Chapter 5

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Range constriction and landscape use of elephants in Maputaland, southern Africa

R.A.R. Guldemond & R.J. van Aarde*

Abstract

We investigated the effects of confinement for spatial and landscape use by elephants in Maputaland. We constructed 95% minimum convex polygons home range areas and used compositional analysis to determine landscape selection. Elephants in southern Mozambique roam freely while those in Tembe Elephant Park are confined. Free-ranging individuals had larger home ranges than those confined by fences. Free-ranging elephants show preference for closed woodlands. Confined elephants show no clear landscape selection, besides avoiding reed beds during the dry season. Home range sizes of elephants in Tembe Elephant Park are not significantly smaller than those predicted by rainfall, based on elephants studied across southern Africa. However, confined elephants have smaller home ranges than free ranging ones. At the same time, providing artificial water may change landscape selection patterns. Park management should reconsider reinstating elephant space use by removing fences and artificial water.

Keywords: artificial water, fences, Maputo Elephant Reserve, rainfall, reed beds, sand forests, Tembe Elephant Park, woodlands.

Introduction

African elephants are generalists and occupy landscapes ranging from semi-deserts to forests (see Blanc *et al*., 2003). Local space use patterns also vary (e.g. Douglas-Hamilton, 1973; Viljoen, 1989). Factors including rainfall (Leuthold & Sale, 1973; Western & Lindsay, 1984; Thouless, 1996; Verlinden & Gavor, 1998), resource distribution (Jachmann, 1983; Osborn, 2003), social interactions (de Villiers & Kok, 1991; Wittemeyer, Douglas-Hamilton & Getz, 2005; Charif *et al*., 2005), site-specific differences in the behaviours of bulls and breeding herds (Leuthold & Sale, 1973; Viljoen, 1989) and landscape heterogeneity (Grainger, van Aarde & Whyte, in press) may all influence landscape use. Artificial disturbances such as human induced compression of elephants into "disturbance free-space" (Lamprey *et al*., 1967; Western & Lindsay, 1984), illegal activities (Jachmann, 1983; Western & Lindsay, 1984) and culling (van Aarde, Whyte & Pimm, 1999) may further influence local space and landscape use.

The development of conservation areas across the distributional range of elephants often limits them to fenced areas. Relatively high human densities around unfenced conservation areas may also restrict movements (Hoare, 1999; Hoare & du Toit, 1999; O'Connell-Rodwell *et al*., 2000). Such restrictions may reduce home ranges, and could thereby intensify the impact that elephants have on vegetation. Few opportunities exist to test this generalisation. Free-ranging and confined elephants living in Maputaland, however, provide for such an opportunity.

Maputaland's elephant population was recently fragmented into two sub-populations. Here, elephants in Tembe Elephant Park are fenced into an area covering 300 km^2. Other elephants in the region roam freely across an area of about 1500 km^2 within Maputo Elephant Reserve and the Futi River Corridor in southern

Mozambique. In this study, we compare home ranges for neighbouring elephants living under these contrasting conditions, but in the same landscapes. We relate our observations to published and unpublished records for elephants across southern Africa. We test the hypothesis that rainfall, rather than constriction explains variation in home range area in elephants. Should confinement influence ranging behaviour we expect that the home ranges of confined elephants to differ from those of free-ranging elephants exposed to similar rainfall conditions.

Materials and methods

The study site

The Tembe Elephant Park (TEP) (27º01'S 32º24'E) is situated in the northern KwaZulu-Natal Province (South Africa) and Maputo Elephant Reserve (MER) (26°25'S, 32°45'E) and Futi River Corridor (FC) in southern Mozambique. Geographically, the FC (~700km^2) connects the TEP (300km^2) and MER (800 km^2) and is now protected by limiting the number of people living here (Soto, Munthali & Breen, 2002). Elephants move freely through the unfenced MER and FC. An electrified elephant-proof fence, situated along the international border between South Africa and Mozambique, separates TEP from FC and MER (Sandwith, 1997). Some 204 elephants live in southern Mozambique, while 179 are presently confined to the TEP (Morley, 2005).

Mean (±SD) annual rainfall, from July to June for southern Mozambique (measured at Changalane from 1980 to 2002) is 757 ± 226 mm. This is similar to the 718 ± 371 mm recorded for TEP (measured at Sihangwane from 1959 to 2002). The cumulative surplus/deficit trends in rainfall (Dunham, Robertson & Grant, 2004) and the duration of the wet and dry seasons are also similar across these areas (Figs. 5.1a

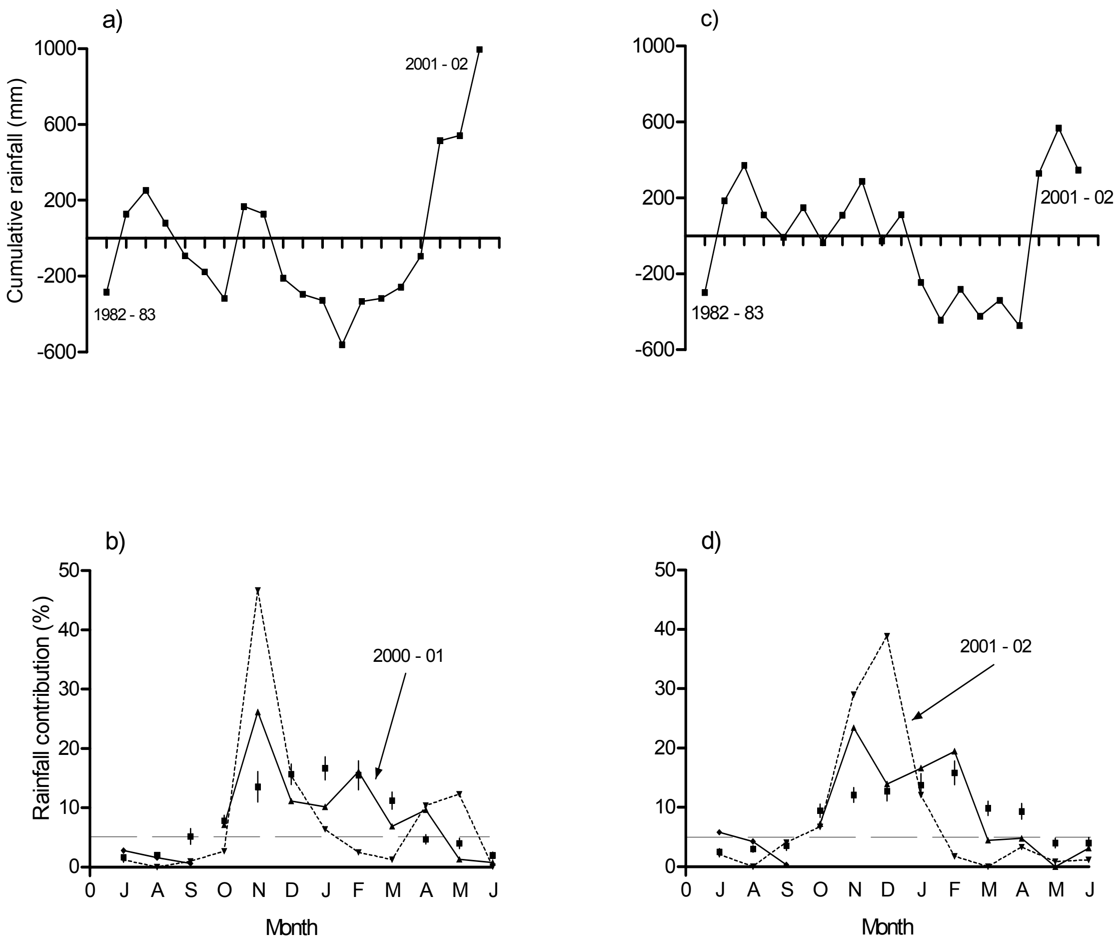

Figure 5.1. The MER & FC (a) and TEP (c) received higher than average rainfall during the study period as shown by the cumulative deficit/surplus rainfall patterns for the respective areas. We define dry seasons by the months contributing less than 5 % of the annual total for (b) MER & FC and (d) TEP. The solid (2000–01) and dotted (2001–02) lines track the monthly rainfall for the study duration. The square blocks and lines indicate the mean (± SE) percentage rainfall typical for each month and the horizontal dashed line indicate the 5% cut-off percentage in monthly rainfall contribution defining the wet and dry seasons (see text for details).

& c). We define wet and dry based on the percentage contribution of monthly rainfall to the mean annual rainfall. Each dry season month contributed less than 5 % to the annual rainfall. Subsequently, we deemed May to September as the dry season months, while the wet season months of October to April accounted for > 80 % of the annual rainfall (Figs. 5.1b & d).

A supervised vegetation classification using ERDAS IMAGINE 8.7 software (Leica Geosystems GIS & Mapping LLC, Illinois) of Maputaland provided information on the dominant landscape types for the study area (Harris *et al*. in review, using a cloud free partial scene ID 167-79 of 30 August 1999*). We grouped landscapes into forests (combining sand, swamp and coastal dune forests), closed woodlands, open woodlands and reed beds (Kappa statistic = 80%). The relative sizes of the landscapes between southern Mozambique and TEP are similar with forests contributing 31% vs. 33%, closed woodlands 37% vs. 44%, open woodlands 30% vs. 23% and reed beds 3% vs. < 1% respectively.

Sampling design

The study period from October 2000 to September 2002 provided information on the locations of elephants that roamed across the area for two wet and dry seasons. Here nine elephants were fitted with satellite collars (ST–14 Platform Transmitters Terminal, Telonics, Arizona, USA). These included one bull and three cows in TEP and three bulls and two cows in southern Mozambique. The collar on the bull in TEP failed after one year, and one of the bulls collared in southern Mozambique did not record information during the 2002 (second) dry season. All transmitters were active

* "In all sites, we took GPS points demarcating vegetation and vegetation transitions. Many of these points trained our signatures for vegetation mapping, using supervised classification techniques with maximum likelihood decision rules. Each vegetation map was smoothed with a 3X3 majority filter to remove pixel scatter, and received validation via a kappa statistic" (from Harris *et al.* in review).

for 24 hours and inactive for 48 hours thereby providing at least one location each third day. Location accuracy ranged from 0–350m (class 2 & 3 accuracy; Argos, 2000). The number of locations of each elephant for each season are summarised in Table 5.1.

We used computerised databases, the African Elephant Bibliography (http://www.elephant.chebucto.net) and hand searches through references lists (cited in this chapter's reference list) to find studies with home range estimates for elephants bounded between the 10º and 28º latitudes south of the equator. We excluded data for forest elephants (*Loxodonta cyclotis* Matchie, 1900) and those occurring in the hybrid zone delineated by Roca, Georgiades & O'Brien (2004). Data on elephant locations currently collected by CERU across southern Africa, supplemented the information of the collated studies (Jackson & Erasmus, unpublished report). We also documented rainfall and whether elephants' movements were constrained by fences and/ or through the provision of artificial waterholes.

Data analyses

We calculated seasonal home ranges for each elephant as the 95 % minimum convex polygon (MCP; see White & Garrott, 1990) using Ranges 6 v1.2 software (Kenward, South & Walls, 2003). The number of locations per individual may influence estimates of the home ranges (Girard *et al*., 2002) and we tested for stabilisation of these with incremental analysis (Kenward *et al*., 2003).

Spatial and temporal autocorrelation (Swihart & Slade, 1985) may bias the interpretation of elephant home range and landscape preference. Autocorrelation is analogous to pseudoreplication, which implies that replicates used in inferential statistics are dependent (Hurlbert, 1984). Here, the position of an animal at time $t + \Delta t$

Table 5.1. Number of locations (class 2 and 3; with 0–350m accuracy) for the collared elephants in each season in Tembe Elephant Park and southern Mozambique. The values in brackets are the respective Schoener ratios measuring the serial autocorrelation of the location data.

	Wet season 1	Dry season 1	Wet season 2	Dry season 2
Tembe Elephant Park				
Bull	320 (0.31)	132 (0.20)		
Breeding herds	270 (0.26)	195 (0.29)	181 (0.34)	316 (0.42)
Breeding herds	288 (0.31)	212 (0.34)	196 (0.37)	355 (0.34)
Breeding herds	153 (0.63)	100 (0.32)	86 (0.82)	165 (0.46)
Southern Mozambique				
Bull	203 (0.08)	186 (0.03)	162 (0.09)	48 (0.38)
Bull	209 (0.13)	164 (0.04)	156 (0.41)	259 (0.18)
Bull	118 (0.46)	96 (0.13)	109 (0.30)	264 (0.05)
Breeding herds	145 (0.27)	105 (0.45)	71 (0.14)	231 (0.26)
Breeding herds	247 (0.19)	192 (0.26)	185 (0.27)	308 (0.21)

is dependent of its position at time *t*, so that we can predict an animals position based on its previous position. We assessed the level of autocorrelation of the location data with the Schoener's ratio, following Swihart & Slade (1985). When the ratio is < 2, the location data are serially autocorrelated (Swihart & Slade, 1985).

We used the compositional method (Aebischer, Robertson & Kenward, 1993) to analyse seasonal second and third order (see Johnson 1980 for a detailed description of terminology) landscape selection. Second order selection relates the proportional use of landscape patches within each elephant's home range relative to its availability in the total elephant range. Third order selection reflects on the relative number of location points in each landscape patch within each elephant home range. We define availability as the proportional contribution of each landscape in the total elephant range. We replaced missing values (landscapes with zero values) with 0.001, which is one order of magnitude lower than the lowest proportional value in the usage of landscapes (following Aebischer *et al*., 1993).

The studies we collated used one of three approaches to estimate home range sizes. These included individual recognition (mark-recapture methods), VHF radio and satellite/ GPS based platforms (e.g. Leuthold, 1977; Dunham, 1985; Douglas-Hamilton, 1998). These methods reported 3 to 1051 locations per individual elephant over periods ranging from 3 to 24 months. We omitted estimates that used less than 30 location points (based on Seaman *et al*., 1999). We log_{10}–transformed all home ranges and rainfall data before analysis (Sokal & Rohlf, 1995) and distinguished between fenced and unfenced elephant populations.

Results

Our satellite-tracking database yielded a mean (±SD) of 189 ± 77.3 elephant locations per season for each individual in southern Mozambique and TEP. Mean seasonal home range area stabilised at 136 ± 65.9 locations and we consider our estimates robust. All the elephants in this study location data were serially autocorrelated, that is, the Schoener ratios for all the individuals range from 0.03 to 0.82 (Table 5.1).

Elephant bull(s) had larger home ranges than breeding herds in both TEP and southern Mozambique (Table 5.2). The dry season home ranges for both sites were also smaller than in the wet seasons but, with the exception of the elephant bull in TEP not as prominent, as documented elsewhere. Irrespective of season and sex of the elephant, home ranges in TEP, were at least three times smaller than for those elephants in southern Mozambique.

Table 5.3 compares the second and third order selection of the elephants in our study. During our study, elephants in southern Mozambique used closed woodlands more than expected relative to its availability. These elephants did not show any preference for reed beds, open woodlands and sand forests. However, if we compare the relative number of locations of elephants in their respective home ranges, sand forests ranked first, non-significantly in the wet and significantly in the dry seasons. Again, the number of locations in the rest of the landscapes was relative to their availability within the elephants' home ranges.

The overall pattern in elephants' landscape use in TEP is less clear. Only in the wet seasons, did closed and open woodlands rank higher in their relative use than sand forests and reed beds. There is, however, no detectable difference between the two woodland types, or between sand forests and reed beds. In the dry season, elephants did not use any landscape more than expected by its availability. However,

Table 5.2. Mean (±SD) seasonal home ranges (km^2) calculated with 95% Minimum Convex Polygon for breeding herds and bulls in Tembe Elephant Park and southern Mozambique for the wet and dry seasons. (*n* represents the number of individuals).

		Tembe Elephant Park	Southern Mozambique
Herds	Wet seasons	139.3 ± 79.2 (*n* = 3)	353.9 ± 104.2 (*n* = 2)
	Dry seasons	80.0 ± 9.5 (*n* = 3)	253.7 ± 109.3 (*n* = 2)
Bull(s)	Wet seasons	295.7 (*n* = 1)	716.9 ± 327.6 (*n* = 3)
	Dry seasons	139.6 (*n* = 1)	639.3 ± 223.5 (*n* = 3)

Table 5.3. Hierarchical second (a) and third (b) order landscape selection for elephants in (i) Tembe Elephant Park and (ii) southern Mozambique. (SF = Sand forest, CW = Closed woodland, OW = Open woodland and RB = Reed beds).

	(i) Tembe Elephant Park	(ii) Southern Mozambique
(a) Second order landscape selection		
Wet seasons	CW = OW >>> SF > RB	CW >>> RB > OW > SF
Dry seasons	SF > RB > CW > OW	CW >>> RB > OW > SF
(b) Third order landscape selection		
Wet seasons	SF > OW > CW > RB	SF > RB > CW > OW
Dry seasons	OW > CW > SF >>> RB	SF >>> RB > CW > OW

= Equal preference, > NS preference ($P>0.05$), >>> Significant preference ($P<0.05$)

when we compare number of location points relative to landscape availability within their respective home ranges, elephants used the reed beds significantly less in the dry season. Finally, in the wet season, elephants used the landscapes relative to their contribution within the individual home ranges.

We collated sufficient information on elephant home ranges from ten studies that yielded data on home range areas for 93 individuals across southern Africa. The CERU database provided information on a further 52 and this study nine elephants. Mean annual rainfall between the sites ranged from less than 100 up to 1200 $mm.a^{-1}$. Elephant home range decreased significantly with an increase in mean annual rainfall ($F_{1,151}$ = 112.08; P < 0.0001; r^2 = 0.43) (Fig. 5.2), with no significant difference between fenced and unfenced study areas ($F_{1,151}$ = 0.44; P = 0.51).

Discussion

The elephant population in Maputaland functioned as a singular entity before its fragmentation by the fences erected around Tembe Elephant Park between 1983 and 1989. The electrified elephant-proof fence that spans the Mozambique-South Africa border effectively divided the population into two fragments. The elephants in southern Mozambique remained unfenced and could therefore roam freely. The scenario here is very similar to that elsewhere across sub-Saharan Africa, where electric fences restrict the movements of elephants (Addo Elephant National Park, Kruger National Park). High densities of people may also hinder free passage (e.g. Hoare & du Toit, 1999; O'Connell-Rodwell *et al*., 2000). Restriction conceivably may reduce home range sizes, thereby increasing the intensity of landscape utilisation and the apparent impact of elephants. Home ranges, however, are known to be influenced by elephants' social interactions, landscape heterogeneity and rainfall (e.g.

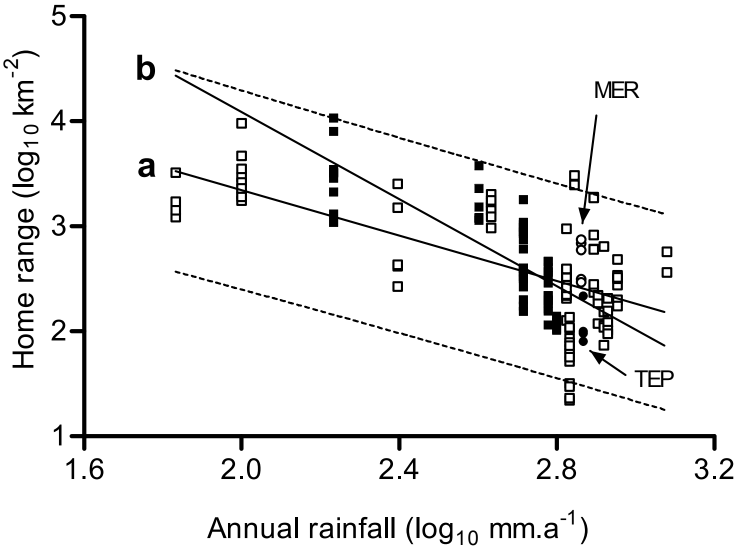

Figure 5.2. Elephant home ranges decrease significantly with an increase in mean annual rainfall for both the unfenced (open squares/ line marked **a**) and fenced (filled squares/ line marked **b**) elephant populations. Arrows indicate the home range sizes of elephants in southern Mozambique (closed circles) and Tembe Elephant Park (open circles). Regression lines are only for illustrative purposes and the dashed lines indicate the 95% confidence interval for the unfenced elephant populations.

Verlinden & Gavor, 1998; Charif *et al*., 2005; Grainger *et al*., in press). Our study across Maputaland, where the rainfall is similar, excludes such influences. With a component of the elephant population restricted by fences, while the other roamed freely, we had an opportunity to assess the influence of restriction on range use. By addressing the apparent impact of confinement in view of the relevance of rainfall variation elsewhere across southern Africa, we could further assess the consequences of restriction on home range use.

The importance of location data being autocorrelated attracts a large amount of attention in the ecological literature (*e.g.* Schoener, 1981; Swihart & Slade, 1985; Legendre, 1993; Hansteen, Andreassen & Ims, 1997; Rooney, Wolfe & Hayden, 1998; de Solla, Bonduriansky & Brooks, 1999). This debate divides between statistical (Schoener, 1981; Swihart & Slade, 1985) and biological relevance (Rooney *et al*., 1998; de Solla *et al*., 1999) of spatial and temporal autocorrelation. Statisticians suggest sub-sampling the data by increasing the time-period between location points until achieving independence – known as time to independence (TTI) (Swihart & Slade, 1985). However, de Solla *et al*., (1999) argue that such a destructive sub-sampling scheme reduces significant biological relevance. They base their argument on the infrequent sampling procedures, such as 'bursts' of location points with variable time-periods between sampling occasions. We obtained our elephant location data systematically at regular time intervals (Rooney *et al*., 1998; de Solla *et al*., 1999). Besides Cushman, Chase & Griffin (2005), no previous study on elephant space or landscape use incorporated the influence of autocorrelation in interpreting their results. Increasing the time-periods between location points in their study did not decrease autocorrelation (Cushman *et al*., 2005). They did show, however, that the complex pattern of elephants' space use behaviour is linked to the onset of regional rainfall. This example highlights the biological relevance of autocorrelated data (see de Solla *et al*., 1999).

Elephants confined to the TEP have smaller home ranges than those roaming freely across southern Mozambique. This was irrespective of sex and season, or despite the similar rainfall patterns between sites during our study. For example, breeding herds in southern Mozambique had home ranges comparable to the total size of TEP, whereas those in the Park only used a third of the area available to them. This is the same as elephants living elsewhere under similar conditions, such as in Addo Elephant National Park (103 km^2) and Pilanesberg National Parks (500 km^2), where elephants use between 10-50% of the available area (Whitehouse & Schoeman, 2003; Slotow & van Dyk, 2004). However, home ranges of elephants in southern Mozambique for this study are also three times larger than a previous assessment for elephants in this population (Ntumi *et al*., in press). Both studies used satellite technology and the 95% MCP in calculating home ranges, using a similar delineation of seasons and rainfall. Sample sizes (number of individuals collared) for both studies are low, and differences may reflect normal variation in elephants' home range in southern Mozambique. From this we may conclude that the home ranges of elephants not constricted by fences in Maputaland vary more than confined elephants.

Landscape selection by elephants in Maputaland confirms their general widespread and catholic requirements. Elephants in southern Mozambique use reed beds and closed woodlands more than expected by their availability alone, with the rest of the landscapes used non-selectively throughout the year. Our results differ from de Boer *et al*. (2000) and Ntumi *et al*. (in press), both whom indicated sand forests and the Futi flood plains to be the preferred landscapes for elephants in southern Mozambique. However, de Boer *et al*. (2000) and Ntumi *et al*. (in press) only differentiate between forests and open woodland, with closed woodlands incorporated into the sand forests. Their observation that elephants prefer sand forests therefore may principally be due to them attending to closed woodlands or forests other than sand forests.

In spite of the similarities between the study conditions, i.e. the spatial extent (area of coverage), studies differed in formulating the landscape information (Lillesand & Kiefer, 2000). In their preference assessment, both de Boer *et al*. (2000) and Ntumi *et al*. (in press) relied on maps where polygons, rather than raster data, defined the landscape units onto which they placed the elephants' locations. These homogenous units have a lower spatial resolution and contain inherently less information (Lillesand & Kiefer, 2000). Here, the 'user defined decision rules' (Lillesand & Kiefer, 2000) applied after landscape classification may cause small patches of a particular landscape, often important to an elephant to be masked by the dominant single landscape type of the area (Lillesand & Kiefer, 2000). Maputaland is very heterogeneous at the finest landscape resolution and using raster data (at the 25 X 25 m pixel resolution), we managed to retain this regional heterogeneity. We therefore consider our landscape preference analysis of elephants for this region to be more robust.

The confinement of elephants to TEP changes the proportional availability of landscapes in Maputaland to them, and the provision of water may further disrupt their selection patterns. Surface water in southern Mozambique is not a limiting factor, and management does not provide artificial water. Elephants in southern Mozambique were consistent in their landscape selection patterns throughout the study period. This is in contrast to TEP, where the landscape selection of elephants is less clear. In fact, our results only indicate elephants to avoid reed beds during the dry season. Reed beds in the Muzi swamps in TEP are associated with natural surface water. Elephants are water dependent (Sukumar, 2003), and their avoidance of these areas during the dry season is against expectations. This may be a response on the provision of artificial water that characterised TEP during our study period.

Home range areas of elephants decreased with an increase in mean annual rainfall. Our results agree with Osborn (2004) and Sukumar (2003)), who related the home ranges of males and females separately with rainfall. Rainfall may not be the sole variable that elephants respond to, since rainfall is positively related with primary productivity and herbivore biomass in savanna systems (e.g. Phillipson, 1975; Coe, Cumming & Phillipson, 1976; Bell, 1982; East, 1984; Fritz & Duncan, 1994; Fritz *et al*., 2002). Consequently, primary productivity rather than rainfall may be a determinant of elephant home range size.

From our results, constricting elephants, such as in TEP, did not significantly influence the home range sizes along the rainfall gradient. However, our analysis has limitations, often associated with these quantitative assessments (Gates, 2002). More studies reported on range use of elephants in the mesic than arid and sub-tropical regions. The rainfall range against which we predicted enclosed elephants' space use was narrower than the free roaming populations. Another factor is that of estimating elephant home ranges using different sampling and statistical methods (e.g. White & Garrott, 1990). We excluded home range estimates of some 40 elephants due to insufficient sampling or statistical reporting. Often studies did not report on the study duration, sample size (both number of individuals and locations per individual), frequency of data acquisition, or partitioned between the sexes and seasons. These variables may influence the overall interpretation of elephants' space use patterns (e.g. Hall-Martin, 1987; Thouless, 1998).

The limitations mentioned above lead us to visually assess the rainfall-home range relationships. Home ranges areas for elephants confined by fences in arid regions appear to be larger than the free roaming populations. The opposite is true in the mesic regions, which induce a steeper decline in the slope in this relationship. Again, the systematic placement of waterholes in confined areas may explain this, since we know that these influence range use (see Grainger *et al*., in press). Artificial waterholes in the drier regions may provide opportunity for elephants to expand their home ranges as resources deteriorate. It may also allow elephants in mesic regions to remain in areas beyond which may be permitted by primary production. Both cases allow elephants to use areas for extended periods, and not give vegetation the opportunity to recover from impact induced by elephants.

We conclude that fences and the artificial provision of water may disrupt space utilization and landscape preference of elephants in TEP. However, home ranges sizes are within the expected variation allowed for by rainfall. Elephants in southern Mozambique have however, higher variation in space utilization that may negate the potential negative impact they have on vegetation.

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