingency test (Sachs 1982), where R is the number of distance-to-water categories and $C = 2$. These tests detect as significant small changes between the percentages of area in each distance-to-water category because our sample sizes are very large (e.g. the northern and southern regions respectively contain 9,269 and 9,136 1 km x 1 km grid cells).

The results of these tests, however, are not directly relevant to our understanding of how herbivore distributions may be affected by changes in the percentage of area in each distance-to-water category. The questions of interest focus instead on the percentage of KNP areas that are far from water sources. These results must be interpreted in the context of particular management objectives and species' characteristics. Thus we combine our 1 km distance-to-water categories and focus on four distance-to-water categories relevant to herbivore movements, specifically 0-2 km, 2-5 km, 5-10 km, and >10 km. For example, estimates of 5 to 10 km have been proposed as the distance that large, mobile, water-dependent herbivores will travel from water sources (Thrash and Derry 1999). We chose to break the 5 km distance-to-water category into areas within 2 km of water sources and areas between 2-5 km from water sources so that our comparisons are also relevant for species that are expected to remain close to water sources.

RESULTS

Surface Water Availability Patterns

Patterns of surface water availability in the KNP differ greatly between the two water source assemblages. In the total water source assemblage, 91% and 95% of the area in the northern and southern regions, respectively, occurs within 5 km of water sources during dry years (Fig. 3). Additionally, the location of areas more than 5 km from water sources is not consistent, but varies according to the location of dry season rainstorms (Fig. 4). Differences exist, however, between patterns of surface water availability in the northern and southern regions. Particularly noticeable is the fact that the southern region contains a larger percentage of area within 2 km of water sources than the northern region during both wet and dry years (Fig. 3). These differences correspond with the increasing north to south rainfall gradient described by Gertenbach (1980) and with the higher average annual and dry season rainfall in the southern versus northern region observed in this study. The northern region also shows a slightly larger difference than the southern region in the percentage of area within 2 km of water sources during wet versus dry years.

In the persistent water source assemblage, 78% and 84% of the area in the northern and southern regions, respectively, occurs within 5 km of water sources during dry years (Fig. 5 and 6). The percentage of area within 5 km of water sources is smaller in the persistent versus total water source assemblage because the persistent water source assemblage is composed primarily of boreholes and perennial water sources and hence excludes many ephemeral water sources. Additionally, differences between the

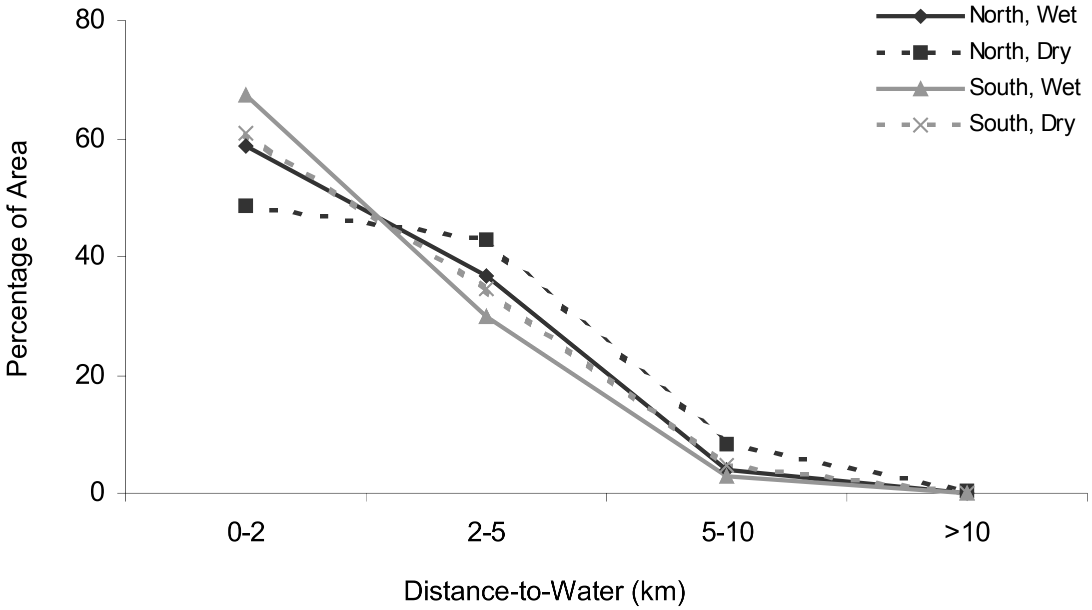


Figure 3. The distribution of area among four distance-to-water categories is plotted for the total water source assemblage in the northern and southern regions during wet and dry years.

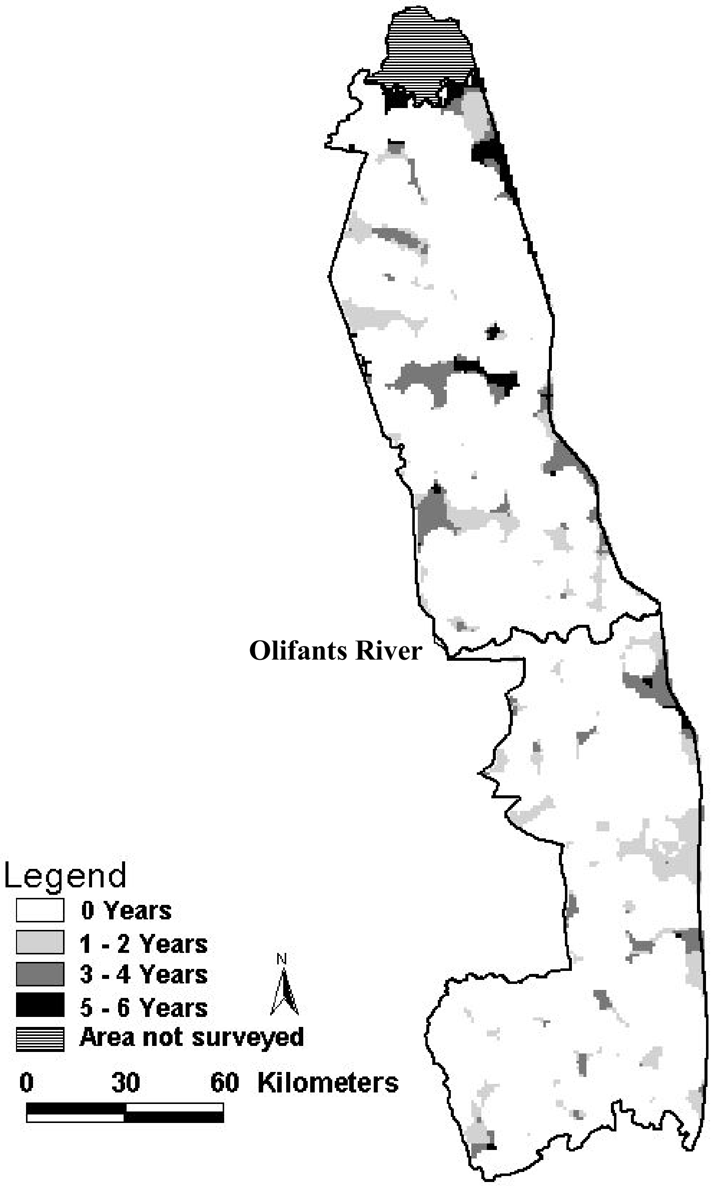


Figure 4. Temporal and spatial heterogeneity in the total water source assemblage are depicted for dry years. A GIS was used to determine the number of dry years (out of a total of six) each 1 km x 1 km grid cell was more than 5 km from a water source. Maps produced for wet years have fewer areas that are consistently more than 5 km from a water source. The locations of these areas, however, may differ between wet and dry years because of the variability in the location of dry season rainstorms.

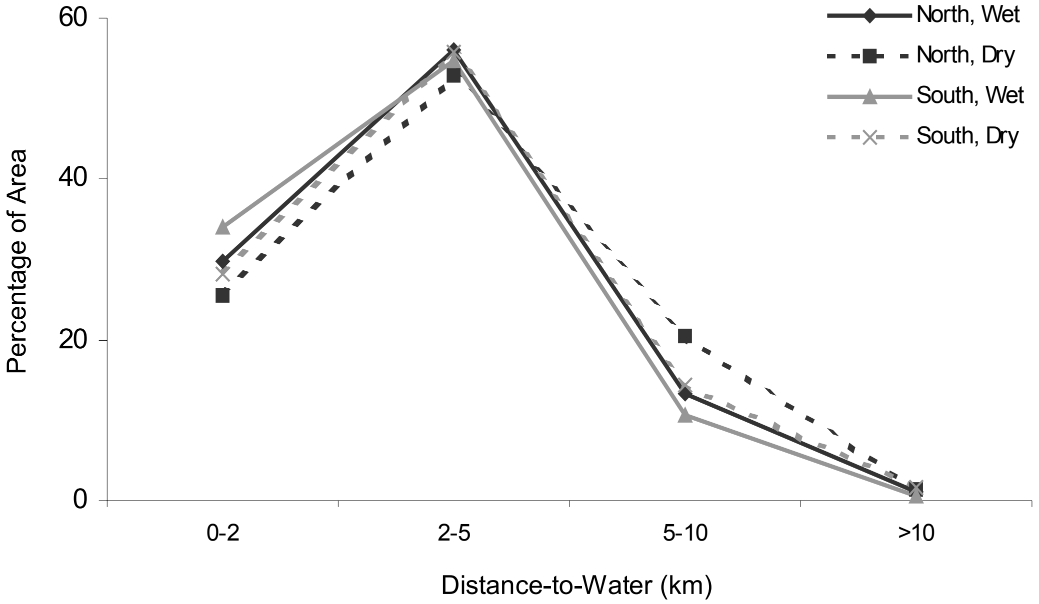


Figure 5. The distribution of area among four distance-to-water categories is plotted for the persistent water source assemblage in the northern and southern regions during wet and dry years.

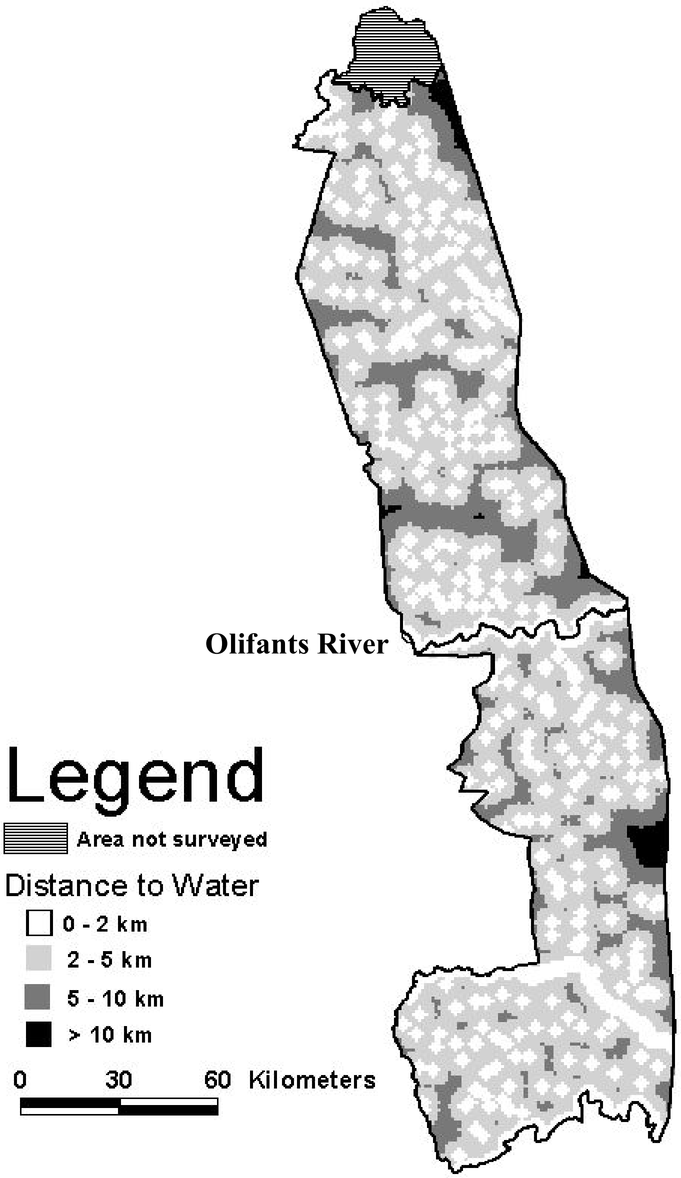


Figure 6. The spatial distribution of various distance-to-water categories during dry years is mapped for the persistent water source assemblage. Persistent water sources in dry years represent a subset of the persistent water sources in wet years. Hence, a greater percentage of area occurs close to persistent water sources in wet versus dry years.

percentage of area within 2 km of water sources in the northern and southern regions are smaller in the persistent versus total water source assemblage (compare Fig. 5 with Fig. 3). The difference between the percentage of area within 2 km of water sources during wet and dry years is smaller for the persistent versus total water source assemblage in the northern region and is similar for both assemblages in the southern region (compare Fig. 5 with Fig. 3).

Consequences of Borehole Removal

Differences between patterns of surface water availability in the northern and southern regions are magnified when all of the KNP boreholes are removed from the total water source assemblage (Fig. 7). In particular, a large proportion of the southern region remains close to water sources during wet and dry years. In the northern region, however, the distribution of area is spread more evenly across the distance-to-water categories during dry years. Additionally, differences in patterns of surface water availability between wet and dry years are more pronounced in the northern versus southern region.

Examination of the changes produced by borehole removal also emphasizes the differences between the northern and southern regions (Fig. 8). In general, borehole removal has a greater effect on patterns of surface water availability in the northern region, which is characterized by lower average annual and average dry season rainfall. Specifically, closing all of the KNP boreholes during dry years increases the percentage of area that occurs beyond 5 km of water sources from 9% to 28% in the northern region

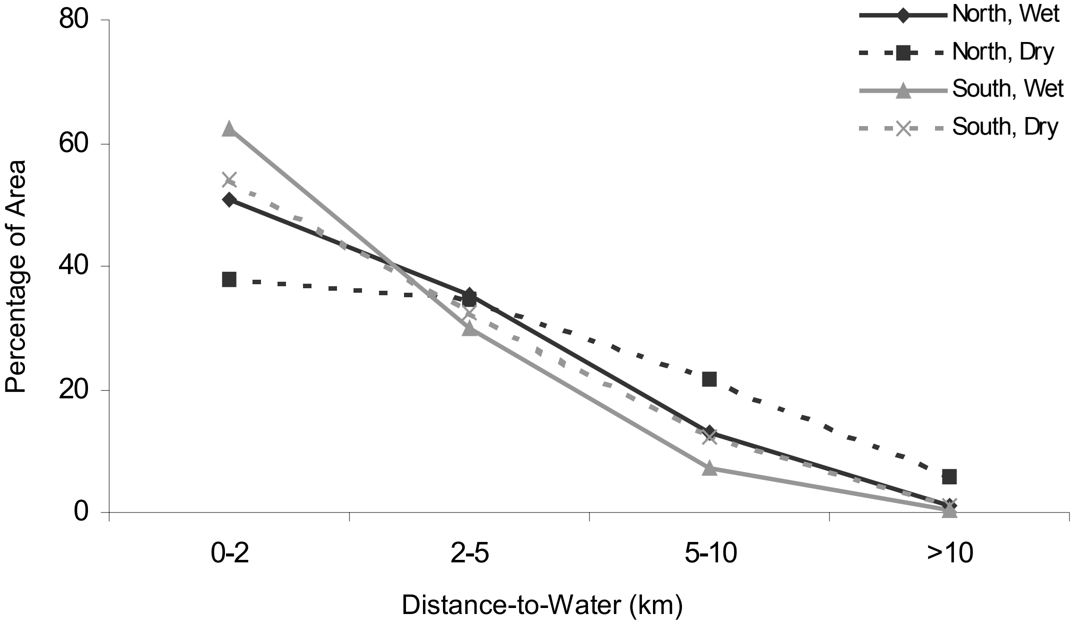
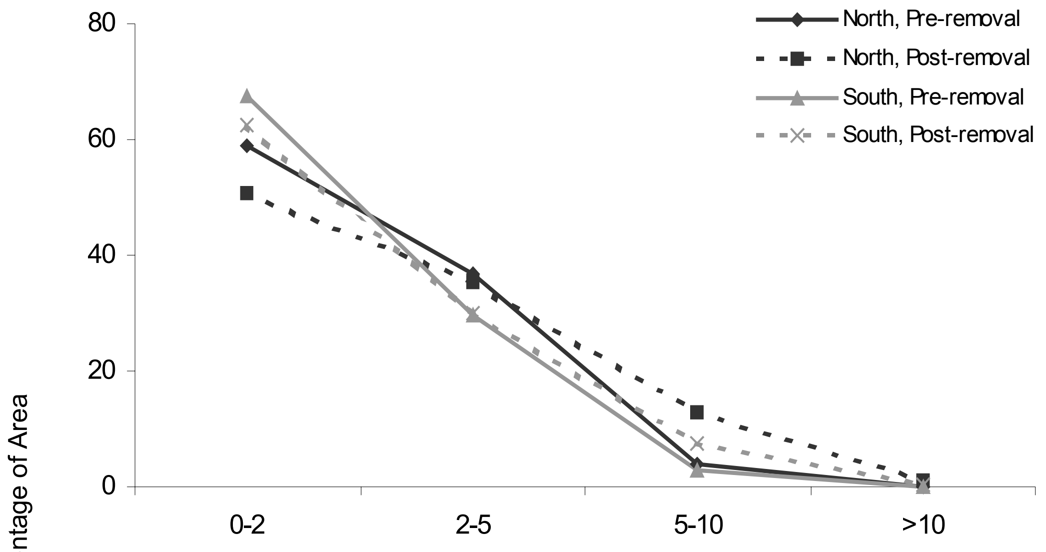


Figure 7. The distribution of area among four distance-to-water categories following the removal of all KNP boreholes from the total water source assemblage is plotted for the northern and southern regions during wet and dry years.

A) Wet Years



B) Dry Years

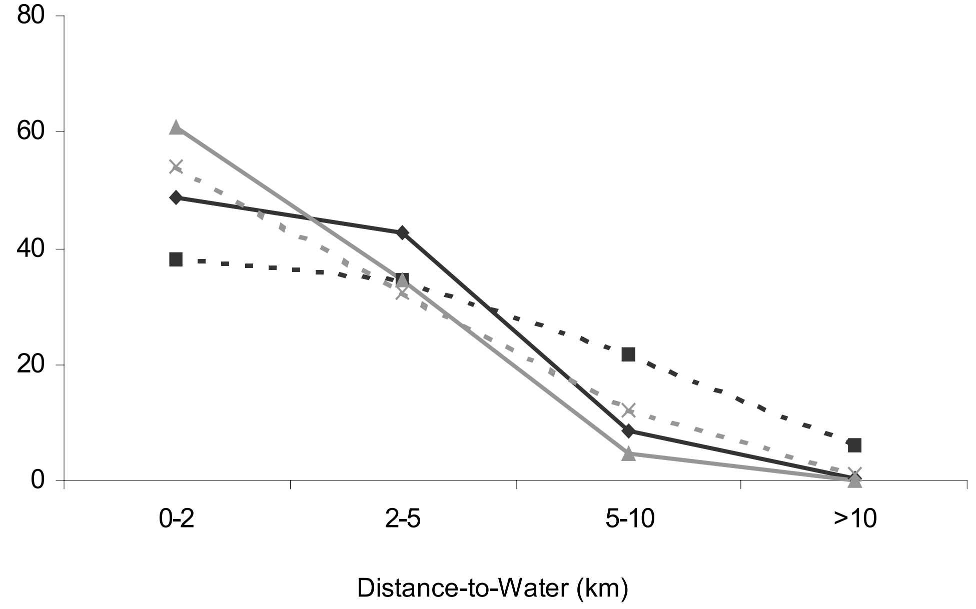


Figure 8. The distribution of area among four distance-to-water categories before and after the removal of boreholes from the total water source assemblage is compared in the northern and southern regions during wet and dry years.

and from 5% to 13% in the southern region (Fig. 8). Although borehole removal produces an increase in the amount of area more than 5 km from water sources in both regions, the location of this area varies based upon the occurrence of dry season rainstorms (Fig. 9) and few areas are consistently more than 5 km from water sources.

Removing all of the KNP boreholes from the persistent water source assemblage creates a large difference between patterns of surface water availability in the northern and southern regions (Fig. 10). In particular, during dry years a greater percentage of area occurs beyond 10 km from persistent water sources in the northern versus southern region. Additionally, a large difference occurs between patterns of surface water availability during wet versus dry years in both regions.

As expected, removing all of the KNP boreholes from the persistent water source assemblage had a large impact on patterns of surface water availability because boreholes comprise a large proportion of this assemblage. In general, complete borehole closure causes a change from regions in which a majority of the area occurs within 5 km of persistent water sources to regions in which a substantial percentage of the area occurs beyond 10 km of persistent water sources (Fig. 11). For example, removing all boreholes during dry years increases the percentage of area beyond 10 km of persistent water sources from 1% to 50% in the northern region and from 1% to 38% in the southern region (Fig. 11). These changes suggest that borehole removal isolates the remaining persistent water sources, creating little area within 5 km of persistent water sources (Fig. 12).

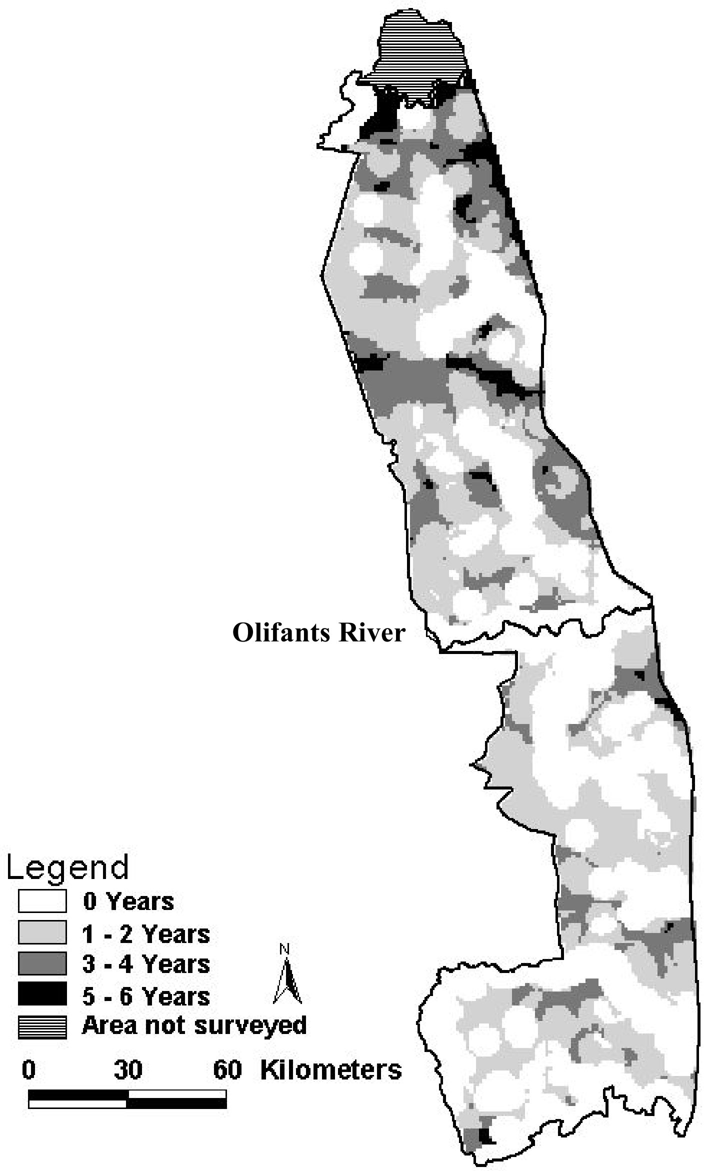


Figure 9. Temporal and spatial heterogeneity following the removal of all KNP boreholes from the total water source assemblage are depicted for dry years. A GIS was used to determine the number of dry years (out of a total of six) each 1 km x 1 km grid cell was more than 5 km from a water source. Maps produced for wet years have fewer areas that are consistently more than 5 km from a water source. The locations of these areas, however, may differ between wet and dry years because of the variability in the location of dry season rainstorms.

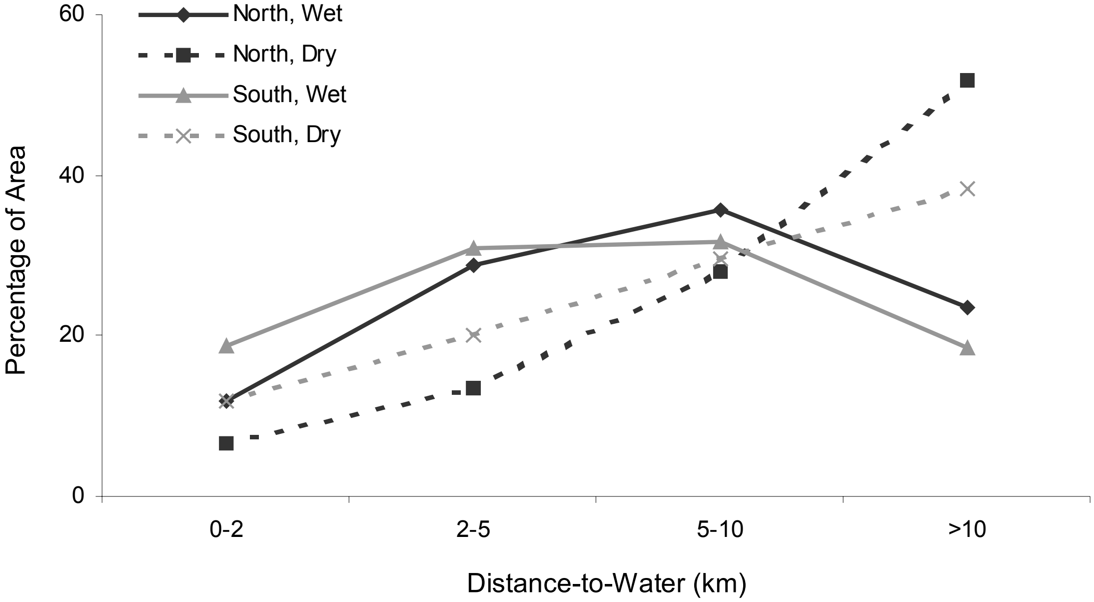
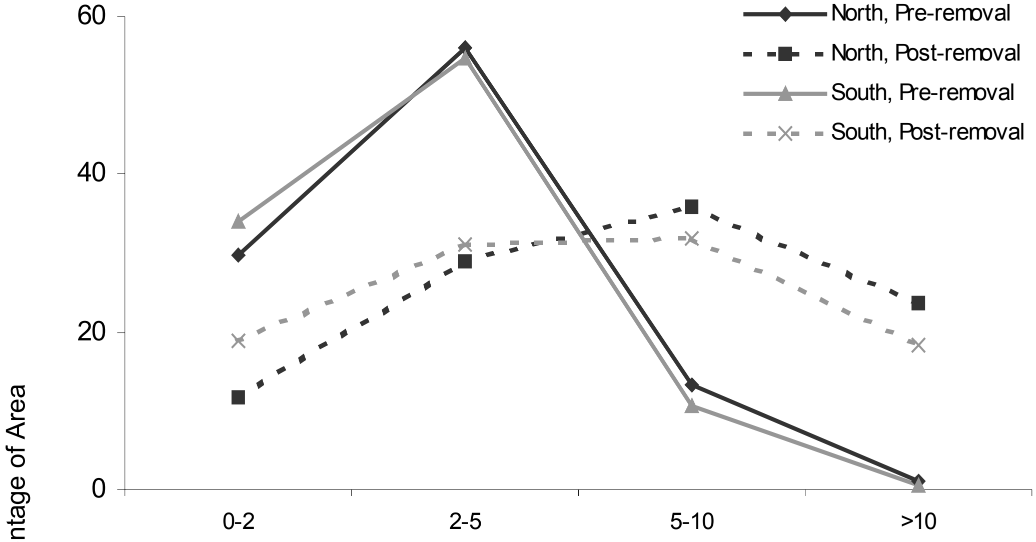


Figure 10. The distribution of area among four distance-to-water categories following the removal of all KNP boreholes from the persistent water source assemblage is plotted for the northern and southern regions during wet and dry years.

A) Wet Years



B) Dry Years

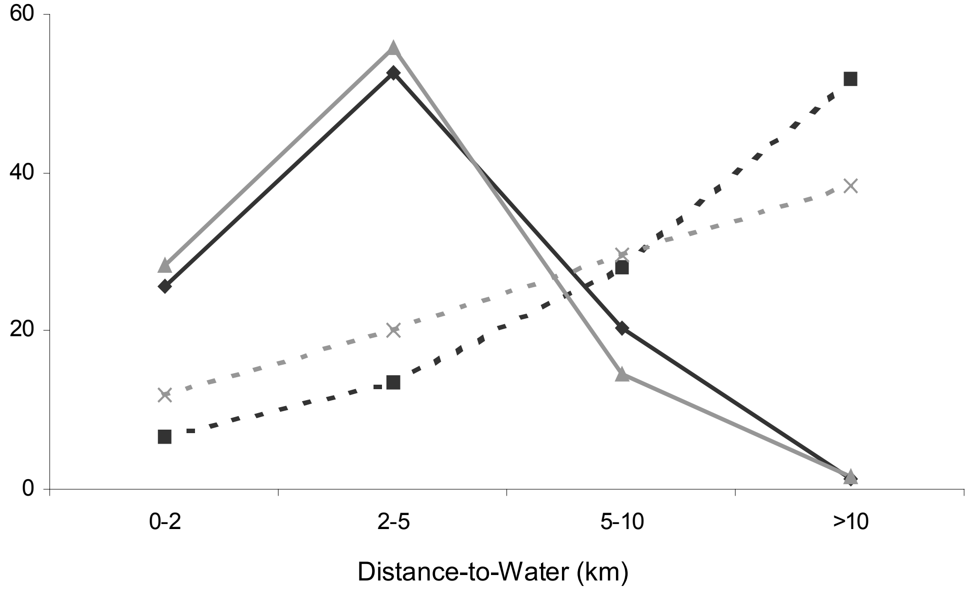


Figure 11. The distribution of area among four distance-to-water categories before and after the removal of boreholes from the persistent water source assemblage is compared in the northern and southern regions during wet and dry years.

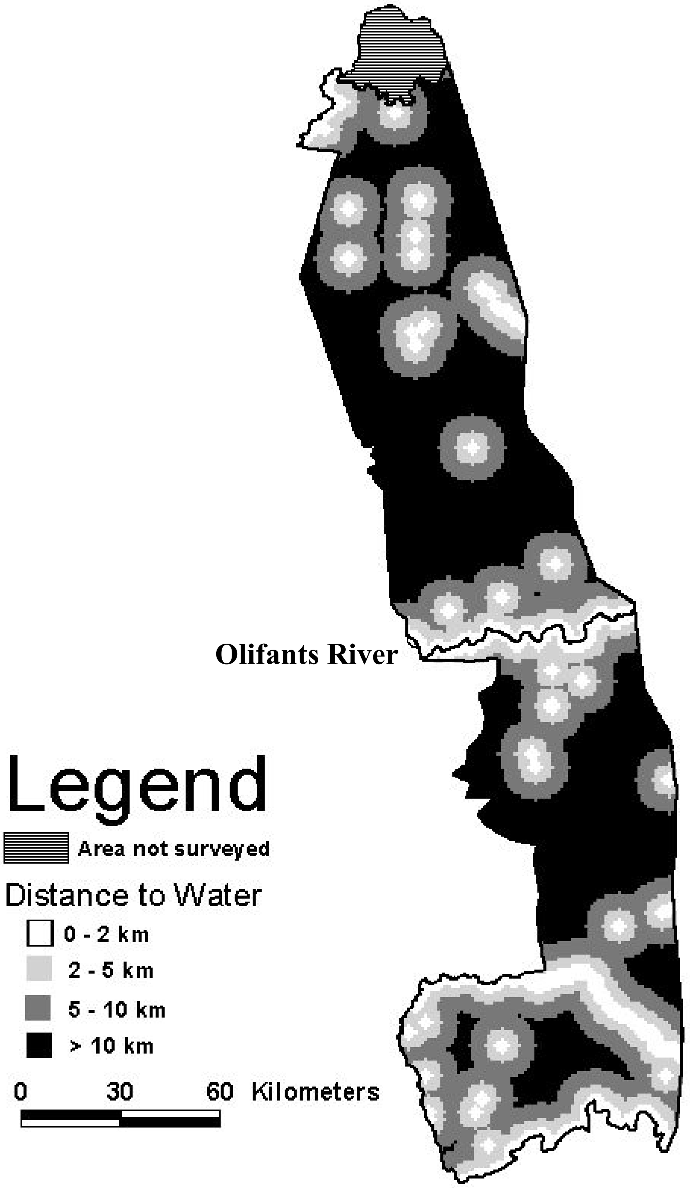


Figure 12. The spatial distribution of various distance-to-water categories during dry years is mapped following the removal of all KNP boreholes from the persistent water source assemblage. Persistent water sources in dry years represent a subset of the persistent water sources in wet years. Hence, a greater percentage of area occurs close to persistent water sources in wet versus dry years.

DISCUSSION

Manipulating Surface Water Availability:

Temporally and Spatially Heterogeneous Water Sources

In the KNP, the total water source assemblage is spatially heterogeneous over a range of temporal scales. In the total water source assemblage, complete borehole removal does increase the percentage of area that occurs beyond 5 km of the water sources from 9% to 28% in the northern region and from 5% to 13% in the southern region. This increase, however, does not necessarily imply that borehole removals allow managers to control patterns of surface water availability at a scale that is meaningful to herbivore distributions. Previous studies have used general estimates of 5 to 10 km as the distance that large, mobile herbivores may travel from water sources (Thrash and Derry 1999). Farther traveling distances, however, have also been documented. For example, buffalo (*Syncerus caffer*), zebra (*Equus burchelli*), and wildebeest (*Connochaetes taurinus*) may range 10-30 km from water sources to meet their forage requirements (Estes 1991). Additionally, elephants (*Loxodonta africana*) have been observed to occur 15-24 km from water sources during drought conditions (Owen-Smith 1988). Following borehole removal, only 6% of the area in the northern region and 1% of area in the southern region occur more than 10 km from water sources during dry years (Fig. 8).

Furthermore, removing boreholes from the total water source assemblage creates few areas that are consistently more than 5 km from water sources (Fig. 9) because the locations of the ephemeral water sources contained in this assemblage vary temporally and spatially according to dry season rainstorms. Some herbivore species may disperse to patches in which a dry season rainstorm has occurred to obtain access to forage that would otherwise occur too far from water sources or to obtain access to higher quality forage if the rainfall produces a green flush of vegetation. Whether a particular species generally follows a dispersal or concentration strategy depends on several factors including body size and behavioral characteristics. For example, water-dependent species that are small and/or territorial are more likely to concentrate near persistent water sources than large, mobile species. Hence, results from the total water source assemblage suggest that large, mobile herbivores, which disperse to areas experiencing dry season rainstorms, will continue to have access to a majority of the KNP's area after borehole closure.

The exact percentage and location of areas that occur beyond the range of large, mobile herbivores depends on rainfall; specifically, this area will be larger in areas or years with lower rainfall. Caution must therefore be used in generalizing the relationship between herbivore distributions and water sources across areas with different rainfall patterns. For example, boreholes were removed in a northeastern section of the KNP in an attempt to reverse roan antelope declines (Harrington et al. 1999). Borehole removals were expected to increase the percentage of area far from water sources and therefore decrease the potential negative effects of high densities of water-dependent herbivores on the more water-independent roan population. Following the borehole removals, zebra numbers were reduced and roan numbers stabilized (Harrington et al. 1999). This case study appears to support the hypothesis that surface water availability can be manipulated to manage herbivore populations. Analyses of surface water availability patterns throughout the KNP, however, reveal that generalizing the results obtained in the northern region to the southern region may be inappropriate. The northern region, and particularly the far northern patches, is characterized by lower average annual and dry season rainfall and consequently borehole removal in this region produced the greatest increase in the percentage of area far from water sources.

In general, analyses of the total water source assemblage suggest that our capacity to create large-scale changes in surface water availability decreases with increasing rainfall and increasing temporal and spatial heterogeneity in natural water sources. Manipulating surface water availability under conditions in which water sources vary temporally and spatially may be even more difficult than our results suggest. The KNP aerial census data potentially under-represents the heterogeneity of this water source assemblage, because small pools caused by dry season rainstorms occurring before or after the census may not be recorded.

Manipulating Surface Water Availability:
Permanent Water Sources

In the KNP, the availability of persistent water sources should influence the distribution patterns of herbivore species that remain in areas that regularly contain water sources. In contrast to the total water source assemblage, removing boreholes from the persistent water source assemblage considerably increased the percentage of area more than 10 km from persistent water sources, particularly during dry years (Fig. 11). This result is a direct consequence of the fact that the persistent water source assemblage is composed primarily of boreholes and perennial rivers. In the KNP, perennial rivers may occur as far as 175 km apart. Removing boreholes, therefore, creates large tracts of area that are more than 10 km from persistent water sources (Fig. 12).

Consequently, herbivore populations that depend solely on persistent water sources may be concentrated in smaller areas and face barriers to movement during the dry season. The degree of range contraction will depend on the species' habitat preference. For example, some species may be concentrated near perennial rivers because riparian habitat satisfies both their forage and water requirements. It is unlikely that borehole removal will directly affect such species. These populations may, however, be indirectly affected by increased competition and predation if borehole removal increases the number of species that concentrate in riparian habitat.

In contrast to perennial rivers, the impact of boreholes on habitat characteristics is limited to a local area. While further research is needed to determine the generality of previous piosphere studies in the KNP, these studies suggest that alteration of forage characteristics may only occur within several hundred meters of a borehole (Thrash 1998, Thrash and Derry 1999). Thus, it is unlikely that these habitat changes explain the relationship between boreholes and herbivore distributions. Rather, boreholes may be an important determinant of herbivore distributions because they provide access to regions that would otherwise be unavailable to less mobile, water-dependent herbivores. Therefore, removing all of the KNP boreholes significantly decreases the potential distribution range for such species. This range contraction may result in a reduction of population sizes.

Future Research Priorities

Patterns of surface water availability in the KNP reveal the paramount necessity of conducting future research to determine how herbivore populations respond to temporal and spatial heterogeneity in water sources. In particular, a better understanding of how herbivore distributions are influenced by the location of dry season rainstorms is needed. Specific issues that future research should address include:

- Identification of species that disperse to patches where dry season rainstorms have occurred;
- Determination of the rate of dispersal to these patches;
- Measurement of the total time spent in these patches;
- Determination of the amount of rainfall required to cause dispersal.

In addition, this research should incorporate a multi-scale perspective as an explicit acknowledgment that herbivores may respond to temporal and spatial heterogeneity in water sources at multiple scales. For example, it is possible that large-scale distribution patterns, such as the location of herbivore home ranges, are influenced by perennial water sources. Local distribution patterns, however, may be influenced by ephemeral water sources at a range of temporal scales.

CONCLUSION

Until we obtain a better understanding of how herbivore distributions are influenced by temporal and spatial heterogeneity in water sources, we suggest that caution must be used in generalizing conclusions about the relationship between herbivore populations and water sources. Specifically, our analysis of surface water availability in the KNP suggests that relationships between herbivore populations and water sources documented in a particular location may not be applicable to an area with different rainfall patterns. Such applications have been made among studies conducted in

South Africa, Botswana, Kenya, and Australia. Conclusions derived from these studies need to be re-evaluated within a context that specifically accounts for rainfall derived differences in water source heterogeneity.

The hypothesis that surface water availability can be manipulated to manage the distribution and size of herbivore populations in African savanna ecosystems assumes that surface water availability is a primary determinant of herbivore distributions and that surface water availability can be manipulated at scales that influence herbivore distributions. These assumptions pervade the literature, influencing the interpretations and generalizations of studies dealing with the relationship between surface water availability and the characteristics of herbivore populations. Additionally, the influence of these assumptions can be seen in the dearth of studies that rigorously evaluate the relative and potentially synergistic influences that water sources and other factors, such as forage conditions and culling, exert on herbivore populations. To progress in our understanding of the ecology and management of African savanna herbivores, we must move beyond an uncritical acceptance of these assumptions. This viewpoint encourages the development of broad questions about the role multiple interacting factors play in determining the distribution and size of herbivore populations.

ACKNOWLEDGEMENTS

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