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Elephants and low rainfall alter woody vegetation in Etosha National Park, Namibia

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Abstract

Elephants, the distribution of water sources and below-average rainfall may threaten the survival of woody plants in Etosha National Park, Namibia. We base our assessment of such interactions on the satellite tracking of six elephant herds following a 17-year record of fixed-point photographs. These showed that woody plant survival increased and spatial use by elephants decreased at greater distances from water sources. We conclude, therefore, that elephants may be an important factor in reducing woody plant survival. The low rainfall typical of our study period may also have limited survival. A continued decline in vegetation, aggravated by elephants, could compromise local conservation efforts. Our study emphasizes the importance of studying interactions between animals, plants and water before supplementing water sources as a management action.

Keywords: *Loxodonta africana*; Fixed-point photographs; Rainfall; Survival; Water augmentation

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1. Introduction

Conservation in Africa continues to benefit from the large stretches of land set aside as protected areas (Western, 2003). The erection of fences around some of these areas and the artificial supply of water, however, could influence conservation efforts. For instance, fencing fragments landscapes and may speed up the extinction of species by compromising species–area relationships (Rosenzweig, 2003). The inverse relationship between the size of East African parks and the rates of extinctions for mammals support this (Soulé et al., 1979; Newmark, 1996). Competition may accelerate such extinctions (Owen-Smith, 1996). Fences also may prevent populations from adjusting their ranges when confronted by climate change (Ogutu and Owen-Smith, 2003).

Water sources alter the way animals use landscapes. For instance, in South Africa's Kruger National Park, artificial water sources induced a decline in roan antelope (*Hippotragus equinus*) numbers by favouring zebra (*Equus burchelli*) and blue wildebeest (*Connochaetes taurinus*) (Owen-Smith, 1996; Harrington et al., 1999). While supplying water may benefit ungulates in the short term, starvation during droughts could compromise long-term viability (Owen-Smith, 1996; Gaylard et al., 2003). This may hold for Etosha National Park where most water sources are artificial.

Etosha is fenced, extends over 22,900 km^2 and contains 63 artificial and natural perennial water sources. Some 4410 km^2 is made up of saline pans that contain no woody plants and where water accumulates only during the rainy season. The Park's 2000 savanna elephants (*Loxodonta africana*) have dominated the browsing guild for the past 20 years (Etosha Ecological Institute, unpublished data). Their numbers fluctuated widely before the construction of waterholes during the 1960s and the completion of a perimeter fence in 1973. Before 1960, neither water sources nor elephants were present across large stretches of Etosha during the dry season. Today, elephants remain in the Park through the year (De Villiers and Kok, 1984; Lindeque, 1988). Both male and female elephants in Etosha drink daily during the dry season, moving large distances between water sources when they spend little time feeding (de Villiers and Kok, 1984, 1988). Through the wet season, however, they disperse over larger areas (Lindeque and Lindeque, 1991).

Elephants often change the structure and composition of the vegetation, particularly in areas close to water sources (Ben-Shahar, 1993; Brits et al., 2002). Increased browsing around waterholes during the dry season may enhance local mortality of woody plants (De Villiers and Kok, 1988). The effects that elephants have on vegetation may be confounded by those of fire (Dublin et al., 1990; Eckhardt et al., 2000), drought (Tafangenyasha, 1997; Van de Vijver et al., 1999) and/or other browsers (Ben-Shahar, 1993; Styles and Skinner, 2000; Barnes, 2001). Browsing by these herbivores may also suppress seedling regeneration and recruitment (Prins and Van Der Jeugd, 1993). Elephants, however, are likely to cause the greatest reduction in the numbers of established woody plants (Barnes, 2001).

The effect of drought and fire on plant survival should not change with distance from water. We therefore predict that elephants and other browsers that forage preferentially close to water sources should induce distance gradients in the survival of woody plants. In this study, we assess the influence of distance from water on the survival of woody plants. To do this we evaluated fixed-point photographs taken over a 17-year period from 1984 to 2001 throughout Etosha and related elephant landscape preferences to distance from water.

2. Methods and materials

2.1. Study area

Etosha National Park is situated in north-central Namibia (19°S 16°E). Mean monthly maximum temperatures vary from 25 to 35 °C and mean monthly minimum temperatures vary from 6 to 18 °C in winter and summer, respectively (de Villiers and Kok, 1988). Rain falls during the summer months and changes along an east–west rainfall gradient across the Park. Since 1980, the annual rainfall was mostly below the long-term average (Etosha Ecological Institute, unpublished data).

Besides elephants, the arid to semi-arid savanna woody vegetation in Etosha supports a browsing guild comprising black rhino (*Diceros bicornis bicornis*), giraffe (*Giraffa camelopardalis*), kudu (*Tragelaphus strepsiceros*), steenbok (*Raphicerus campestris*) and Damara dik-dik (*Madoqua kirkii*). Eland (*Taurotragus oryx*), springbok (*Antidorcas marsupialis*) and black-faced impala (*Aepyceros melampus petersi*) are mixed feeders. Important woody plants include *Acacia newbrownii, Acacia reficiens, Acacia erioloba, Acacia mellifera, Colophospermum mopane*, *Boscia foetida*, *Combretum apiculatum, Commiphora spp., Grewia spp., Terminalia prunioides*, *Terminalia sericea* and *Ziziphus mucronata* (De Villiers and Kok, 1988).

2.2. Spatial use by elephants

We fitted six elephant cows in different breeding herds (14–28 individuals) with GPS-satellite neck collars (model AWT SM2000E, Africa Wildlife Tracking) using procedures sanctioned by the ethics committee of the University of Pretoria. Elephant locations were logged separately for consecutive seasons from 2002 to 2004 (Table 1). Data were only available for three elephants during the 2003/2004 dry season.

Once daily, locations were logged to an accuracy of 9.0 ± 3.0 m (mean $\pm$ S.D.; $n = 6$). These locations were grouped into distance classes (0–4, $>$4–8, $>$8–12, $>$12–16 and $>$16 km) away from 63 artificial and natural perennial water sources. We used a third-order compositional analysis (Johnson, 1980; Aebischer et al., 1993) to determine the ranks of preference for each distance class and season. The number of locations within each distance class served as surrogates for spatial use. The relative contribution of a distance class to each elephant's home range indicated availability (see Aebischer et al., 1993).

We used the Animal Movement extension (Hooge and Eichenlaub, 1997) of ArcView GIS 3.3 (ESRI, Inc., 2002) to estimate 95% fixed Kernel home ranges using

Table 1
Number of GPS locations, logged once daily, for each elephant during the different seasons

Elephant ID	November 2002–April 2003 (wet season)	May 2003–October 2003 (dry season)	November 2003–April 2004 (wet season)	May 2004–October 2004 (dry season)
1	137	175	144	—
2	138	176	133	—
3	132	155	164	115
4	110	176	49	—
5	138	178	170	104
6	133	178	162	114

least squares cross validation (LSCV) smoothing. This approach provides greater accuracy than other methods when basing range estimates on more than 30 locations (Seaman et al., 1999). We followed Swihart and Slade (1985), who advocated using only one or two locations per day over a period of several months for each animal. This results in statistically valid samples for which the effect of autocorrelation becomes almost negligible.

2.3. *Woody plant survival*

The Etosha Ecological Institute took fixed-point photographs at the same locations and in the four ordinal directions at 440 points in 1984, 1990, 1996 and 2001 (see Hipondoka and Versfeld, 2003). From this series, we excluded fixed points that did not include woody vegetation, for which photographs did not overlap fully, or where photographs were either damaged or missing. Consequently, 150 fixed points yielded data for further analyses.

For each of the fixed points, we counted the number of recognizable woody plants (trees and shrubs that appeared taller than 0.5 m) present in 1984 and noted their subsequent presence or absence. We also counted the number of woody plants recruited. Each of the 150 fixed points was placed into the same distance classes used for the analysis of spatial use by elephants. We expressed overall survival as the percentage of individuals present during 1984 that we could account for in photographs taken in 2001. We also estimated woody plant survival separately for each of the fixed-points and time intervals from 1984 to 1990, 1990 to 1996 and 1996 to 2001. We used a log-linear model (Sokal and Rohlf, 1995) to identify any relationships between distance, time interval and survival. We related the survival of woody plants to actual distances from water using a logistic regression analysis following the proc logistic procedure (SAS v. 9.1, SAS Institute, Cary, North Carolina, USA).

2.4. *Rainfall*

We treated rainfall data for the western (Otjovasandu), central (Okaukuejo) and eastern (Namutoni) regions of the Park separately. We considered yearly rainfall lower than the long-term mean as indicative of a dry spell. These data were collected between 1954 and 2004 for Okaukuejo and 1970 and 2004 for both Namutoni and Otjovasandu. We also compared the long-term mean annual rainfall to the mean values between 1984 and 2001.

3. Results

3.1. Spatial use by elephants

A compositional analysis showed that the six elephants preferred to use areas within 4 km of water more than other areas during all seasons (Table 2). These areas, which account for 14% of the Park area (excluding the saline pans), experienced greater elephant use during the dry seasons. We could not ascribe use of areas further than 4 km from water to relative preferences during the wet season.

3.2. Distance from water and woody plant survival

Of the 1676 individual woody plants identified on the photographs taken during 1984, most (79%) were still present in 2001. Only 26 woody plants were recruited over the same period. The best-fit log-linear model indicated that survival of these plants at the 150 fixed-points varied with distance from water. Survival was similar for the different time intervals between years when photographs were taken ($\chi^2 = 16.7$, df. $= 18$, $p = 0.54$). The probability of woody plant survival increased significantly with distance from water ($\chi^2 = 26.2$, df. $= 1$, $p<0.001$; Fig. 1), where the probability of survival (p) at any given distance (X) is given by $p = 1/[1 + e^{-(0.9743+0.0418X)}]$.

Table 2
Relative preference ranking derived from a compositional analysis (see Aebischer et al., 1993) for five distance classes from water over several seasons in Etosha National Park

Distance class (km)	Area (km^2)	2002/03		2003/04	
		Wet season	Dry season	Wet season	Dry season
0–4	2591	2	3	1	4
>4–8	5226	0	1	0	2
>8–12	4478	0	1	0	2
>12–16	2951	0	1	0	0
>16	7620	0	0	0	1
Cows (n)		6	6	6	3

The greater the absolute value the greater the preference.

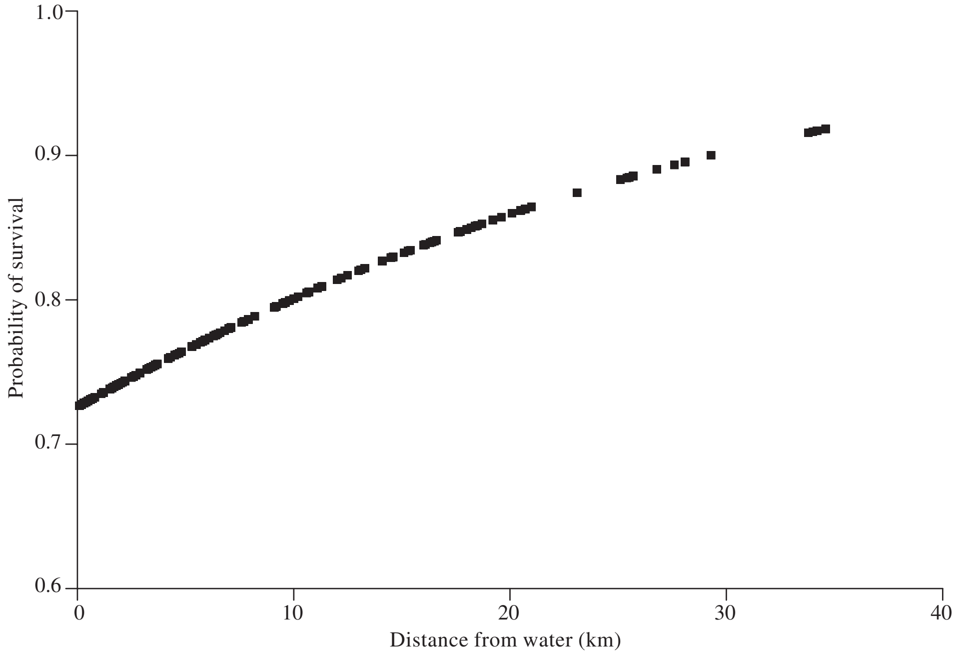

Fig. 1. The probability of woody plant survival in Etosha National Park as a function of distance from water based on the logistic regression analysis.

3.3. Rainfall

The eastern and central regions of Etosha experienced below-average rainfall for 13 (76%) of the 17 years of our study from 1984 to 2001. In the west, nine (53%) of the 17 years received rain below the long-term average (Fig. 2). Over this period, average annual rainfall (Namutoni: 419 mm; Okaukuejo: 322 mm; Otjovasandu: 279 mm) was lower than the long-term mean (Namutoni: 436 mm; Okaukuejo: 354 mm; Otjovasandu: 287 mm) for all three regions.

4. Discussion

Food and water availability influence the way elephants use landscapes. For instance, elephants concentrate near water sources in the dry season and disperse during the wet season (Owen-Smith, 1988; Wittemyer, 2001; Osborn and Parker, 2003). This pattern holds for Etosha (see De Villiers and Kok, 1984; Lindeque and Lindeque, 1991), where elephants preferred to use areas within 4 km of water throughout the year. Relative to the dry season, ranging during the wet season seems less dependent of distance from perennial water sources, as seasonal water sources are widely available.

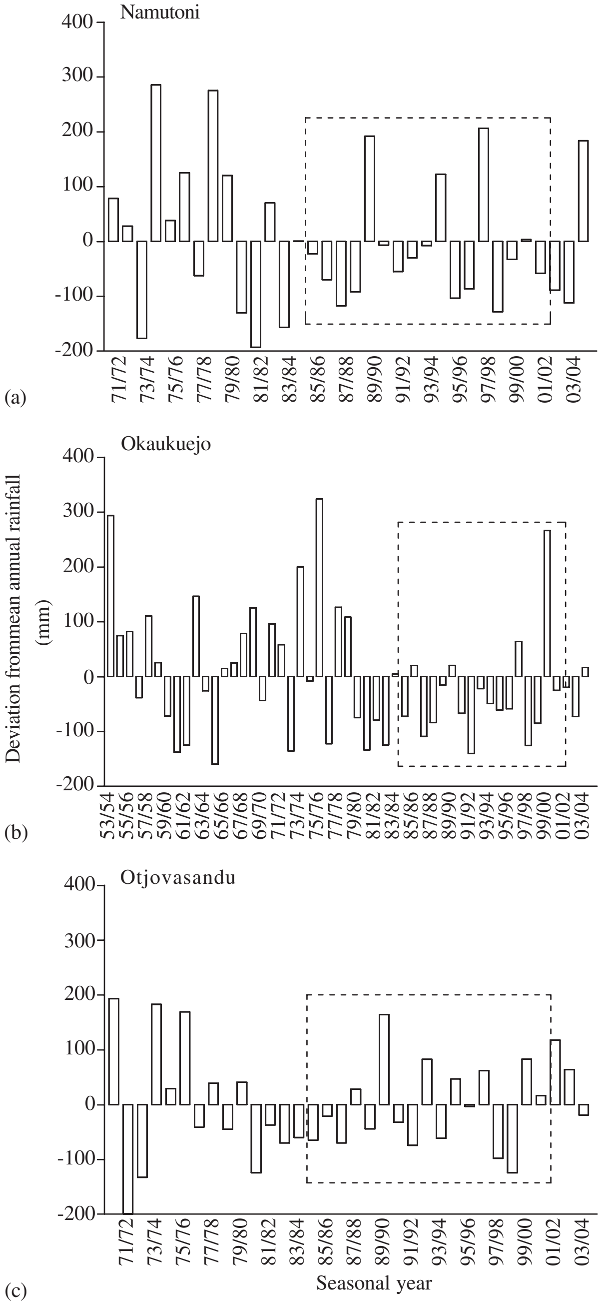

Fig. 2. Deviations from the long-term mean annual rainfall (normalized to zero) for the (a) eastern, (b) central and (c) western parts of Etosha National Park. Stippled blocks indicate the period over which we studied the survival of woody plants. Note that the *x*-axis differs between regions and depicts seasonal years (1 July–30 June).

With elephant activity focussed on areas near water sources, we predicted greater impact on woody vegetation here—our findings support this. The development of piospheres around water sources in response to trampling and foraging, as we noted for Etosha, is well-documented (Owen-Smith, 1996; Thrash, 1998). For example, in northern Botswana, elephants damaged more woody plants close to permanent water sources (Ben-Shahar, 1993). Moreover, in the Kruger National Park, the supplementation of water caused widespread elephant-induced damage of woody vegetation (Gaylard et al., 2003).

Independent of distance from water, mortality exceeded recruitment of woody plants in Etosha from 1984 to 2001. Survival varied greatly, but overall increased with distance from water. Our study on spatial use by elephants followed the period for which we assessed woody plant survival. In spite of this, it is no coincidence that areas that experienced the highest intensity of elephant use also experienced the lowest rate of woody plant survival. De Villiers and Kok (1984) and Lindeque and Lindeque (1991) noted the same patterns of spatial use for elephants in Etosha. Therefore, we believe roaming behaviour was similar during the period of decline in woody plants that we documented. While elephants may be instrumental in reducing survival of woody plants, this does not exclude the role of other herbivores.

Areas within 4 km of perennial water sources account for 14% of the area of the Park, excluding the pans. This may influence the roaming behaviour of water-dependent animals, thereby accounting for other changes in Etosha's vegetation. At one extreme, dependence on water in altered landscapes may influence a variety of species (see Laws, 1970; Laws et al., 1975; De Villiers and Kok, 1988; Owen-Smith, 1996; Cumming et al., 1997; Ogutu and Owen-Smith, 2003). Of particular concern to Etosha is its population of endangered black rhinos. These rhinos forage primarily on woody plants of intermediate height (Owen-Smith, 1988) and may therefore become food-limited.

Average rainfall during our study period was low and for most years, below the long-term mean. These relatively dry conditions may also have reduced survival and recruitment. Our study design, however, did not allow us to relate rainfall to survival. Rain falls unevenly across Etosha and without point-specific rainfall values, an assessment of the influence of rainfall on woody plant survival is impossible. Global climate change may increase the incidence of droughts through southern Africa (Tyson and Preston-Whyte, 2000). In Etosha, this could lead to a continued decline in vegetation and when aggravated by elephants, compromise conservation (Ogutu and Owen-Smith, 2003). Our study emphasizes the importance of studying interactions between animals, plants and water before supplementing water sources as a management action.

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