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Elephant spatial use in wet and dry savannas of southern Africa

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Abstract

The influence of elephants on woody vegetation cover varies from place to place. In part this may be due to the way elephants utilize space across landscapes and within their home ranges in response to the availability and distribution of food. We used location data from 18 cows at six study sites across an east to west rainfall gradient in southern Africa to test whether wet- and dry-season home-range sizes, evenness of space use within seasonal home ranges and range overlap between seasons and between years, differed between wet and dry savannas. We then tested whether the quantity, distribution and seasonal stability in vegetation productivity, a coarse measure of food for elephants, explained differences. Elephants in wet savannas had smaller wet- and dry-season home ranges and also returned to a higher proportion of previously visited grid cells between seasons and between years than elephants living in dry savannas. Wet-season home-range sizes were explained by seasonal vegetation productivity while dry-season home-range sizes were explained by heterogeneity in the distribution of vegetation productivity. The influence of the latter on dry-season home ranges differed among structural vegetation classes. Range overlap between seasons and between years was related to inter-seasonal and inter-annual stability in vegetation productivity, respectively. Evenness of elephant spatial use within home ranges did not differ between savanna types, but it was explained by seasonal vegetation productivity and heterogeneity in the distribution of vegetation productivity during the wet season. Differences in elephant spatial use patterns between wet and dry savannas according to vegetation structure and season may need to be included in the development of site-specific objectives and management approaches for African elephants.

Introduction

Large herbivores change the structure, composition and function of ecosystems (Hobbs, 1996; Pickup, Bastin & Chewings, 1998; Wallis de Vries, Bakker & van Wieren, 1998; Sankaran, Ratnam & Hanan, 2008). When confined to conservation areas these changes may be undesirable (McShea, Underwood & Rappole, 1997; O'Connor, Goodman & Clegg, 2007). African elephants *Loxodonta africana* alter savannas by reducing the abundance of trees (Barnes, 1983), which may transform woodlands to shrublands (Smallie & O'Connor, 2000; Guldemond & van Aarde, 2008). Past management of elephants consequently focussed on reducing numbers to reduce impact. However, the link between herbivore numbers and the impact they have on other species is not simple (Gordon, Hester & Festa-Bianchet, 2004; for an elephant-related discussion see van Aarde, Jackson & Ferreira, 2006; and van Aarde & Jackson, 2007).

Elephant impacts may be accentuated when seasonal home ranges overlap, or when individuals utilize the same areas in consecutive years, thus providing no respite to species affected by elephants (see Owen-Smith *et al.*, 2006). In addition, the impacts of elephants may not be the same for all places (Mapaure & Campbell, 2002; Baxter & Getz, 2005; Sankaran *et al.*, 2008). While woody cover in general correlates negatively with elephant densities in many places, the effects of elephants can be negligible or even marginally positive in other places (Mapaure & Campbell, 2002; Baxter & Getz, 2005). Hence, impact may be associated with variation in the intensity of elephant spatial utilization, as well as with their numbers and the environmental context within which such impacts occur.

African savannas can be divided into dry, climatically driven and wet, disturbance-driven systems (Sankaran *et al.*, 2005). The nature and strength of interactions between species in savanna ecosystems therefore differ according to rainfall (see Sankaran *et al.*, 2005; Baxter & Getz, 2008). Because elephant spatial utilization is influenced by rainfall (Western & Lindsay, 1984; Thouless, 1998; Verlinden & Gavor, 1998), differences in elephant spatial use between wet and dry savannas may partially explain differences in the impacts of elephants among places. Certainly, the distribution and availability of food, which also influence elephant spatial use (Murwira & Skidmore, 2005; Chamaillé-Jammes, Valeix & Fritz, 2007*a*; Wittemyer *et al*., 2007*a*; Harris *et al*., 2008) are related to rainfall (Scholes, Bond & Eckhardt, 2003), and may also differ between wet and dry savannas. Food availability may be better in wet than dry savannas where the annual precipitation is relatively low; and seasonal changes in food availability may also differ between wet and dry savannas. In wet savannas, a longer duration and greater volume of rainfall may render seasonal differences in food availability less pronounced than in dry savannas. These differences may influence elephant returns to previously utilized areas within seasons, between seasons and between years.

In this study we tested whether three measures of elephant spatial use (home-range size, evenness of spatial use within home ranges and repeated spatial use between seasons and between years) differed between wet and dry savannas. We then assessed whether temporal (seasonal) and spatial trends in the distribution of food availability within home ranges and within structural vegetation types explained differences in our three elephant spatial use measures. We used vegetation productivity [indexed by the normalized difference vegetation index (NDVI)], as a coarse measure of food availability for elephants (Murwira & Skidmore, 2005; Chamaillé-Jammes *et al*., 2007*a*; Wittemyer, Rasmussen & Douglas-Hamilton, 2007*b*). Our assumptions and expectations are summarized in Table 1.

Materials and methods

Study sites

We studied spatial use by elephants in six study sites associated with conservation areas in southern Africa across a west to east rainfall gradient that ranged from 376 to 802 mm mean annual precipitation. This gradient extended from Etosha National Park (Namibia) in the west to South

Table 1 The assumptions and expectations of our study

Vegetation productivity		Expectations		
Attribute	Assumptions	NDVI	Elephant spatial use at the landscape scale	Elephant spatial use within home ranges
Spatial distribution of vegetation productivity	Vegetation productivity is higher in wet than dry savannas	NDVI values are higher in wet than dry savannas	Elephant home ranges are smaller in wet than dry savannas	Spatial use within home ranges is not influenced by vegetation productivity
	Vegetation productivity is more uniformly distributed in wet than dry savannas	Variability in NDVI values is greater in dry than wet savannas	Elephant home ranges are smaller in wet than dry savannas	Spatial use within home ranges is more uniform in wet than dry savannas
	Seasonal differences in total vegetation productivity are less pronounced in wet than dry savannas	Seasonal differences in NDVI values are smaller in wet than dry savannas	Seasonal differences in elephant home-range sizes are less pronounced in wet than dry savannas	Seasonal differences in spatial use intensity within home ranges are less pronounced in wet than dry savannas
	Seasonal differences in the heterogeneity in the distribution of vegetation productivity are less pronounced in wet savannas than dry savannas	Seasonal differences in the variability in NDVI values are smaller in wet than dry savannas	Seasonal differences in elephant home-range sizes are less pronounced in wet than dry savannas	Seasonal differences in uniformity of spatial use within home ranges are less pronounced in wet than dry savannas

		NDVI within grid cells	Repeated use of space by elephants over time
Inter-seasonal and inter-annual stability of vegetation productivity	The spatial distribution of vegetation productivity between wet and dry seasons and from year to year within seasons is more stable in wet than dry savannas	From season to season, NDVI values within grid cells are more stable in wet than dry savannas	Between wet and dry seasons elephants use a higher proportion of the same grid cells in wet than dry savannas
		From year to year, within seasons, NDVI values within grid cells are more stable in wet than dry savannas	From year to year within seasons, elephants use a higher proportion of the same grid cells in wet than dry savannas

NDVI, normalized difference vegetation index.

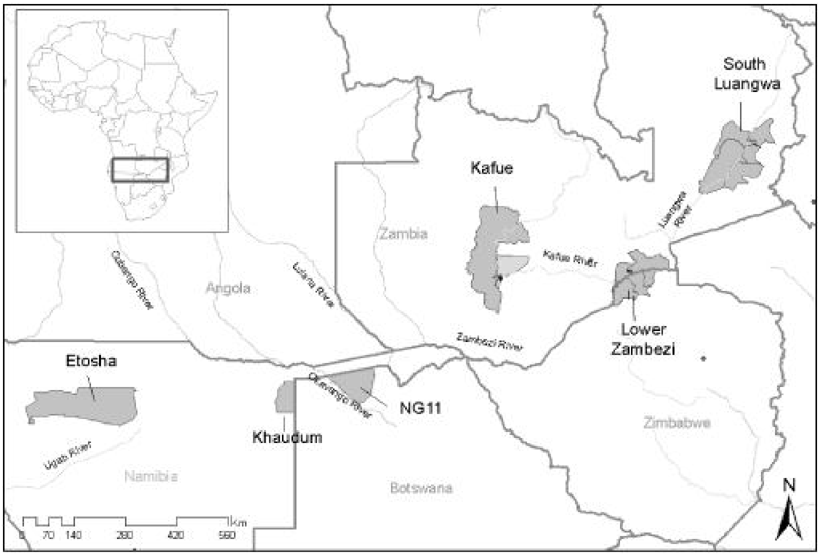


Figure 1 Location of study sites across southern Africa.

Luangwa National Park (Zambia) in the east (Fig. 1). According to the rainfall-derived savanna types defined by Sankaran *et al.* (2005), Etosha (centroid 19°00′S, 16°00′E), Khaudum (centroid 19°00′S, 20°40′E), and Ngamiland Section 11 (NG11, centroid 18°40′S, 22°40′E) were dry, climatically driven savannas, while Kafue (centroid 15°20′S, 25°40′E), Lower Zambezi (centroid 15°30′S, 29°30′E) and South Luangwa (centroid 13°00′S, 31°30′E) were wet disturbance-driven savannas. The boundaries of study sites were defined by the furthest extent of elephant locations associated with each conservation area over the study period. Based on the Global Land Cover 2000 Project (Mayaux *et al.*, 2003), the relative proportions of woody and herbaceous cover differed among study sites. In addition, because Kafue, Lower Zambezi and South Luangwa were unfenced, and elephants ranged beyond conservation area boundaries, these three study sites included areas where croplands were mixed with open vegetation. Boreholes in Etosha and Khaudum provided additional drinking water for wildlife. Kafue was situated beside a large artificial lake. In Kafue, rivers, lakes, pans and other wetlands also provided surface water, as was the case in NG11, Lower Zambezi and South Luangwa.

Data

We used location datasets for 18 elephant cows from the six study sites (three cows per study site). Each of these cows lived in a breeding herd and was fitted with a neck collar containing a satellite tracking unit (Africa Wildlife Tracking, Pretoria, South Africa). The dataset for each cow included daily locations during two consecutive wet and two consecutive dry seasons. Elephants at each site were tracked for 2-year periods between December 2002 and March 2006 (Table 2). Daily locations were advanced by 2 hours every week, thereby reducing the likelihood of these locations being dictated by diurnal activity rhythms.

We extracted monthly rainfall data from weather stations close to, or within each study site. For Khaudum, where no such weather stations existed, we calculated monthly mean values from interpolated rainfall surfaces available from http://www.worldclim.org/. We used monthly rainfall data to distinguish between wet and dry seasons. We defined core wet seasons as those sequential months that cumulatively received 70% of the annual rainfall. Core dry seasons were those sequential months that received $<2\%$ of the annual rainfall (Table 2).

We used the NDVI as a measure of vegetation productivity. We downloaded NDVI data for each month from December 2002 to March 2006 from http://free.vgt.vito.be/. Data were at a resolution of 1 km^2, with NDVI values calculated from 10 day composites of remotely sensed images from SPOT4 and SPOT5 satellites.

Elephant spatial use

We calculated three measures of spatial use. Home-range size served as a measure of spatial use at the landscape scale. Utilization uniformity measured how evenly elephant locations were spaced within home ranges. Repeated visits to grid cells between seasons and between years served as a measure of inter-seasonal and inter-annual spatial use intensity.

For each elephant we calculated 95% fixed kernel home-range sizes using the Animal Movement Extension (Hooge & Eichenlaub, 1997) for two core wet seasons and two core dry seasons, using ArcView GIS 3.3 (Environmental Systems Research Institute Inc., Redlands, CA, USA). For each elephant we also calculated the seasonal differences in home-range size as wet-season values minus the following dry-season values.

We used a clumping index (R) of elephant locations within home ranges as a measure of how evenly elephants used space. For each elephant- and season-specific set of locations, we calculated the observed average nearest

Table 2 Mean annual precipitation and core seasons for study sites

Study site	Mean Annual Precipitation (standard deviation) (mm)	Collection period (years)	Core season months Wet season 1	Wet season 2	Dry season 1	Dry season 2
Etosha	376 (112)	25	December 2002–March 2003	December 2003–March 2004	June 2003–September 2003	June 2004–September 2004
Khaudum	524[a]	50	December 2004–March 2005	December 2005–March 2006	June 2005–September 2005	June 2006–September 2006
NG11	430 (190)	20	December 2004–March 2005	December 2005–March 2006	June 2005–September 2005	June 2006–September 2006
Kafue[b]	783 (234)	17	December 2003–March 2004	December 2004–March 2005	June 2003–September 2003	June 2004–September 2004
Lower Zambezi	667 (204)	10	December 2004–March 2005	December 2005–March 2006	June 2005–September 2005	June 2006–September 2006
South Luangwa	802 (145)	21	December 2004–March 2005	December 2005–March 2006	June 2005–September 2005	June 2006–September 2006

Mean annual precipitation was calculated from monthly data from weather stations within or in close proximity to study areas. For Khaudum only, monthly data were obtained from interpolated rainfall surfaces downloaded from the worldclim website http://www.worldclim.org/. Numbers in brackets are standard deviation of the mean. Core wet seasons were those consecutive months that cumulatively received 70% of the annual rainfall. Core dry seasons were those months that cumulatively received $<2\%$ of the annual rainfall.

[a] No standard deviation available.

[b] Note the order of core seasons for Kafue is asynchronous with those of other study sites.

neighbour distance (d_o). We then randomly distributed a similar number of locations and also estimated an average nearest neighbour distance (d_e). From these we derived R as d_o/d_e. Values >1 reflected dispersed distributions (uniform utilization), those <1 were clumped (patchy utilization), while values of 1 represented a random distribution (see Mitchell, 2005). For each elephant we also calculated seasonal differences in utilization uniformity as wet-season values minus the following dry-season values.

Our measure of inter-seasonal and inter-annual repeated visits between core seasons was the fraction of the total area visited in both core seasons (inter-seasonal: wet and dry; dry and wet; inter-annual: wet and wet; dry and dry). To calculate this we divided each elephant- and season-specific home range into grid cells of $5\,\text{km}^2$ and calculated the fraction of the total number of grid cells visited in either season that was visited during both seasons. We assumed that $5\,\text{km}^2$ represented most of an elephant cow's daily operating range, taking into account their daily water requirements (Stokke & du Toit, 2002; de Beer *et al.*, 2006; Smit, Grant & Devereux, 2007).

We compared season-specific home-range size and utilization uniformity with two-tailed *t*-tests (Zar, 1984). For inter-seasonal and inter-annual repeated visits we used the non-parametric Kolmogorov–Smirnov test.

Vegetation productivity

We divided each study site into $1\,\text{km}^2$ grid cells (the resolution of our NDVI data). For each grid cell we calculated the sum of the maximum NDVI values (one value per month) for the core seasons for which we studied elephants. The mean of the summed values of grid cells measured seasonal vegetation productivity (Pettorelli *et al.*, 2005), and the standard deviation of the summed values among grid cells measured heterogeneity in the spatial distribution of vegetation productivity (Murwira & Skidmore, 2005). For each study site we also calculated seasonal differences from the wet to the dry season for each measure. We grouped the study sites according to wet and dry savanna types and compared our vegetation productivity measures between savanna types using two-tailed *t*-tests.

We also calculated season-specific vegetation productivity measures for grid cells within study sites grouped according to structural vegetation classes (Table 3), defined by Eiten (1968) and consistently assigned by Mayaux *et al.* (2003) across the whole of the African continent in the Global Land Cover 2000 Project.

To measure the stability in the spatial distribution of vegetation productivity for each study site between seasons (wet to dry and dry to wet), and between years (wet to wet and dry to dry), we calculated a temporal autocorrelation of the sum of maximum NDVI grid-cell values between seasons and between years (see Rossi *et al.*, 1992 for explanation). To do this, we created a lagged-scatter plot (Chatfield, 1975) for all grid cells of each study site for each seasonal combination (wet to dry; dry to wet; wet to wet and dry to dry). On the scatter plot, every grid cell represented a point with the sum of maximum NDVI values at time (t) on the x-axis, and the sum of maximum NDVI values at time ($t+1$) on the y-axis. Pearson's correlation coefficient r for each seasonal combination served as a measure of stability.

We grouped our study sites according to savanna types and compared the measures of intra-seasonal and inter-annual stability in the spatial distribution of vegetation productivity with two-tailed *t*-tests.

Table 3 Proportion of the total number of grid cells (1 km^2) of each study site falling into structural vegetation classes as defined by Mayaux *et al.* (2003)

Study site	Tree canopy cover > 40%. Canopy height > 5 m	Tree canopy cover between 15 and 40%. Canopy height > 5 m	Shrub canopy cover > 15%. Canopy height < 5 m. Sparse tree layer < 15%	Shrub canopy cover > 15%. Canopy height < 5 m. No tree layer	Tree and shrub canopy cover < 20%. Herbaceous cover > 40%	Shrub canopy cover < 20%. Herbaceous cover between 15 and 40%	Herbaceous cover between 5 and 15% without shrub canopy	Herbaceous cover between 1 and 5%	Swamp bushland and grassland	Areas where croplands were mixed with open vegetation
Etosha					0.03	0.47	0.30	0.01		
Khaudum				0.35	0.55	0.11				
NG11		0.17	0.02	0.70	0.11				0.09	
Kafue	0.01	0.60	0.24	0.01						0.12
Lower Zambezi	0.03	0.16	0.37	0.07	0.06	0.01				0.31
South Luangwa			0.50	0.02						0.48

Elephant spatial use and vegetation productivity

We regressed elephant home-range sizes (pooled for wet and dry savannas), our measure of utilization uniformity and our measure of inter-seasonal repeated visits against season-specific vegetation productivity measures per site and per vegetation structural class for each site.

Selection within home ranges

We compared maximum NDVI for visited 5 km^2 grid cells within each 10 day period with the same number of randomly selected 5 km^2 grid cells (pseudo-absences; Engler, Guisan, & Rechsteiner, 2004). We permutated this procedure 10 000 times (see Gentle, 1943) and proposed a null model that the mean value of visited grid cells was drawn from the same distribution as values from randomly selected grid cells within the same 10 day period. We rejected the null model if $P < 0.05$. For each elephant- and season-specific set of 10 day time periods, we calculated the proportion of periods where the mean maximum NDVI of visited grid cells was higher, and significantly ($P < 0.05$) higher, than that for randomly selected grid cells.

We further assessed whether elephant cows selected for areas of higher NDVI within structural vegetation classes (Mayaux *et al.*, 2003). We removed the effect of time on NDVI values by calculating a residual maximum NDVI ($rC_{j(t)}$) value for each grid cell of each elephant's seasonal home range for each 10 day NDVI data period as follows

$$rC_{j(t)} = C_{j(t)} - \sum_{j=1}^{n} C_j / m_{(t)}$$

where $C_{j(t)}$ is the maximum NDVI value of cell j at time t, and m is the mean maximum NDVI value of all grid cells at time t. We then used a one-tailed t-test (Zar, 1984) to compare mean residual maximum NDVI for visited grid cells with the same number of randomly selected grid cells within each structural vegetation class that was represented in each elephant- and season-specific home range for the first wet and the first dry season of our study. We then calculated the proportion of residual mean maximum NDVI values that were higher for visited than randomly selected grid cells for wet and dry savannas.

Results

Elephant spatial use

Home ranges

Home-range sizes of elephant cows from dry savannas were three- and four-fold those of elephants from wet savannas during the wet and dry seasons, respectively (two-tailed t-test: wet season, $t = 3.35$, d.f. = 34, $P = 0.002$; dry season, $t = 3.50$, d.f. = 34, $P = 0.001$) (Fig. 2a). Although seasonal differences between wet- and dry-season home-range sizes

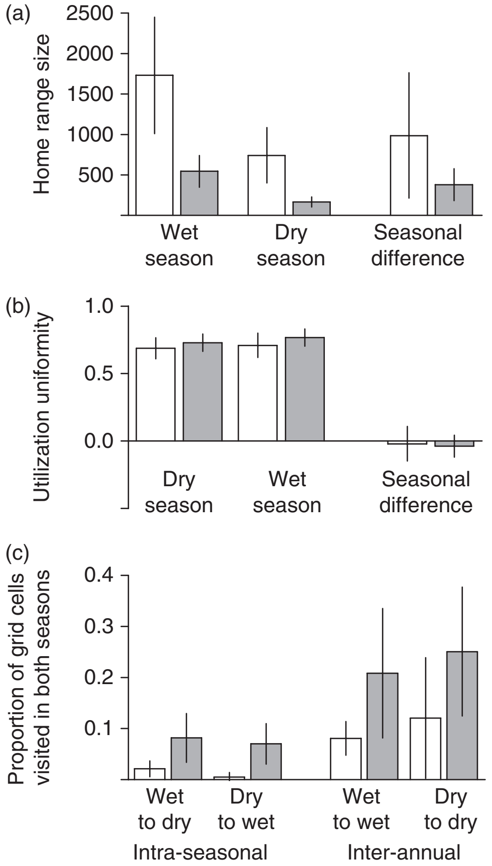


Figure 2 Elephant spatial use in wet (shaded bars) and dry (clear bars) savannas. We show (a) home-range sizes calculated as the area of 95% kernel density (km^2) and, (b) utilization uniformity as the clumping index (R) of elephant- and season-specific locations, for nine elephants from three wet savanna study sites (three per site), and nine elephants from three dry savanna study sites (three per site), for two wet seasons pooled and two dry seasons pooled. In (a) and (b) seasonal differences for home-range sizes and utilization uniformities were calculated as wet-season values minus the following dry-season values. We also show (c) the inter-seasonal and inter-annual repeated visits in wet and in dry savannas calculated as that fraction of grid cells visited in either season that were visited in both seasons. All bars are mean ± 95% confidence interval.

were larger in dry than wet savannas (Fig. 2a), this was not significant ($t = 1.60$, d.f. = 34, $P = 0.118$).

Utilization uniformity within home ranges

Contrary to our expectation, we found no evidence that elephants from wet savannas utilized the space within their home ranges more evenly than their dry savanna counterparts in the wet season, (two-tailed t-test: $t = 0.846$, d.f. = 34, $P = 0.403$) or in the dry season ($t = 1.10$, d.f. = 34, $P = 0.277$) (Fig. 2b). Furthermore, seasonal differences in utilization uniformity within home ranges did not differ between wet and dry savannas, as expected ($t = 0.24$, d.f. = 34, $P = 0.815$) (Fig. 2b).

Repeated visits between seasons and from year to year within seasons

Elephant cows living in wet savannas revisited a higher proportion of previously visited grid cells between seasons. Elephants from wet savannas revisited between two- and seven-fold the proportion of grid cells between seasons and in the same season from year to year than those living in dry savannas (Fig. 2c). Differences were significant from the wet season to the following dry season (Kolmogorov–Smirnov test, $P < 0.01$), from the dry season to the following wet season ($P < 0.01$), and from one wet season to the next wet season ($P < 0.01$). From one dry season to the next dry season, this difference was not significant ($P > 0.05$).

Vegetation productivity

Seasonal vegetation productivity (mean sum of maximum NDVI)

Our results supported our expectation that vegetation productivity was higher in wet than dry savannas (Fig. 3a). However, this difference was significant only for the wet season (two-tailed t-test: $t = 2.52$, d.f. = 10, $P = 0.03$), and not for the dry season ($t = 1.77$, d.f. = 10, $P = 0.11$) (Fig. 3a).

We had expected that seasonal differences in vegetation productivity would be larger for dry than wet savannas; however, the opposite was the case ($t = 2.05$, d.f. = 10, $P = 0.07$) (Fig. 3a).

Heterogeneity in the spatial distribution of vegetation productivity (standard deviation sum of maximum NDVI)

Our expectation that the spatial distribution of NDVI would be more heterogeneous in dry savannas than wet savannas did not hold in either the wet season (two-tailed t-test: $t = 0.26$, d.f. = 10, $P = 0.80$), or the dry season ($t = 0.04$, d.f. = 10, $P = 0.97$) (Fig. 3b). Our expectation that seasonal differences in the spatial heterogeneity of vegetation productivity would be less pronounced in wet than dry savannas was also not supported ($t = 0.25$, d.f. = 10, $P = 0.81$) (Fig. 3b).

Inter-seasonal and inter-annual stability in the distribution of vegetation productivity (temporal autocorrelation in sum maximum NDVI)

Contrary to our expectations, the spatial stability in the distribution of vegetation productivity did not significantly differ between wet and dry savannas for any of our seasonal combinations (Fig. 3c) as follows: from the wet season to the dry season: (two-tailed t-test: $t = 1.20$, d.f. = 4, $P = 0.30$); from the dry season to the wet season ($t = 1.26$, d.f. = 4, $P = 0.28$); from one wet season to the next ($t = 0.40$, d.f. = 4, $P = 0.71$); from one dry season to the next ($t = 0.04$, d.f. = 4,

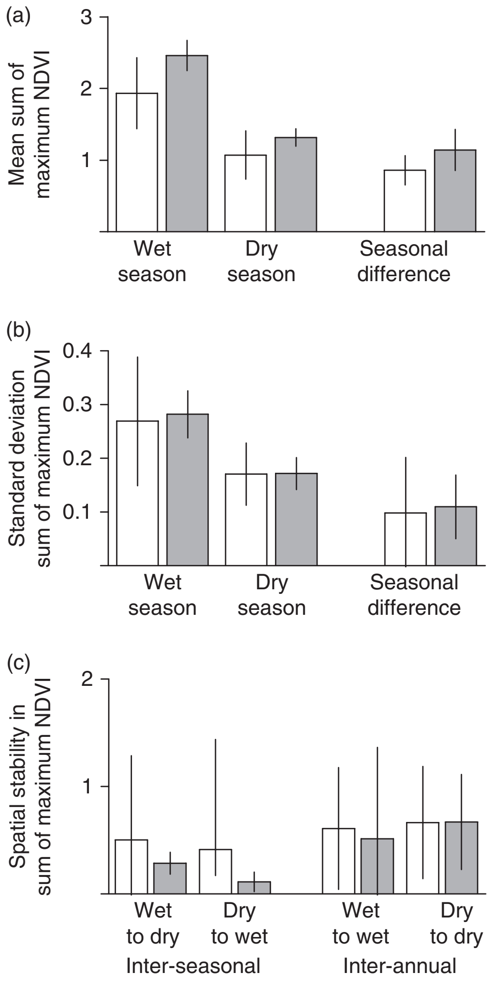


Figure 3 Vegetation productivity measures for three wet (shaded bars) and three dry (clear bars) savanna study sites for two wet seasons pooled, and two dry seasons pooled. We show (a) seasonal vegetation productivity (mean sum of maximum NDVI), (b) heterogeneity in the spatial distribution of seasonal vegetation productivity (standard deviation sum of maximum NDVI), and (c) inter-seasonal and inter-annual stability in the distribution of maximum NDVI within grid cells (mean Pearson's *r*, see 'Materials and methods'). All bars are mean ±95% confidence interval.

$P = 0.97$). However, variation in the stability of the distribution of vegetation productivity among wet savanna study sites was relatively small compared with that of dry savanna study sites from the wet to the dry season and the dry to the wet season (Fig. 3c).

Elephant spatial use and vegetation productivity

Our results confirmed that elephant spatial use was a function of seasonal vegetation productivity (mean sum of maximum NDVI), heterogeneity in the distribution of vegetation productivity (standard deviation in sum of maximum NDVI) and its spatial stability from season to season. This, however, varied across measures and between seasons (Figs 4–6).

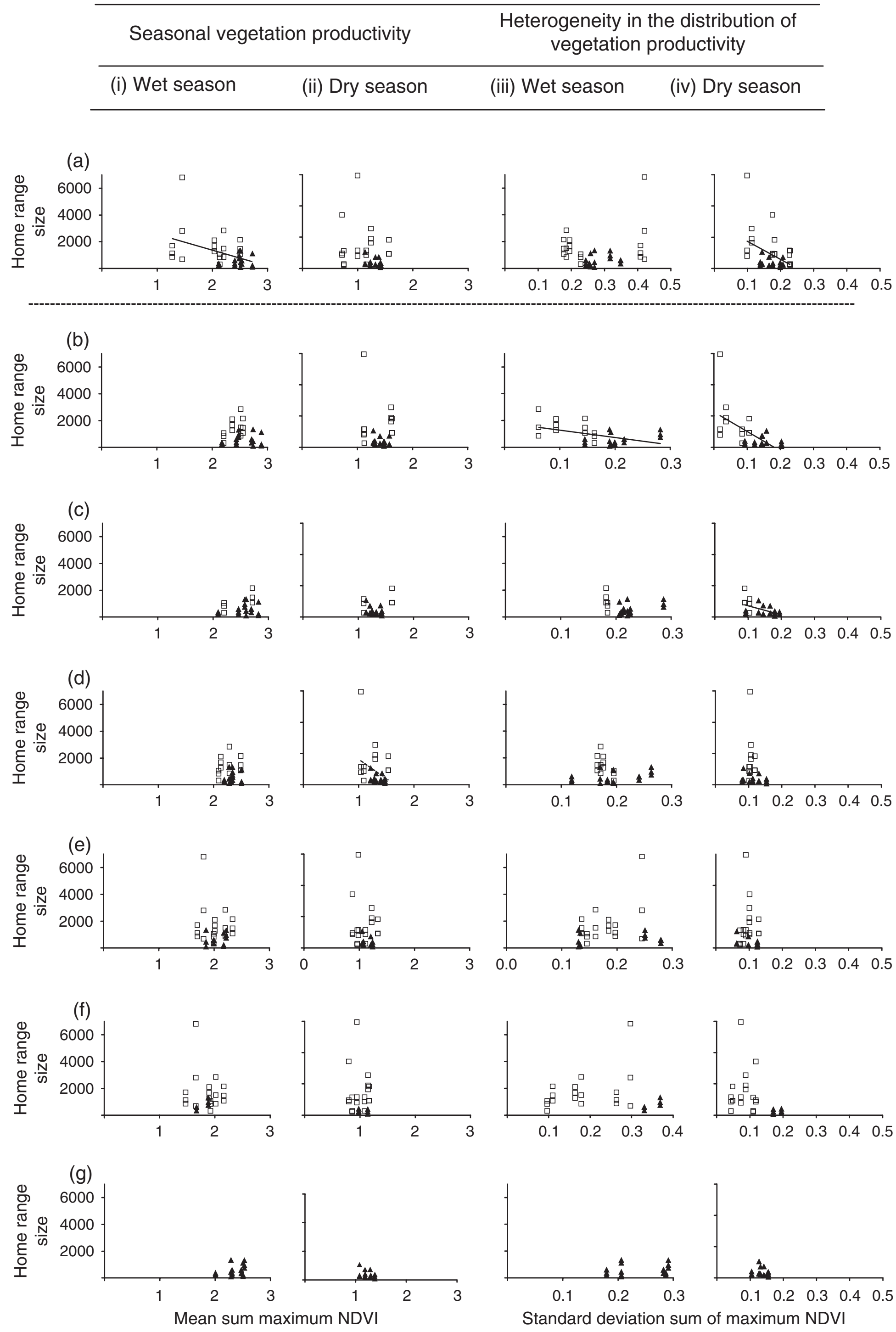
Home-range sizes during the wet season decreased with increasing seasonal vegetation productivity for all grid cells within study sites ($y = -1193x + 3759$, $r^2 = 0.18$, $F_{1,34} = 7.5$, $P = 0.01$) (Fig. 4a) but not for grid cells within structural vegetation classes (Fig. 4b–g).

Heterogeneity in the distribution of vegetation productivity also influenced elephant home-range sizes. Dry-season home-range sizes decreased with increasing heterogeneity in seasonal vegetation productivity calculated for all grid cells within study sites ($y = -5758x + 1441$, $r^2 = 0.17$, $F_{1,34} = 1.5$, $P = 0.01$) (Fig. 4a) and for grid cells within structural vegetation classes within study sites where: (1) the tree canopy cover varied from 15 to 40% and canopy height was >5 m ($y = -6246x + 1127$, $r^2 = 0.35$, $F_{1,28} = 15$, $P < 0.001$); (2) the shrub canopy cover was $>15\%$, canopy height was <5 m and there was a sparse tree layer of $<15\%$ ($y = -2849x + 642.7$, $r^2 = 0.26$, $F_{1,22} = 7.7$, $P < 0.01$). During the wet season home-range sizes also decreased with increasing heterogeneity in the distribution of seasonal vegetation productivity calculated for grid cells belonging to the structural vegetation class where tree canopy cover varied from 15 to 40% and canopy height was >5 m ($y = -5473x + 1823$, $r^2 = 0.23$, $F_{1,28} = 8.54$, $P < 0.007$) (Fig. 4b).

Seasonal vegetation productivity also influenced how evenly elephants utilized the space within their home ranges, but only during the wet season. Utilization uniformity of wet-season home ranges increased with increasing seasonal vegetation productivity calculated for all grid cells within a study site ($y = 0.11x + 0.46$, $r^2 = 0.11$, $F_{1,34} = 4.2$, $P = 0.05$) (Fig. 5a), and for grid cells within structural vegetation classes where the shrub canopy cover was 20% and herbaceous cover varied between 15 and 40% ($y = 0.33x + 0.07$, $r^2 = 0.22$, $F_{1,22} = 6.2$, $P = 0.03$) (Fig. 5f). Utilization uniformity decreased with increasing seasonal vegetation productivity within structural vegetation classes within study sites where croplands are mixed with open vegetation ($y = -0.43x + 1.7$, $r^2 = 0.39$, $F_{1,16} = 10$, $P = 0.006$) (Fig. 5g).

The heterogeneity in the distribution of vegetation productivity also influenced how evenly elephants utilized the space within their home ranges, but only during the wet season (Fig. 5). Elephants utilized their wet-season home ranges less evenly with increasing heterogeneity in the distribution of seasonal vegetation productivity calculated for all grid cells within study sites ($y = -0.97x + 0.98$, $r^2 = 0.29$, $F_{1,34} = 14.14$, $P < 0.001$) (Fig. 5a), and for grid cells within structural vegetation classes per study sites where: (1) the shrub canopy cover was $>15\%$, canopy height was <5 m, and a sparse tree layer of $<15\%$ was present ($y = -1.56x + 1.1$, $r^2 = 0.17$, $F_{1,22} = 4.7$, $P = 0.04$) (Fig. 5c); (2) the shrub canopy cover was $>15\%$, canopy height <5 m, and no tree layer existed ($y = -1.14x + 0.95$, $r^2 = 0.11$, $F_{1,28} = 3.5$, $P < 0.07$) (Fig. 5d); (3) the tree and shrub canopy cover was $<20\%$, and herbaceous cover was $>40\%$ ($y = -1.3x + 0.96$, $r^2 = 0.50$, $F_{1,10} = 10.04$, $P < 0.01$) (Fig. 5e); (4) the shrub canopy cover was $<20\%$, and herbaceous cover varied from 15 to 40% ($y = -0.73x + 0.83$, $r^2 = 0.24$, $F_{1,22} = 6.8$, $P < 0.02$) (Fig. 5f).

Repeated visits to grid cells between seasons and between years was related to the stability in the spatial distribution of seasonal vegetation productivity within grid cells. From the dry to the wet season, visits to previously visited grid cells declined with increasing stability in sum of maximum NDVI ($y = -0.082x + 0.064$, $r^2 = 0.20$, $F_{1,16} = 3.9$, $P = 0.06$) (Fig. 6). By contrast, from one dry season to the next, repeated visits increased with increasing stability in sum of maximum NDVI ($y = 0.46x - 0.12$, $r^2 = 0.16$, $F_{1,16} = 2.98$, $P = 0.10$) (Fig. 6). No relationship between repeated visits to grid cells



and stability in sum of maximum NDVI was found for the wet season to the following dry season, or for the wet season to the following wet season (Fig. 6).

Selection within home ranges

In no study site were the mean maximum NDVI values of visited grid cells for any elephant consistently higher than that for randomly selected grid cells (Table 4). By contrast, within structural vegetation classes, grid cells visited by elephants in dry savannas had higher maximum NDVI values than randomly selected grid cells in the wet season for 78% of 18 cases. Mean residual maximum NDVI values of visited grid cells were higher than randomly selected grid cells in 14 of 20 cases (70%) in the wet season for which eight cases were significantly different ($P<0.05$) (Table 5). This was not the pattern for the dry season when only six of 16 cases (38%) were higher for visited grid cells than randomly selected grid cells, of which only two were significant. Elephants in wet savannas only visited grid cells with higher residual maximum NDVI in comparison to that of randomly selected grid cells in 42% of 24 cases during the wet season, when only two of 10 were significant. During the dry season, wet savanna elephants visited grid cells with higher residual maximum NDVI values than randomly selected grid cells in 43% of 21 cases of which seven of 14 were significant.

Discussion

In our study, spatial use by elephants differed between wet and dry savannas. Wet savanna elephants ranged over smaller seasonal home ranges than those living in dry savannas and returned to more than two-fold the proportion of previously visited grid cells between seasons and between years than their dry savanna counterparts.

These repeated visits to the same places within seasons, between seasons and across years may accentuate the impact of elephants on vegetation (see Owen-Smith *et al.*, 2006; O'Connor *et al.*, 2007), particularly on woody vegetation (see Guldemond & van Aarde, 2008 and references therein). Furthermore, together with fire, elephant foraging on woody seedlings and saplings can depress regeneration of woodland areas (Dublin *et al.*, 1990; see also Baxter & Getz, 2005). Hence repeated returns to the same woodland areas within and between seasons could reduce regeneration over longer time scales, particularly since family units discriminate between patches to select the highest density of palatable species (Stokke & du Toit, 2002). This will also influence species composition. Furthermore, elephants may also revisit places to take advantage of compensatory growth of previously impacted vegetation (Jachmann & Bell, 1985; Smallie & O'Connor, 2000), thus reinforcing their impacts at a particular site. The 'legacy' effect (Sankaran *et al.*, 2008), where elephant impacts at a site are dependent on previous levels of elephant activity there, may be consistent with our interpretation. Thus, differences in spatial use patterns between wet and dry savannas may partially explain differences in elephant impacts on woody vegetation at different places (see Guldemond & van Aarde, 2008 and references therein).

The spatial and temporal variability of rainfall induces heterogeneity in primary productivity and thus the quality and distribution of food in savannas (Scholes *et al.*, 2003). Accordingly, we expected that wet savannas, which received higher relative mean annual rainfall over longer wet-season durations than dry savannas, would have higher relative seasonal vegetation productivity (mean sum of maximum NDVI), lower relative heterogeneity in the spatial distribution of vegetation productivity (standard deviation sum of maximum NDVI) and more stable distribution of vegetation productivity between seasons, than dry savannas. Because home ranges reflect an animal's nutritional requirements (see Schoener, 1981), and for elephants smaller ranges suggest higher quality home ranges (Wittemyer *et al.*, 2007*a*), we further expected that differences in the quantity, distribution and stability of vegetation productivity as a coarse measure of food availability (Murwira & Skidmore, 2005; Chamaillé-Jammes *et al.*, 2007*a*; Wittemyer *et al.*, 2007*b*), should explain differences between wet and dry savanna elephant spatial use patterns above.

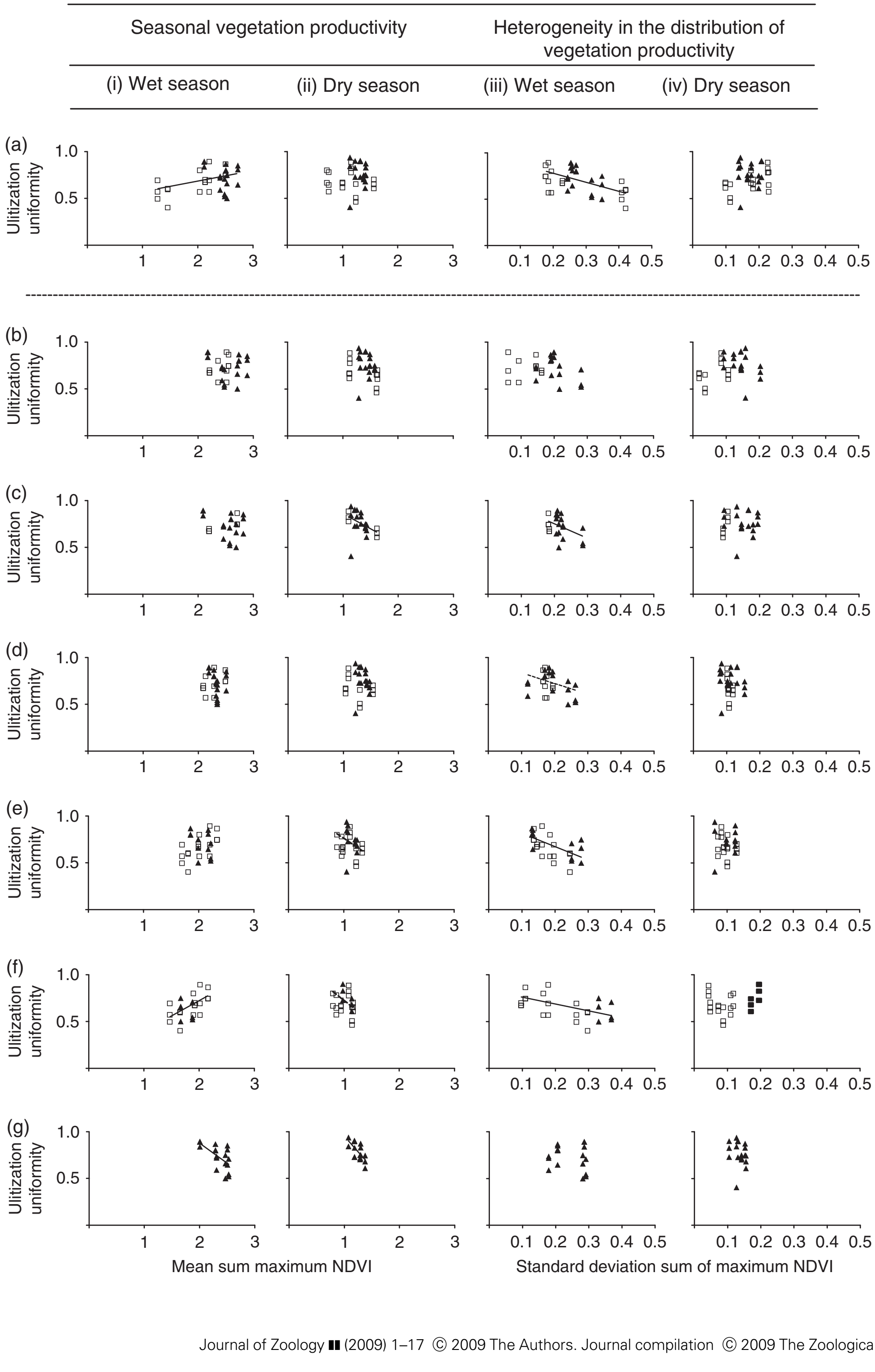
In support of our expectations, seasonal vegetation productivity was higher in wet than in dry savannas during the wet season, and correspondingly wet-season elephant home-range sizes decreased with increasing seasonal vegetation productivity. Furthermore, elephant spatial use within wet-season home ranges became more even with increasing seasonal vegetation productivity. In contrast, however,

◀

Figure 4 Home-range size (km^2) as a function of seasonal vegetation productivity and heterogeneity in the spatial distribution of vegetation productivity calculated for (a) all grid cells within a study site; and (b–g) grid cells within a study site belonging to structural vegetation classes (land cover classes) as defined by Mayaux *et al.* (2003). For (a), plots comprise data from nine elephants from three wet (▲) (three per study site), and nine elephants from three dry (□) (three per study site) for two wet seasons pooled and two dry seasons pooled. For (b–g) plots are as for (a), but comprise data only from study sites with that structural vegetation class present (as shown in brackets). Lines were fitted only in cases where a significant relationship ($P<0.05$) (solid line), or ($P<0.10$) (dashed line) existed. Structural vegetation classes shown are for: (b) Tree canopy cover between 15 and 40% with a canopy height >5 m (Khaudum, NG11, Kafue, Lower Zambezi, South Luangwa). (c) Shrub canopy cover $>15\%$ with a canopy height <5 m and a sparse tree layer $<15\%$ (NG11, Kafue, Lower Zambezi, South Luangwa). (d) Shrub canopy cover $>15\%$ with a canopy height <5 m and no tree layer (Khaudum, NG11, Kafue, Lower Zambezi, South Luangwa). (e) Tree and shrub canopy cover $<20\%$ and herbaceous cover $>40\%$ (Etosha, Khaudum, NG11, Lower Zambezi, South Luangwa). (f) Shrub canopy cover $<20\%$ and herbaceous cover between 15 and 40% (Etosha, Khaudum, NG11, Lower Zambezi). (g) Areas where croplands were mixed with open vegetation (Kafue, Lower Zambezi, South Luangwa).

vegetation productivity was not more homogeneously distributed in wet than dry savannas, as expected, nor was the distribution of vegetation productivity between seasons more stable in wet than dry savannas. Even so, elephant spatial use was influenced by these two vegetation productivity measures. During the dry season, home-range sizes decreased, and during the wet-season elephant spatial use within home ranges became more even with increasing heterogeneity in the distribution of vegetation productivity.

These results suggest the influence of vegetation productivity on elephant spatial use changes according to seasonal resource limitations, most likely that of surface water availability and seasonal food preferences. During the wet season elephant breeding herds are less dependent on the



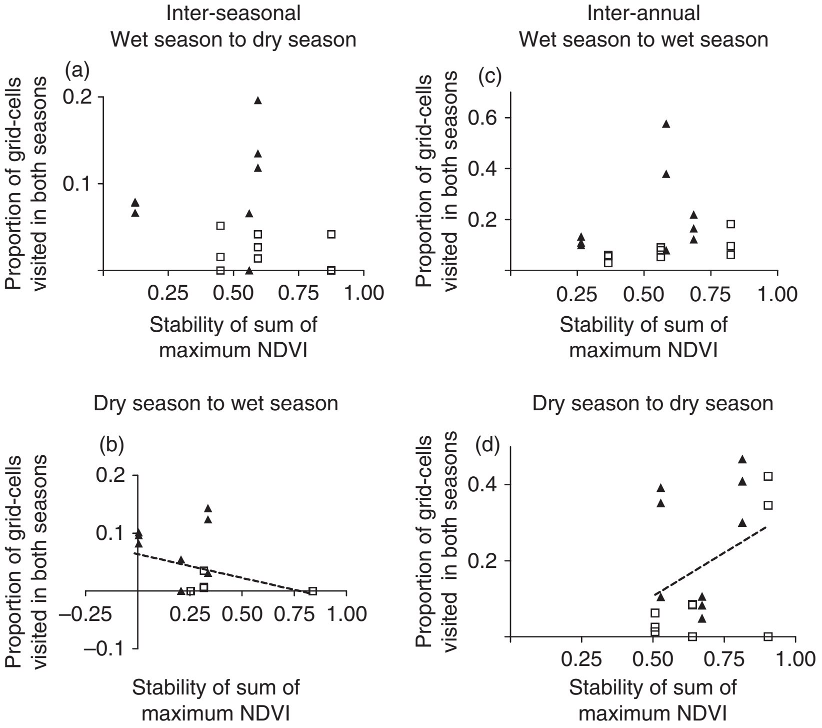


Figure 6 Relationships between the proportion of repeated visits to grid cells between seasons for nine elephants from three wet savanna study sites (▲) (three per site), and nine elephants from three dry savanna study sites (□) (three per site), and the stability in the spatial distribution of sum of maximum NDVI (see 'Materials and methods') from the (a) wet to dry season; (b) dry to wet season; (c) wet to wet season; (d) dry to dry season. Lines were fitted only in cases where a significant relationship ($P<0.10$) existed.

distribution of permanent surface water sources and therefore may range further and wider than during the dry season, when they typically remain in close proximity to surface water to provide for young and neonate needs (Stokke & du Toit, 2002; Redfern *et al.*, 2005; Chamaillé-Jammes, Valeix & Fritz, 2007*b*; Smit *et al.*, 2007; Wittemyer *et al.*, 2007*a*). Hence the availability of surface water defines key-resource areas by shaping the seasonal restriction of the foraging range (Chamaillé-Jammes *et al.*, 2007*b*, 2008). Our result that home-range size was influenced by vegetation productivity only during the wet season is consistent with food resources being an important determinant of elephant spatial use when elephant breeding herds are less restricted by the availability of surface water. In contrast, during the dry season, the lack of influence of seasonal vegetation productivity is consistent with surface water being the primary determinant of foraging range. The apparent lack of selection by both wet and dry savanna elephants within structural vegetation classes within dry-season home ranges is also consistent with the suggestion that water is a key determinant for elephant spatial use during this season. However, the decrease in dry-season home-range sizes with increasing heterogeneity in the distribution of vegetation productivity suggests that when surface water is limited, elephant foraging may be more efficient in heterogeneous landscapes (Grainger, van Aarde & Whyte, 2005; Murwira

Figure 5 Utilization uniformity (average nearest neighbour statistic) as a function of seasonal vegetation productivity and heterogeneity in the spatial distribution of vegetation productivity calculated for (a) all grid cells within a study site; and (b–g) grid cells within a study site of different structural vegetation classes (land cover classes) as defined by Mayaux *et al.* (2003) see below for descriptions. For (a), plots comprise data from nine elephants from three wet (▲) (three per study site), and nine elephants from three dry (□) (three per study site) for two wet seasons pooled and two dry seasons pooled. For (b–g) plots are as for (a), but comprise data only from study sites with that structural vegetation class present (as shown in brackets). Lines were fitted only in cases where a significant relationship ($P<0.05$) (solid line), or ($P<0.10$) (dashed line) existed. Structural vegetation classes shown are for: (b) Tree canopy cover between 15 and 40% with a canopy height >5 m (Khaudum, NG11, Kafue, Lower Zambezi, South Luangwa). (c) Shrub canopy cover >15% with a canopy height <5 m and a sparse tree layer <15% (NG11, Kafue, Lower Zambezi, South Luangwa). (d) Shrub canopy cover >15% with a canopy height <5 m and no tree layer (Khaudum, NG11, Kafue, Lower Zambezi, South Luangwa). (e) Tree and shrub canopy cover <20% and herbaceous cover >40% (Etosha, Khaudum, NG11, Lower Zambezi, South Luangwa). (f) Shrub canopy cover <20% and herbaceous cover between 15 and 40% (Etosha, Khaudum, NG11, Lower Zambezi). (g) Areas where croplands were mixed with open vegetation (Kafue, Lower Zambezi, South Luangwa).

Table 4 Proportion of 10 day time periods where mean maximum NDVI values of visited grid cells were higher than for randomly selected grid cells

	Proportion of times mean maximum NDVI is higher for visited than randomly selected grid cells								
Elephant	All seasons combined	Wet 1		Dry 1		Wet 2		Dry 2	
Etosha 3	0.90	0.88	*0.50*	0.90	*0.50*	0.92	*0.67*	0.90	*0.40*
Etosha 5	0.85	0.67	*0.33*	1.00	*0.67*	0.92	*0.33*	0.90	*0.30*
Etosha 6	0.59	0.78	*0.33*	0.45	*0.09*	0.58	*0.00*	0.56	*0.42*
Khaudum 4	0.59	1.00	*0.33*	0.38	*0.13*	0.27	*0.18*	0.73	*0.09*
Khaudum 5	0.46	0.57	*0.00*	0.63	*0.00*	0.33	*0.00*	0.40	*0.30*
Khaudum 6	0.58	0.67	*0.56*	0.50	*0.00*	0.67	*0.36*	0.45	*0.00*
Botswana 6	0.51	0.62	*0.14*	0.38	*0.00*	0.58	*0.08*	0.22	*0.11*
Botswana 8	0.54	0.80	*0.40*	0.38	*0.13*	0.36	*0.00*	0.50	*0.25*
Botswana 10	0.47	0.50	*0.00*	0.38	*0.13*	0.58	*0.17*	0.38	*0.25*
Kafue 1	0.54	0.45	*0.09*	0.29	*0.00*	0.70	*0.00*	0.71	*0.00*
Kafue 3	0.74	0.67	*0.17*	0.86	*0.00*	0.86	*0.29*	0.60	*0.00*
Kafue 8	0.63	0.67	*0.25*	0.43	*0.00*	1.00	*0.17*	0.43	*0.14*
Zambezi 1	0.49	0.44	*0.00*	0.42	*0.14*	0.43	*0.08*	0.71	*0.00*
Zambezi 3	0.74	0.50	*0.00*	0.86	*0.00*	0.81	*0.27*	1.00	*0.29*
Zambezi 6	0.51	0.44	*0.11*	0.43	*0.14*	0.58	*0.33*	0.57	*0.29*
Luangwa 1	0.60	0.60	*0.20*	0.44	*0.11*	0.67	*0.17*	0.67	*0.22*
Luangwa 3	0.53	0.44	*0.11*	0.55	*0.00*	0.42	*0.00*	0.62	*0.13*
Luangwa 5	0.62	0.67	*0.33*	0.56	*0.11*	0.44	*0.00*	0.61	*0.19*

Each core season was divided into 12 time periods of 10 days. For each elephant and season we report the proportion of periods that the maximum NDVI values for visited grid cells was higher than that for an equal number of randomly selected grid cells within that elephant- and season-specific home range. In italics, we also report the proportion of times that the difference was significant according to a one-tailed *t*-test ($P<0.05$).

NDVI, normalized difference vegetation index.

& Skidmore, 2005; de Beer & van Aarde, 2008), particularly because the spatial configuration of food and water is critical during this season (Harris *et al*., 2008).

Bearing in mind that seasonal vegetation productivity differed between wet and dry savannas but heterogeneity in the distribution of vegetation productivity did not, we conclude that differences in vegetation productivity between wet and dry savannas explained differences in wet-season elephant home ranges, but that differences between dry-season home-range sizes in wet and dry savannas may be influenced by factors other than differences in vegetation productivity alone.

Vegetation structure differed between wet and dry savannas. Wet savannas mainly comprised tree- and shrub-dominated structural vegetation classes, while dry savannas mainly comprised structural vegetation classes where shrub and herbaceous cover predominated. Vegetation structure has a large influence on NDVI values (see Mayaux *et al*., 2003; Geerken, Zaichik, & Evans, 2005), and therefore on vegetation productivity. Our analysis of suggests elephant spatial use as a function of vegetation productivity within structural vegetation classess, that vegetation structure explains the differing influence of vegetation productivity on elephant spatial use between seasons. Because grasses have relatively high NDVI values during the wet season (van Bommel *et al*., 2006), the lack of influence of vegetation productivity within any one structural vegetation class on wet-season home-range sizes appears consistent with elephants primarily selecting grasses during this season (O'Connor *et al*., 2007), regardless of structural vegetation class. Hence, consistent with our conclusion above, the difference in seasonal vegetation productivity between wet and dry savannas regardless of vegetation structure accounted for differences in home-range size during the wet season.

In contrast, during the dry season, the influence of heterogeneity in the distribution of vegetation productivity on dry-season home-range sizes was important in tree- and shrub-dominated structural vegetation classes which were represented only in the wet savanna study sites. Because grasses senesce during the dry season elephants switch to browse to meet nutritional requirements (O'Connor *et al*., 2007). The higher heterogeneity in the distribution of vegetation productivity in these structural vegetation classes may therefore reflect higher availability of the required combination of browse and water (Harris *et al*., 2008). If so, differences in vegetation structure between wet and dry savannas rather than vegetation productivity alone may explain the differences in elephant spatial use between wet and dry savanna types during the dry season.

Differences in vegetation structure between wet and dry savanna types may also explain why seasonal stability in vegetation productivity, which did not differ between wet and dry savannas, nevertheless influenced elephant repeated visits. Repeated visits from one dry season to the next increased with the increasing stability of vegetation productivity,

Table 5 NDVI values for visited and randomly selected grid cells within land cover classes

Study site and elephant code	Proportion of cases	Tree canopy cover >40%. Canopy height >5 m		Tree canopy cover between 15% and 40%. Canopy height >5 m		Shrub canopy cover >15%. Canopy height <5 m. Sparse tree layer <15%		Shrub canopy cover >15%. Canopy height <5 m. No tree layer		Tree and shrub canopy cover <20 %. Herbaceous cover >40%		Shrub canopy cover <20%. Herbaceous cover between 15% and 40%		Herbaceous cover between 5% and 15% without shrub canopy		Swamp bushland and grassland		Areas where croplands were mixed with open vegetation	
		R	V	R	V	R	V	R	V	R	V	R	V	R	V	R	V	R	V
Wet season																			
Etosha																			
3		▨	▨	▨	▨	▨	▨	▨	▨			**−0.002**	**0.064**[a]			▨	▨	▨	▨
5		▨	▨	▨	▨	▨	▨	▨	▨			**0.019**	**0.025**	**−0.003**	**0.025**[a]	▨	▨	▨	▨
6		▨	▨	▨	▨	▨	▨	▨	▨	0.084	0.070	**−0.043**	**0.010**[a]			▨	▨	▨	▨
Khaudum																			
4	Dry savannas	▨	▨	▨	▨	▨	▨	0.055	0.041	**−0.026**	**0.027**[a]	**−0.020**	**0.004**	▨	▨	▨	▨	▨	▨
5	0.78	▨	▨	▨	▨	▨	▨			0.005	−0.009	**0.002**	**0.012**	▨	▨	▨	▨	▨	▨
6		▨	▨	▨	▨	▨	▨	**0.033**	**0.057**[a]	**−0.027**	**−0.009**	**−0.054**	**0.009**[a]	▨	▨	▨	▨	▨	▨
NG11																			
6		▨	▨	**−0.020**	**0.040**[a]			**−0.008**	**0.005**			▨	▨	▨	▨			▨	▨
8		▨	▨	**0.004**	**0.047**[a]			**0.001**	**0.016**			▨	▨	▨	▨			▨	▨
10		▨	▨					−0.014	−0.037			▨	▨	▨	▨			▨	▨
Kafue																			
1				0.012	−0.014	**0.007**	**0.014**			▨	▨	▨	▨	▨	▨	▨	▨	−0.010	−0.013
3				0.061	0.060	**0.010**	**0.016**			▨	▨	▨	▨	▨	▨	▨	▨	−0.024	−0.034
8		**0.046**	**0.011**[a]	**0.019**	**0.038**	0.030	0.024			▨	▨	▨	▨	▨	▨	▨	▨	**−0.035**	**−0.025**
Lower Zambezi																			
1	Wet savannas					0.052	0.041			−0.098	−0.136			▨	▨	▨	▨	−0.022	−0.087
3	0.42					0.023	0.015			**0.020**	**−0.036**[a]			▨	▨	▨	▨	**−0.015**	**0.010**
6						0.028	0.028							▨	▨	▨	▨	−0.012	−0.032
South Luangwa																			
1						**0.055**	**0.063**			▨	▨	▨	▨	▨	▨	▨	▨	**−0.014**	**−0.009**
3						0.026	0.026			▨	▨	▨	▨	▨	▨	▨	▨	0.005	−0.020
5						0.058	0.029			▨	▨	▨	▨	▨	▨	▨	▨	**0.008**	**0.019**
Dry season																			
Etosha																			
3		▨	▨	▨	▨	▨	▨	▨	▨			**0.006**	**0.018**[a]			▨	▨	▨	▨
5		▨	▨	▨	▨	▨	▨	▨	▨			**0.009**	**0.025**[a]	0.005	−0.014	▨	▨	▨	▨
6		▨	▨	▨	▨	▨	▨	▨	▨			0.002	0.001	−0.013	−0.020	▨	▨	▨	▨
Khaudum																			
4	Dry savannas	▨	▨	▨	▨	▨	▨	**−0.009**	**−0.004**	0.001	−0.008			▨	▨	▨	▨	▨	▨
5	0.38	▨	▨	▨	▨	▨	▨			0.004	0.002	**−0.010**	**−0.001**	▨	▨	▨	▨	▨	▨
6		▨	▨	▨	▨	▨	▨			0.001	0.000			▨	▨	▨	▨	▨	▨

Table 5. Continued.

Study site and elephant code	Proportion of cases	Tree canopy cover >40%. Canopy height >5 m		Tree canopy cover between 15% and 40%. Canopy height >5 m		Shrub canopy cover >15%. Canopy height <5 m. Sparse tree layer <15%		Shrub canopy cover >15%. Canopy height <5 m. No tree layer		Tree and shrub canopy cover <20 %. Herbaceous cover >40%		Shrub canopy cover <20%. Herbaceous cover between 15% and 40%		Herbaceous cover between 5% and 15% without shrub canopy		Swamp bushland and grassland		Areas where croplands were mixed with open vegetation	
		R	V	R	V	R	V	R	V	R	V	R	V	R	V	R	V	R	V
NG11																			
6		▨	▨					−0.020	−0.027			▨	▨	▨	▨	0.178	0.142	▨	▨
8		▨	▨					**−0.058**	**−0.042**			▨	▨	▨	▨	0.041	0.025	▨	▨
10		▨	▨					**−0.040**	**−0.034**			▨	▨	▨	▨	0.050	0.043	▨	▨
Kafue																			
1				0.010	−0.007	0.004	−0.002			▨	▨	▨	▨	▨	▨	▨	▨	**−0.014**	**−0.013**
3				**0.013**	**−0.002**[a]	−0.007	0.005			▨	▨	▨	▨	▨	▨	▨	▨		
8						**0.005**	**−0.023**[a]			▨	▨	▨	▨	▨	▨	▨	▨	0.010	0.012
Lower Zambezi																			
1	Wet savannas	0.055	0.040			**−0.022**	**−0.006**[a]							▨	▨	▨	▨		
3	0.43			0.019	0.026	**−0.005**	**0.017**[a]			**−0.053**	**−0.024**[a]			▨	▨	▨	▨	−0.002	−0.012
6						0.023	0.026							▨	▨	▨	▨	−0.006	−0.018
South Luangwa																			
1		▨	▨	▨	▨			−0.012	−0.014	▨	▨	▨	▨	▨	▨	▨	▨	0.002	0.001
3		▨	▨	▨	▨	0.027	0.018			▨	▨	▨	▨	▨	▨	▨	▨	**0.006**	**0.012**
5		▨	▨	▨	▨	−0.001	−0.010			▨	▨	▨	▨	▨	▨	▨	▨	**−0.008**	**0.004**

Values are the mean residual maximum NDVI of visited (V) and an equal number of randomly selected grid cells (R) within structural vegetation classes defined by Mayaux *et al.* (2003), for each elephant. Values in bold show where NDVI of visited grid cells are higher than that of randomly selected grid cells.

[a] Indicates where differences are significant using a one-tailed *t*-test ($P<0.05$). Grey shading indicates an absence of that structural vegetation class in all elephant locations for that study site. We also show the proportion of cases for dry and for wet savanna study sites where the mean residual NDVI of visited grid cells within land cover classes was higher than that for randomly selected grid cells.

NDVI, normalized difference vegetation index.

while repeated visits from the dry to the wet season decreased within increasing stability of vegetation productivity. Because herbaceous cover that predominated in the dry savanna sites is typically more temporally variable than woody vegetation (see Geerken *et al.*, 2005; van Bommel *et al.*, 2006), elephants living in wet savannas may simply have more opportunity to return to known stable sources of food and water than elephants living in dry savannas. In direct contrast, the decrease in proportion of repeated visits from the dry to the wet season with increasing stability may reflect changes in elephant seasonal preferences and their associated movements from dry-season woody food sources to areas of wet-season grasses (O'Connor *et al.*, 2007). In this case, dry savanna elephants may simply be presented with more choice than wet savanna elephants when water is not limited during the wet season. The low variability observed in the spatial stability of vegetation productivity from the dry to the wet season within wet savanna study sites in comparison to that in dry savanna study sites supports our interpretation. Furthermore, elephants in Etosha and Khaudum (dry savannas) were located on grid cells with higher residual vegetation productivity than randomly selected grid cells where herbaceous cover exceeded 15% in nine of 11 cases during the wet season. In contrast, wet savanna elephants appeared to show little selection for places of higher relative NDVI in any one of the structural vegetation classes during the wet season.

We note that our study did not allow us to consider range overlap between elephants as a measure of spatial use intensity. Such occurrences may amplify impacts where they occur. Furthermore, we were unable to consider the influence of elephant densities on the relationship between elephant spatial use and vegetation productivity. Such consideration may further explain elephant spatial use in relation to water and food resources (e.g. Chamaillé-Jammes *et al.*, 2008). Finally, we stress that we only considered the spatial use patterns of elephant cows as an indication of the movements of family units in this study. Intensity of space use through time of elephant bulls is likely to be dissimilar to that of family units and should also be considered.

Nevertheless, our study showed that the intensity of range utilization in space and through time differed between wet and dry savanna types. In the wet season, these differences could be assigned to differences in vegetation productivity between wet and dry savannas. In the dry season, the influence of vegetation productivity on elephant spatial use differed according to vegetation structure. Differences in the influence of vegetation productivity within different vegetation structural classes is also suggested as explanation for differences in repeated visits between wet and dry savannas. All of these findings may explain the different impacts that elephants have on woody vegetation among sites (see Guldemond & van Aarde, 2008). Elephants contribute to the persistence of woodland and grassland mosaics in savanna systems (Sankaran *et al.*, 2008). Because differences in vegetation structure between wet and dry savanna sites seemed to alter the seasonal influence of vegetation productivity on elephant spatial use during the dry season and between seasons, the intensity of impacts on woody vegetation noted for dry savannas may not be readily extrapolated to wet savannas (see Guldemond & van Aarde, 2008). Differences in elephant spatial use patterns between wet and dry savannas therefore need to be accounted for in the development of site-specific objectives and management approaches for African elephants.

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