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Fences and artificial water affect African savannah elephant movement patterns

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ABSTRACT

The IUCN Redlist considers the African savannah elephant (*Loxodonta africana*) to be "vulnerable" despite it numbering in the 100,000s and having a large geographical range. This seeming paradox stems from how quickly human persecution can eliminate elephants across large areas and how quickly elephant numbers can increase when protected. Much elephant research concentrates on the extent and consequences of elephant persecution. Where elephants thrive, two other human interventions, the provision of artificial water and the construction of fences may have large, and perhaps unintended, impacts on elephant behavior. In general, successful management requires that we understand elephant movements and land-use choices across large areas and long periods. Here, we ask specifically how artificial water and fences might affect these movements. To do this, we first characterize how elephants move in different seasons and landscape types, in different years, and how these patterns change over a region that varies considerably in annual rainfall. We fitted 73 elephants with GPS collars across a large rainfall gradient spanning seven southern African countries over a period of 6 years. We analyzed remotely-sensed environmental data from four satellite borne sensors that measure daily rainfall, weekly temperature, bi-monthly greenness, and summarise human infrastructure. Elephants move approximately 6 km/day in dry landscapes, down to approximately 3 km/day in the wettest ones. Strong seasonal differences modulate geographic differences. Elephants move less, cover less area, and are more faithful to landscapes across years in the dry season than the wet. Water availability drives these seasonal patterns. Seasonal differences in the area covered are less pronounced in wet landscapes where permanent water is more dispersed. Within-day movements reveal that elephants are consistently crepuscular but more active at night than midday when temperatures are high. Direction-changes are centered at midnight when elephants are close to water indicating regular nighttime treks to water. By design, our analyses seek to find general patterns of elephant movements — something that one can achieve only across a large range of locations and ecological conditions — in order to understand the impact of human interventions. We show that both interventions reduce seasonal differences in elephant ranging patterns and increase local impacts of elephants on the vegetation. Artificial water sources allow more extensive dry season ranging, allowing elephants to use — and potentially overexploit — vegetation in areas that would have be otherwise inaccessible to them except in the wet season. Fences cause elephants to "bunch-up" against them during the wet season, again locally increasing the pressure elephants put on their resources.

1. Introduction

We seek effective conservation and management strategies for the African savannah elephant (*Loxodonta africana*, hereafter "elephant") (van Aarde and Jackson, 2007), a species exterminated from much of its large geographical range (Barnes et al., 1999), yet paradoxically sometimes considered too abundant elsewhere (Whyte, 2001). The IUCN Redlist considers this elephant to be "vulnerable" despite it numbering in the 100,000s and having a large geographical range (Blanc et al. 2007; IUCN, 2007). Much elephant research concentrates on the extent and consequences of elephant persecution. Where elephants thrive, successful management requires understanding their movements and land-use choices across large areas and long periods. In such places, two other human interventions, the provision of 'artificial water' and the construction of fences, may have large and perhaps unintended impacts on elephant numbers and behavior. By 'artificial water', we mean water supplies made accessible through boreholes. This study explores the relationship between fences, water and seasonal and within-day movement patterns across diverse landscapes.

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Across the elephant's range, the climate of woodlands and savannahs vary both geographically and seasonally (Sankaran et al., 2005). Water and food resources are patchy, both spatially and temporally. To survive, elephants must move large distances to specific places at specific times (Cushman et al., 2005). One might expect behavior to vary greatly geographically, so there is a critical need to document and compare elephant movements over appropriately large areas. We gathered telemetry data from 73 elephants distributed across seven southern African countries. Data were collected from four satellite borne sensors to remotely sense precipitation, temperature, Enhanced Vegetation Index (a measure of green vegetation), and permanent water across this remote and largely inaccessible landscape. We characterize elephant movements seasonally. We compare their daily movements, the area they explore over 45 days, the degree to which they make repeat visits to the same place each year, and how movements from the same elephant differ from year-to-year. We also characterize within-day movements and explore the relationship between elephant ranging patterns and surface water.

Armed with these baseline data, we then ask whether the two major human interventions to the landscape — artificial water and fences — modify elephant movements and landscape choices and, if they do, what are the conservation implications. Fences are a major factor constraining ungulate movement in African savannahs (Grant et al., 2007; Ogutu and Owen-Smith, 2003), but the areas we consider are very large. Similarly, while some of the areas we discuss provide additional water (Chamaille-Jammes et al., 2007; Smit et al., 2007a,b; Harris et al., 2008), such sources may simply supplement existing natural sources and have no major impact. In fact, we will find that these two interventions have major impacts on elephant behaviour and, as a consequence, they likely impact the areas that elephants occupy.

2. Materials and methods

2.1. Study area

Our study area is a large "T" stretching 2500 km across southern Africa eastward from the hot, arid deserts of Namibia, over the Zambezi watershed, and into the cool moist mountains of Malawi (Fig. 1). The bottom of the "T" grades into the sand forests of South Africa and Mozambique on the edge of the Indian Ocean. The gridded map behind Fig. 1 is a Tropical Rainfall Monitoring Mission satellite average of total annual precipitation from the 6 years of the study (see methods). The reddest areas receive <5 cm rain annually, while the bluest areas receive nearly 2 m annually.

For simplicity, we call this collection of ecosystems "savannahs," except when we need to distinguish particular habitats. We note that they range from dry forests, with a closed canopy and some trees losing their leaves seasonally, through seasonal woodlands (with open canopies), to areas that bushes dominate, to open habitats with few trees. We will notice difference in rainfall, and refer to "dry" and "wet" savannahs, as do Sankaran et al. (2005) and adopt their 65 cm threshold for distinguishing the two. Within this landscape we gathered data from 12 sites across seven countries. (See Supplementary materials for detailed maps of each site including fences, artificial water, and human settlements.)

The 12 sites also differ in the amount of anthropogenic disturbance, vegetation, geology and topography. These variables tended to be correlated with precipitation. Drier areas were generally flatter, more dominated by Kalahari sands, featured more drought tolerant vegetation, and sparser human settlement than wetter areas. We therefore use wet and dry savannahs as proxies for a suite of environmental variables that are highly correlated.

2.2. Data sources

We used data from two classes of information: the locations of elephants — "fixes" — and remotely-sensed data on temperature, rainfall, and landscape greenness. Different satellites provided the latter every few days, at most, and often daily. In addition, we used selected Landsat images with extensive ground-truthing to locate fences, agricultural fields, and permanent water.

2.3. Elephant collaring

We placed telemetry collars on elephants from 12 sites across seven countries (see Supplementary materials). Telonics (Mesa, Arizona, USA) built the first nine collars we used and employed the Argos system to obtain fixes and offload data. The Maputuland elephants carried these pilot collars. The remaining collars were GPS collars build by Africa Wildlife Tracking (Pretoria, South Africa) that uploaded the location data to geostationary satellites approximately daily. All elephant handling operations were conducted under permit from the relevant conservation organization and the animal ethics committee of the University of Pretoria (permit number AUCC-040611-013), and qualified wildlife veterinaries tranquilized the elephants.

Unlike the GPS collars, the Argos collars did not gather fixes at regular intervals. We therefore had to discard more fixes when calculating statistics such as distance travelled that necessitate standardized time intervals between fixes. Additionally, the Argos collars had greater location error than the GPS collars. To control for this, we excluded all fixes from the Argos collars with location errors greater than 350 m (as determined by the Argos error flags). The error in the remaining locations was less than the 250-m pixel size of most of the remotely-sensed imagery and much smaller than the average distance between adjacent fixes. The standard deviation of the fixes from the GPS collars was 50 m.

In Fig. 1, the black points are 71,370 individual elephant fixes from the 73 elephants. We collared from two elephants in the Nyika Plateau to 10 in Ngamiland and Kafue National Park (Fig. 1). Most of the collared elephants were cows and their spatial activities are proxies for those of the breeding herds of which they were members. We collared 14 bulls. We concentrated collaring efforts on females since they are more consistently associated with larger groups of individuals. On average, the locations of a female represent a larger mass of elephants on the landscape than the location of a male.

The GPS collar fix rates were set to collect one fix every eight or 24 h. In practice, numerous data gaps and periods of high frequency sampling made the fix rates much more complex. Experimental collar placement exercises revealed that these were not associated with habitat differences and were largely driven by technical problems with the collars and elephant behaviour such as throwing mud on the collar. The Maputuland elephants were collared in 2000. The Etosha National Park elephants were collared in 2002. All remaining elephants were collared between 2003 and 2005 except three elephants in South Lluangwa National Park collared in 2006. We tracked each elephant for an average of 654 days and 978 fixes. The standard deviations for the number of days tracked and number of fixes were 264 and 441, respectively. We excluded five elephants that had fewer than 250 fixes or were tracked for fewer than 250 days. The remaining 68 elephants were tracked for an average of 691 days and had an average of 1015 fixes. The majority of fixes were separated by 8 h followed by separations of 24 h. The mean separation was 15 h with a few larger intervals up to 685 h. By the end of the study, 16 collars were still providing data. To control for uneven fix rates, we used only those fixes separated by an hour for within-day analyses and 24 h for analyses of movements over longer times.

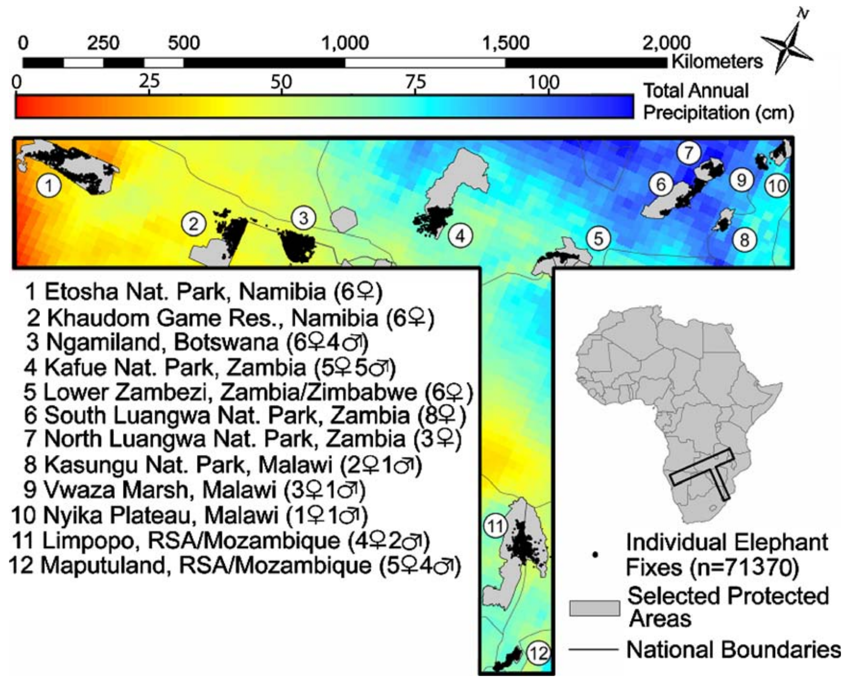

Fig. 1. The spatial extent of the study area. Black points indicate individual elephant fixes. Gray polygons represent selected protected areas. The background is remotely-sensed total annual precipitation ranging from low (red) to high (blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.4. Remotely-sensed data

2.4.1. Landsat

Landsat 7's sensor, the Enhanced Thematic Mapper (ETM+) supplied cloud-free images of our study area from the year 2000 plus or minus a few years (Tucker et al., 2004). We downloaded these images from the Global Land Cover Facility (glcf.umiacs.umd.edu). The spatial resolution of these images is 15 m for panchromatic and 30 m for colour.

We used these images to locate fences, fields, and permanent water. We define permanent water as water supplies that are available year-round, except in the most severely dry years. Over the years of this study, we visited each site several times to geo-reference examples of these features. Our field visits also ensured that permanent water features identified by single-date Landsat images were indeed permanent. We also identified some of the smaller sources of water (springs, etc.) and water under canopies that are not visible from satellite. Despite these precautions, we may have missed several sources of permanent water. We only identified fences large enough to be detectable on Landsat images. These fences tend to be accompanied by access roads on either side. In some cases these fences were electrified. But field visits revealed that electricity was inconsistently active along these electric fences, and fences were often poorly maintained and damaged. The fences were all erected more than 10 years ago.

2.4.2. MODIS vegetation index

The Moderate Resolution Imaging Spectrometer (MODIS) provides a 16-day summary of an Enhanced Vegetation Index, EVI, a measure of the greenness of the landscape (Pettorelli et al., 2005). Studies suggest EVI discriminates high biomass habitats (such as the woodland of our study areas) better than does the related Normalized Difference Vegetation Index (NDVI) (Huete et al., 2002). The spatial resolution of these images is 250 m. We compiled 158 of these images from February 2000 to January 2007. For each year, there are 23 composite images.

Each image has an associated mapping of data quality that, *inter alia*, indicates when clouds degrade the EVI quality. It ranges from 1 (maximum) to 15 (minimum). When each pixel has the maximum data quality — the great majority of the pixels in each image on any given date — we use its EVI. When the data quality is below maximum, we calculate a weighted average of the EVI for that pixel-date weighted against the pixel value for the same date in the other 6 years of the study. We weight each pixel-date with the inverse of the respective qualities.

2.4.3. MODIS temperature

MODIS also provides a Land Surface Temperature and Emissivity 8-day composite. It provides two measurements — the 8-day averages of temperature at approximately 10 AM and midnight. These maps also provide measures of data quality and we processed them in exactly the same way as for EVI.

2.4.4. TRMM rainfall

The Tropical Rainfall Monitoring Mission (TRMM) 3B42 product is merged with calibrated Infrared and other satellite measurements to estimate tropical rainfall every 3 h on a scale of 0.25° spatial resolution, (~28 km, for the areas we consider) (Kummerow et al.,1998). We sum these data to provide daily rainfall totals. The daily rainfall totals were summed to produce annual and monthly precipitation totals.

2.5. Within-day movements

To calculate the distance moved per hour, we required two observations within a short interval (Dai et al., 2007). A small subset of the fixes had times between 15 min to 105 min apart (1-h ±45 min). Such frequent sampling was deliberate, constrained by battery life, and done to assess within-day habitat choices of ambient temperatures for selected locations and seasons (Kinahan et al., 2007). For an elephant to qualify for our within-day analyses, it had to have a minimum of five such pairs of fixes for every one of

the 24, 1-h intervals in a day. Some 31 elephants met this criterion, and the average number of fixes for each hour was 18.

These fixes were concentrated in October and November in Khaudom, Kafue, and particularly Ngamiland — at the end of the dry season at these relatively dry sites — and in December at South Luangwa, North Luangwa, Kasungu, and Vwaza, the wet season at relatively wet sites. While November marks the transition out of the dry season, within-day movement data was unavailable earlier in the dry season. We therefore emphasize that these time periods define relatively drier and wetter conditions but may not necessarily be representative of the entire wet and dry seasons.

2.6. Movements over longer times

For the 68 elephants that had more than 250 fixes and were tracked for more than 250 days, we calculated movements over longer time periods. Four statistics were used to summarise elephant movements of a day or more. (1) We call the distance moved between fixes 24 ± 2 h apart, "displacement." (2) "Area" is the root-mean square displacement of all points in overlapping 45-day windows from their centroid — essentially the radius of movement. The interval is arbitrary, balancing the need for a sufficient sample of days and the need to follow seasonal changes. The units, in meters, are comparable with the previous measure. (3) We measure "fidelity" as distance from the centroid of elephant fixes over a 10-day interval to the centroid of elephant fixes over a 10-day interval a year later. Again, 10 days is arbitrary, but a small interval is required to avoid confounding with potential long distance movements over the long-term. We repeated the analysis with a 5-day interval and the results were similar. (4) We measure "path density" as how often elephants visit an area of fixed size within a season – that is, how densely does the elephant path overlap upon itself. All these measures are closely correlated, though individually they provide different perspectives on elephant movements.

2.7. Statistical analyses

A singular feature of our analysis is its geographical extent. Our objective is not to draw inferences about elephant movements at a particular location, but across many. We have the large sample sizes to allow this. For example, one might conclude that an elephant at one site moved more day-to-day in the dry season than in the wet season. Such inferences require a statistical model of that single elephant's movements, which is not a trivial task (Harris et al., 2008). In our case, we want to know about the typical behaviour of 68 elephants. If suffices to know whether each elephant moved more or less in the wet than in the dry season. Then, we employ a sign test. That is, (to anticipate our first result) we calculate the binomial probability of 53 elephants moving less in the dry season and 15 moving more, given the null expectation of equality. In this case, the excess of elephants moving less in the dry season is significantly different ($p < 0.0001$) from the expectation of the numbers being equal.

In other analyses, we likewise use the measure of an individual elephant as the basic datum and draw conclusions about ensemble patterns across elephants, not on individual elephants themselves. Here we use linear regressions to look for significant relationships with environmental variables such as rainfall. All statistical analyses were performed in R version 2.6.0.

To test our hypothesis that path density increases near fences, we quantify path densities across a landscape and first ask whether they differ seasonally, for we know that elephant movements differ markedly between wet and dry seasons. Then, for the wet season, we can ask whether the proximity to fences modifies path density. We chose 15 km as an *a priori* threshold to distinguish landscapes near fences. The threshold represents the average distance travelled in a few days and resulted in balanced sample pools of fixes near and away from fences. (In the dry season, elephants are closer to permanent water, which in our study sites are generally more than 15 km from fences.)

To calculate elephant path density, we created a 1 km^2 grid over each site. Within each grid cell, we counted the number of elephant fixes that occurred in a 45-day long window. Frequent fixes would inflate path density estimates, so we used fixes separated by a minimum of 22 h, i.e. just less than a day. Conversely, gaps in the data artificially decrease the path density, so we excluded all windows with gaps of 5 days or longer.

The distribution of elephant fixes within grid cells is likely to be a standard, sampling distribution, of which the Poisson process is the simplest. The Poisson has a single parameter, λ, that is normally estimated by the mean of all the outcomes — 0, 1, 2, etc. elephant fixes per grid cell, in our case. The problem is that the observed 0 outcomes are seriously inflated by cells where elephants are never likely to visit because of unsuitable habitat. An alternative estimate of λ comes from noticing that the expected number of observations of one per cell divided by two per cell is 2λ. Put simply, the 1-to-2 count quotient gives an estimate of path density (twice λ) using only observed cells.

For all 68 elephants, we calculated the 1-to-2 count quotient separately from the average of dry season and wet seasons. We used an ANCOVA to test whether season has an effect on the path density. We then chose the subset of all 35 elephants from six sites that had fences. 29 of these elephants spent part of their wet season <15 km from a fence. Thirty four of these elephants spent part of their wet season >15 km from a fence. We used ANCOVA to test whether being near or far from fences influenced the path density.

Throughout, we repeated all analyses excluding the small number of bulls. None of the results were significantly different, as is obvious from inspecting our figures. We caution that the small number of bulls prevents a formal comparison of bulls versus cows — only that including bulls does not alter our results.

A caveat: we used the same data to determine elephant movements across these landscapes — a process that assumes those movements are natural — as we did to examine the influence of artificial water and fences. Does this involve some kind of circularity? As we show in the results, the gradient in movement patterns across the landscape persists *despite* the present degree of modification; we can only assume that the gradient was stronger in a more natural state.

3. Results

3.1. Study sites

Each panel of Fig. 2 summarizes data from a single site. The red band encompasses daily temperature fluctuations. The top of the band is the 10 AM temperature averaged across all the pixels with one or more elephant fixes. The bottom of the band is the corresponding midnight temperature. Using only pixels with elephant fixes excludes lakes, steep slopes, large open pans (such as that at Etosha National Park) where temperatures may be exceptional. Rainfall events are in blue and the green lines show EVI; both again reflect only locations with elephant fixes.

The pale green vertical rectangles represent the extent of the wet season, which we define as the period in which 95% of annual precipitation occurs. Most of the sites have a long dry season. In Etosha, for example, most of the rain falls in only four months of the year. In contrast, the two sites influenced by the Indian Ocean (Limpopo and Maputuland) have only a couple of months without rain.

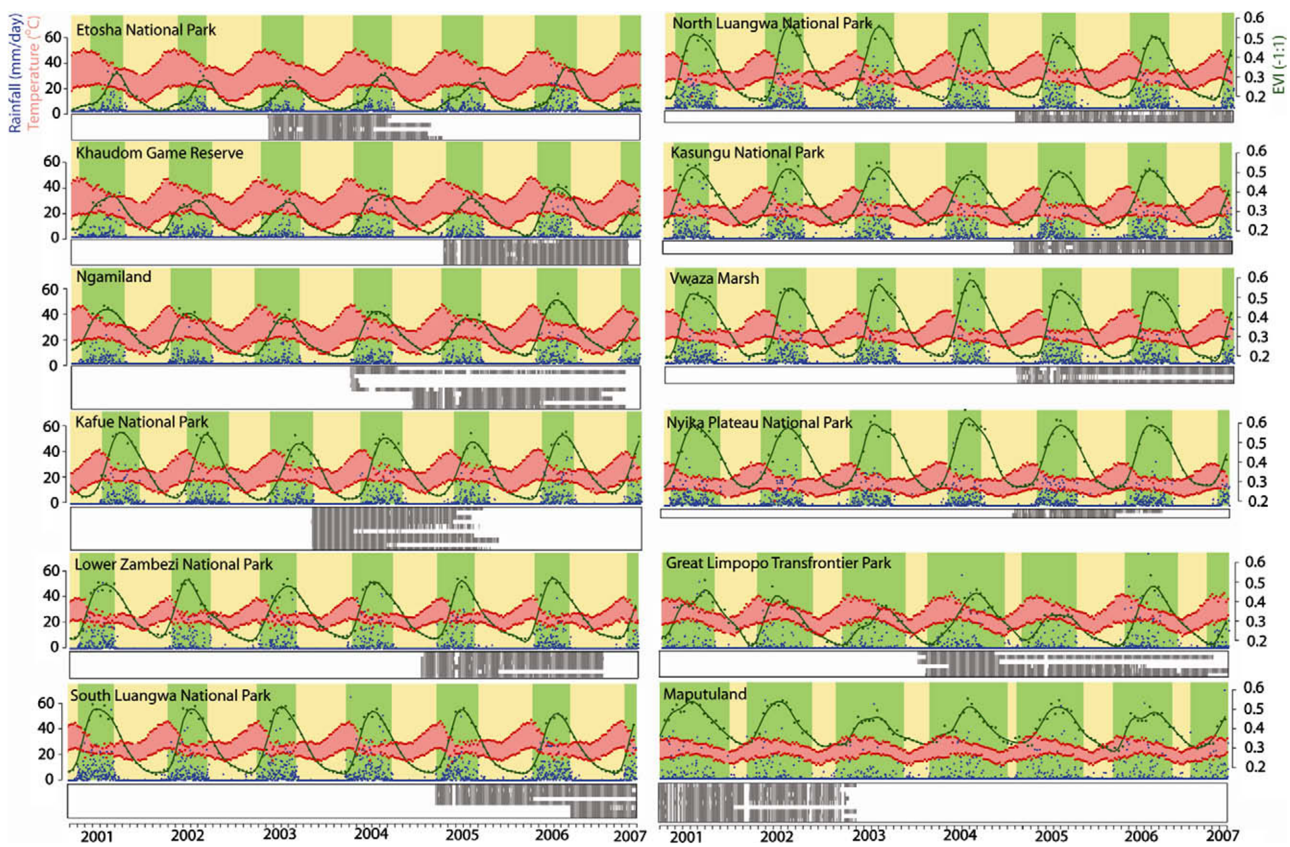

Fig. 2. Temporal trends in temperature, rainfall, and greenness across the study sites. The top graph of each panel has three features, temperature range (red band), EVI (green line), and rainfall (blue points). The green and orange rectangles delineate wet and dry seasons. The bottom graph of each panel shows the elephant fixes at each site where each row represents an elephant. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In Fig. 2, the black vertical lines near the bottom of each panel show the dates of each elephant fix at each site. Each row represents an individual elephant.

3.2. Representation of elephant movement

The basic representation of elephant movements consists of connecting fixes mapped onto a background of relevant ecological variables. To do this, we often colour-code the lines formed using the "colour" — EVI value — of the landscape over the interval on which the satellite measured it. We calculated those EVI values only across those pixels that have one or more elephant fixes.

Fig. 3 shows two examples of the paths of elephants from Ngamiland, Botswana – a relatively arid landscape — and Kasungu National Park, Malawi — a relatively moist landscape. For comparison, we chose only three exemplars of the 10 collared elephants Ngamiland. We produced such maps for all the elephants at the 12 sites to help visualize the main features we wish to describe. (See Supplementary materials.)

The paths connect fixes separated by approximately 24 h (±2 h). The colour of the movement path reflects the average EVI of the background at that point in time, as explained above. Thus, green lines indicate that those movements occurred during the wet season, and orange lines indicate that the movement occurred during the dry season.

At Ngamiland, elephants have a distinct migration. During the dry season, elephant fixes are within 20 km of the water the Okavango River provides. We know from limited data involving hourly elephant fixes (see below) that the elephants drink near midnight at the river then walk inland to feed. Elephant population densities are relatively high here — we completed an elephant survey by helicopter in the dry season of 2004 and counted 1500 elephants over 300 km^2 (Jackson et al., 2008). Given these high densities, it is likely that elephants must travel well away from the water each day to find sufficient food. When rains begin, the elephants move well away from the river and some approach the fence that prevents their crossing into Namibia in the north and a game fence that prevents their moving further to the east. The transition from dry to wet season is abrupt, and elephants move away from the river as soon as good rains begin. From wet to dry season the vegetation changes appear more gradual. The elephant changes are even more marked than with the onset of rains. Elephants return to the river from areas almost 100 km away within 2 days. This is likely a response to the drying of seasonal water sources far from the river. We contrast these elephant movements at Ngamiland with those at Kasungu. At Kasungu they are also seasonal, but not so obviously, and on a very much smaller scale.

3.3. Summaries of overall movement patterns

Fig. 4A shows mean displacements (km/day) for 68 elephants tracked for an average of 691 days plotted against total annual precipitation. The five elephants with insufficient data are not shown. Elephants in drier places move more on average than those in wetter areas ($R^2 = 0.67$, $p < 0.001$).

Elephant movement also varies seasonally. Fig. 4B plots dry season against wet season mean displacements for 68 elephants for which we have both wet and dry season data. Some 53 elephants fall above the 1:1 line (green half), that is, they move more in the wet season compared to 15 that do not ($p < 0.0001$, sign test).

The difference between wet and dry season displacements did not vary with annual precipitation ($p = 0.925$).

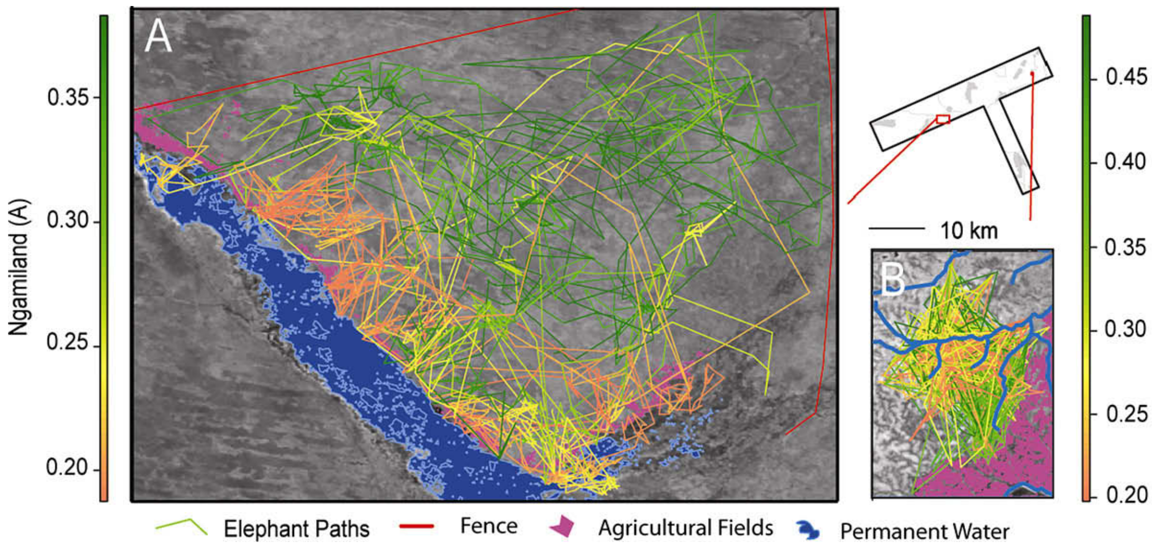

Fig. 3. The movement paths of three elephants (one male and two females) at each of two sites. The map on the left is Ngamiland, Botswana. The map on the right is Kasungu National Park, Malawi. The maps share the same scale (upper left). The colour of the path indicates the average EVI of the background through time. Blue, pink, and red features are permanent water, agricultural fields, and fences, respectively. The grayscale background is average EVI. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

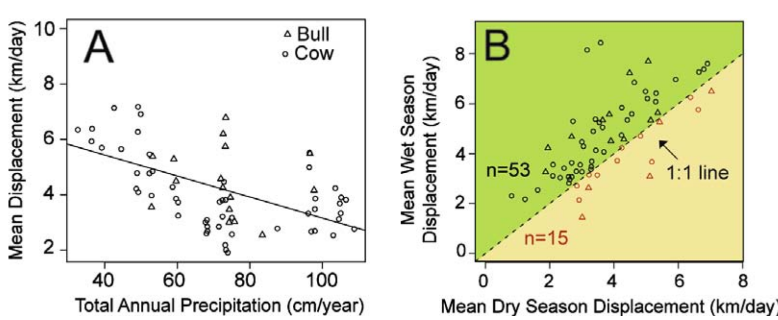

Fig. 4. (A) The mean daily displacement for the 68 elephants with sufficient data (>250 days tracked and >250 fixes) plotted against total annual precipitation ($R^2 = 0.67$). (B) Wet season mean annual displacement plotted against dry season mean annual displacement. The 53 elephants with larger wet season displacements are in black, the 15 with larger dry season displacements are in red. Triangles indicate bull elephants. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The second measure estimates the "area" traversed in a 45-day period. Fig. 5 shows an example from Kafue National Park — a single elephant. To show the calculation, Fig. 5A plots two 45-day windows one in the dry season (orange) and one in the wet (green). For each window, we calculate the centroid — the mean coordinate (shown as orange and green points in Fig. 5A). We then calculate the root-mean square of the distances between each of the fixes and this centroid. One can imagine this as the radius of a circle equivalent to the area explored over the 45-day period. Gaps in the data can erroneously decrease the root-mean square displacement. We excluded all windows with gaps of five days or more.

Fig. 5B shows these "areas" over time expressed as root-mean square distances. The overlapping 45-day windows are in grey and the dry season and wet season example windows in orange and green, respectively. In the dry season, this elephant explored an area equivalent to one with a radius of 12 km, whereas in the wet season it was nearly twice that radius (and so nearly four times the area).

Fig. 5C shows that, like displacement, mean area decreased as mean annual precipitation increased. Importantly, the seasonality of the areas (mean wet season minus mean dry season) decreases significantly with precipitation (Fig. 5D). The slope in the linear model is significant at $p < 0.01$. The slope is still significant even with the removal of the most extreme point ($p < 0.05$).

We have a caveat. Fences and water holes limit the distances moved by elephants and the areas they cover — as we shall show presently. We return to discuss whether these factors alter the conclusions we made in the Discussion.

Fig. 6 deals with year-to-year fidelity. Fig. 6A shows two elephant paths averaged over 10-day windows from 2 years (2005 and 2006) for a single individual elephant, in Lower Zambezi National Park, Zambia. The dotted line represents 2006 and the solid line represents 2005. Each path comprises arrows linking the centroids of elephant fixes assigned to 10-day windows. Both paths start on January 5 (January 1–January 10) and end on August 2 (July 28–August 7). We have data for the last months of 2005, but not 2006, so we use these dates to make the results comparable. The wet season windows are coloured green and the dry season windows are coloured orange. The mean distance from identical 10-day windows across years – for example January 5, 2005 and January 5, 2006 – is the Inter-annual displacement. Small inter-annual displacements mean an elephant is more faithful to a given location among years.

Fig. 6B compares dry and wet season average inter-annual displacements results across all elephants. Some 42 out of 54 elephants have larger average inter-annual displacements in the wet season. That is, an elephant is typically more faithful to its dry season range than its wet season range. The binomial probabil-

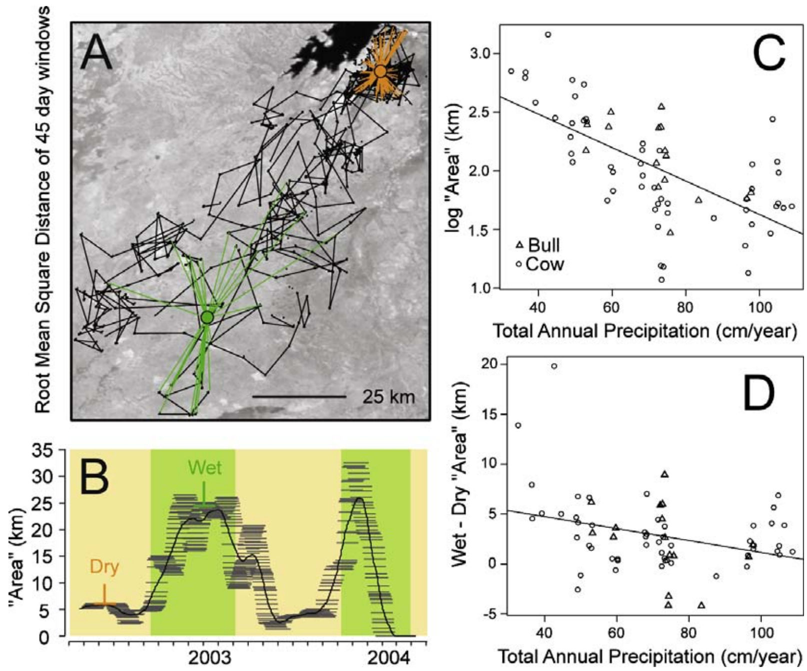

Fig. 5. Estimates of "area" traversed by an elephant (A) The path of a single female elephant from Kafue National Park. The orange lines converge from all points in a 45-day window during the dry season on their centroid. The green lines converge from all points in a 45-day wet season window. (B) The *y*-axis is the root-mean square distance of all points in a 45-day window or the "area". The windows are plotted in grey. The black line is a moving average. The dry and wet season example from Fig. 5a are shown in orange and green, respectively. (C) The log average "area" plotted against average total annual precipitation for each elephant ($R^2 = 0.64$) (D) Seasonality in "area" (wet season minus dry season) plotted against precipitation ($R^2 = 0.53$). Triangles indicate bull elephants.(For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

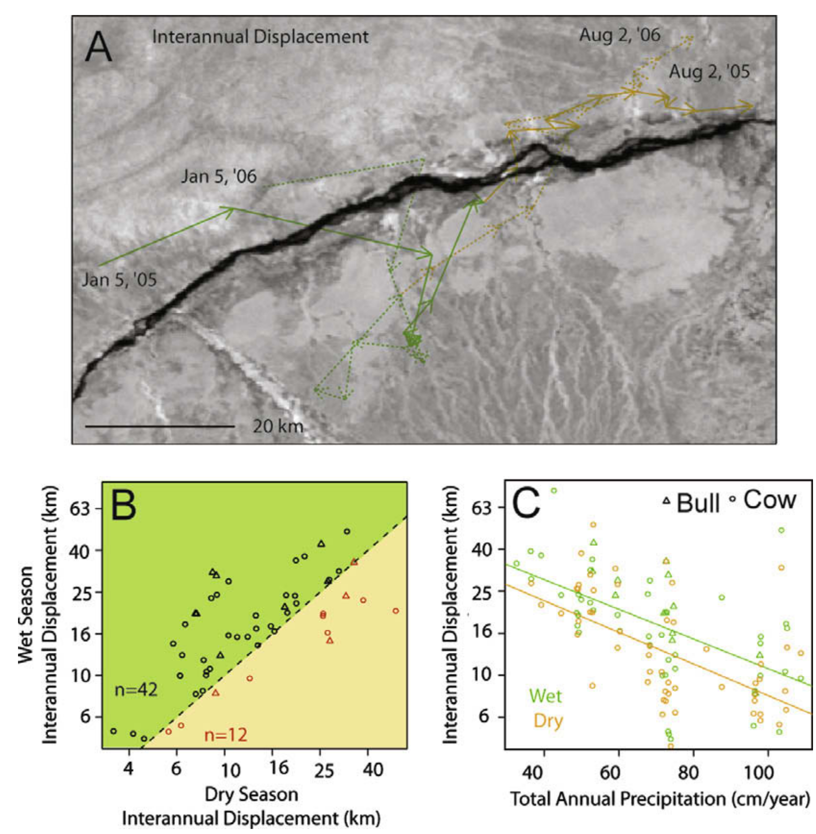

Fig. 6. (A) A simplified path from a female elephant from Lower Zambezi National Park from January 5th to August 2nd for 2005 and 2006. The path is smoothed by 10-day averages. (B) The average inter-annual displacement among years in the dry season plotted against the wet season for 54 elephants. A significant number of elephants have larger inter-annual displacements in the wet season (C) Inter-annual displacement separated by season plotted against mean annual precipitation. The slopes and intercepts of the lines do not differ significantly ($R^2 = 0.51$ and $R^2 = 0.53$ for dry and wet, respectively). Triangles indicate bull elephants. Green and orange represent wet and dry seasons, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ity of this occurring by chance is small ($p < 0.0001$). Fig. 6C plots these inter-annual displacements against mean annual precipitation. Inter-annual displacements are smaller in sites with higher rainfall. Displacements decrease as precipitation increases.

3.4. Within-day movements

The within-day movements from 20 of the elephants took place under relatively dry conditions (<5 mm/day). Movements from the remaining 11 elephants occurred under considerably wetter conditions (>5 mm/day). The differences are partly between wet and dry sites, but time of year also played a role – the movements from wetter sites also occurred at wetter times of years.

Fig. 7A shows the average displacement (meters per hour) calculated from hourly-movements grouped by the 20 elephants moving under dry conditions (orange line) and the 11 elephants moving under wet conditions (green line). Fig. 7B shows the average temperatures for the 2 groups. Bars are ±1 standard error.

Elephants are consistently least active during the middle of the day and night and peak in activity at dusk and dawn. Elephants under dry conditions are considerably more active at night and considerably less so during the middle of the day when temperature peaks. Their dusk activity peak is also delayed and tapers into the night.

Because an elephant path is not straight, the total distances elephants travel accumulate faster than a straight-line drawn between fixes. Fig. 8A shows hourly-movement data for a typical elephant path from Kafue National Park. The path lasts 5 days. The colour of the line indicates the time of day that the movement occurred. The looping behaviour shown here is typical. It results from a relatively straight path from noon (pink) to midnight (light blue), then a sharp turn, and a relatively straight path back.

There are 271 uninterrupted 24-h long elephant paths beginning at noon from 31 elephants. Fig. 8B shows the average cumulative distance travelled from these paths (dashed line). The solid line is the straight-line distance from the first fix of the path (noon). Unlike distance travelled, the straight-line distance is variable. Its pattern results from the looping behaviour described above. Straight-line distance peaks at night (blue rectangle) and then stays relatively constant as the elephant turns and heads in a new direction. Fig. 8C groups the elephant paths by wet (orange line) and dry (green line) conditions as described above. Under dry conditions, elephants travel more overall, but the shapes of the curves are similar.

3.5. Elephant movements and water

Fig. 9A shows the movement paths of all 10 elephants from Ngamiland. (Fig. 3 showed only three exemplars.) Fig. 9B shows the average distance the elephants are from permanent water over time. During the dry season, elephants are metaphorically tethered to the permanent water of the Okavango River. At the driest periods, their daily average is less than 10 km from the river. In the wet season, they average 30–50 km from the river.

Fig. 9C shows hourly-movement data from Ngamiland during the dry season. The elephants are closer to water at night (light blue lines). Indeed, they are closest of all at midnight. They are furthest near the middle of the day, roughly 20 km from water — meaning a 40 km round trip daily. Obviously, selected daily observations at random times would suggest the average of 10 km from water that we have already noticed.

Fig. 10 shows the mean distance from permanent water for all within-day data. Under drier conditions ($n = 20$ elephants), elephants average about 4 km from water during the day and are significantly nearer the water at night (9 PM–2 AM). Under wetter conditions ($n = 11$ elephants), the pattern is a much weaker and there is more overlap among the standard deviations. The elephants are likely even closer to seasonal sources that we cannot detect. The patterns were similar when grouped by sex (see Supplementary materials).

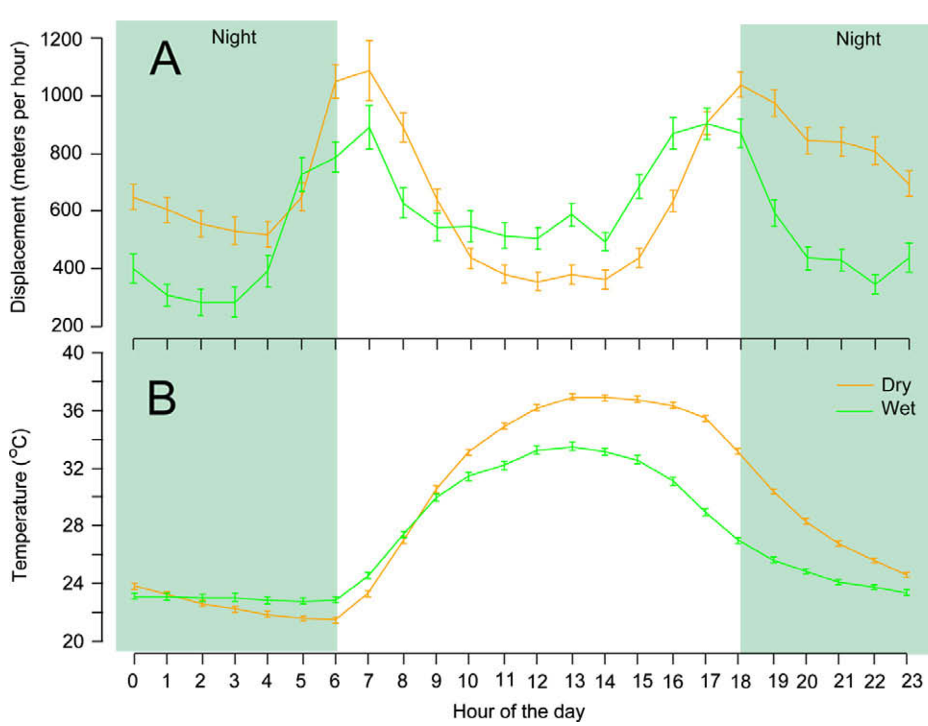

Fig. 7. (A) Within-day displacements by hour grouped by elephants moving under dry conditions (orange line) and elephants moving under wet conditions (green line). (B) Temperature by hour grouped by elephants moving under dry conditions (orange line) and by elephants moving under wet conditions (green line). Bars indicate ±1 standard error. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

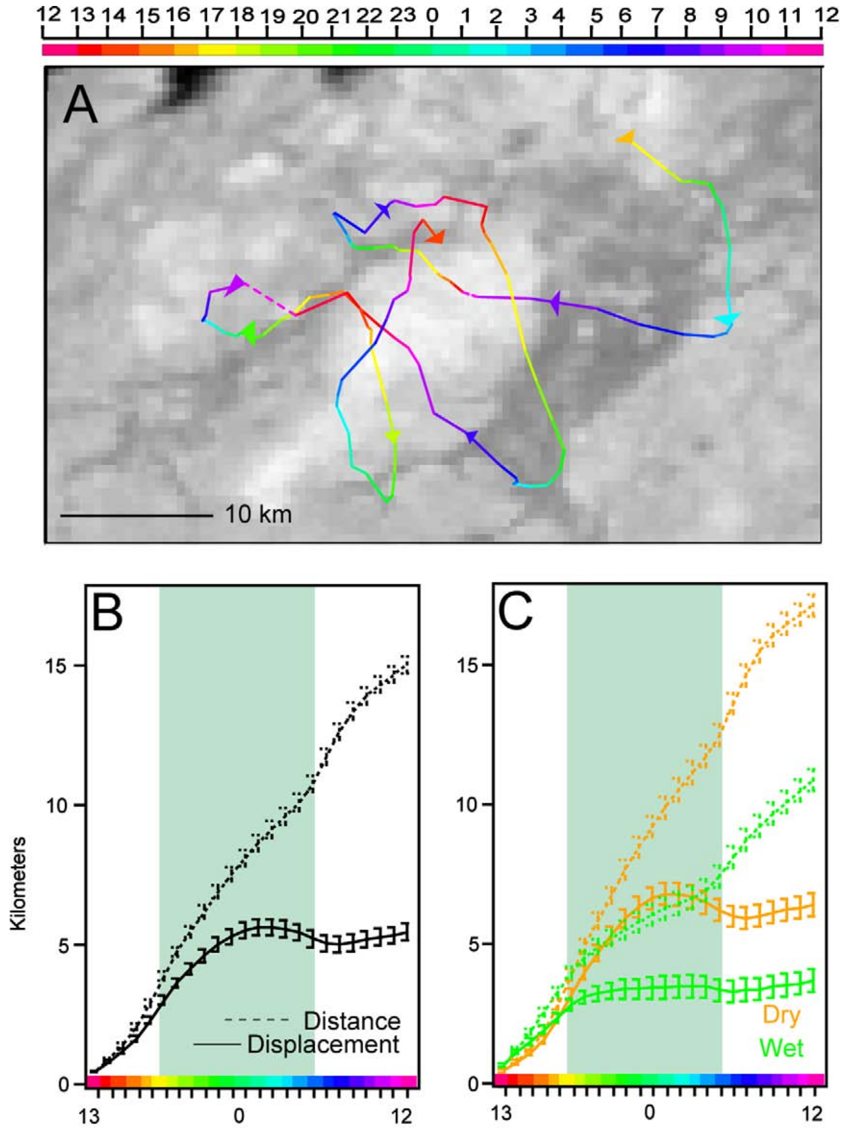

Fig. 8. (A) A 5 day long path of hourly-movement data from a single elephant in Kafue National Park. Arrows indicate the direction of the path; colour indicates time of day. The black areas are a lake, the darker grey areas are a dambo, while the lighter grey areas are woodlands. (B) The average cumulative distance travelled (dashed line) and displacement (solid line) for 271 paths beginning at noon and lasting 24 h for 31 elephants. The *x*-axis shows hour of the day and the blue rectangle indicates night. (C) The average cumulative distance travelled (dashed line) and displacement (solid line) grouped by dry (orange line) and wet (green line) conditions, respectively. Bars indicate ±1 standard error. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Ten km has been used in other studies as an arbitrary cut off for landscapes near and far from water supplies (Redfern et al., 2003; Western and Lindsay, 1984). When elephants have access to artificial water, we hypothesize that their dry season ranging patterns will cover an area greater than a 10 km buffer around natural year-round water supplies. Fig. 11 shows elephant movement in Khaudom Game Reserve. The only natural year-round water is near the northern end of the reserve. Even this source disappears in dry years.

From the Ngamiland results, one might expect the Khaudom Game Reserve elephants to be restricted to within 10 km of this ephemeral source. If so, the addition of artificial waterholes has greatly increased the dry season range of elephants in this reserve supporting our hypothesis.

Smit et al. (2007a) caution that it is difficult to extrapolate patterns from one elephant population to the next. But we note that the pattern of being close to water is general. Across all sites, of more than 34,000 dry season elephant fixes, 71% are within 5 km of a known water source, 84% are within 10 km, and 93% within 15 km. The only other site with extensive artificial water near the collared elephants is Etosha National Park, where the pattern of dry season movement is similar to Khaudom Game Reserve.

3.6. Path density and the role of fences

Fig. 12C plots these path density quotients (see Section 2) for each elephant. The slope of the graph is indeed significantly steeper ($p < 0.0001$ ANCOVA, F-value = 749.13, n = 68/68 dry/wet, df = 138) for the dry season points indicating that the elephant movements are denser during the dry season. These results are consistent with displacement and area results, which are correlated with path density (see Figs. 4 and 5).

In Fig. 11, the Botswana–Namibia border fence at the eastern edge of the area appears to strongly limit the eastward movements of elephants. Does the presence of fences cause elephant movement paths to overlap more increasing the path density?

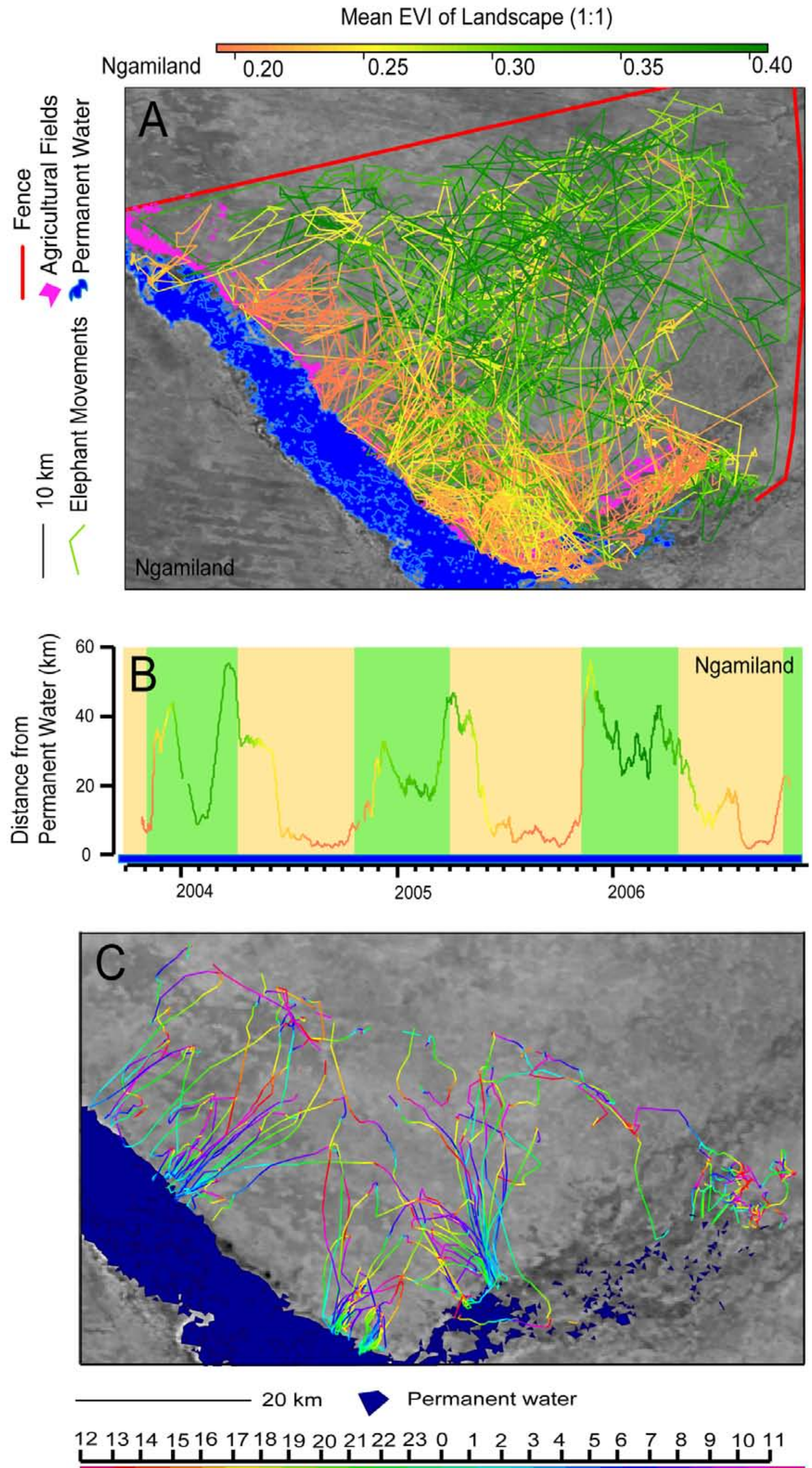

Fig. 9. (A) Movement paths of 10 elephants at Ngamiland. The colour of the path indicates the mean EVI when the movement occurred. The dark blue represents permanent water. (B) Distance from permanent water averaged across all the Ngamiland elephants plotted over time. The colour of the line is the mean EVI. The vertical rectangles delineate the wet and dry seasons. (C) Hourly-movement data from 6 elephants in Ngamiland. Colour indicates time of day. Nighttime fixes — light blue lines — are concentrated near water. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 12A shows a single elephant movement path from Etosha National Park. The red line is a fence that encloses the park. As before, the colour of the line indicates the greenness of the landscape – green lines represent wet season movements, orange lines represent dry season movements. The blue points are water holes while and the red line is a fence. Fig. 12B plots the distance to the fence over time. During the wet season, the elephant movements concentrate near the fence.

Fig. 12D tests whether elephant movements become denser when closer to fences. Here, we compute the 1-to-2 count quotient

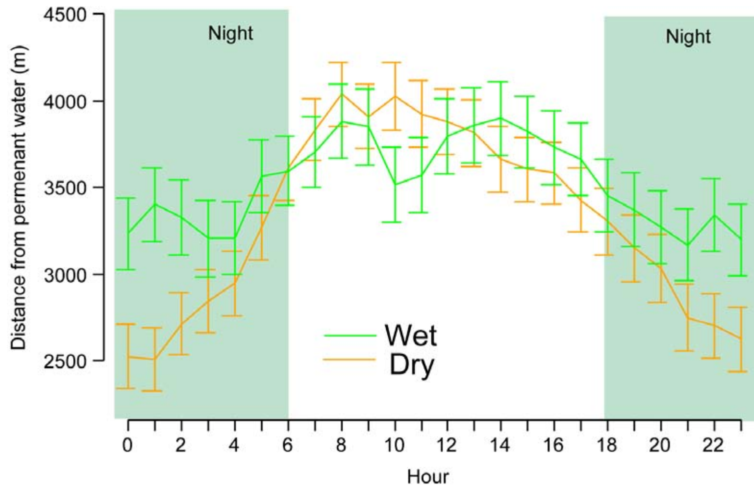

Fig. 10. Mean distance from permanent water by hours of a day across all elephant within-day data ($n = 20$ elephants for dry conditions and $n = 11$ elephants for wet conditions) within 20-km of permanent water grouped by dry (orange) and wet (green) conditions. Blue bars indicated night. The error bars are ±1 s.d. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

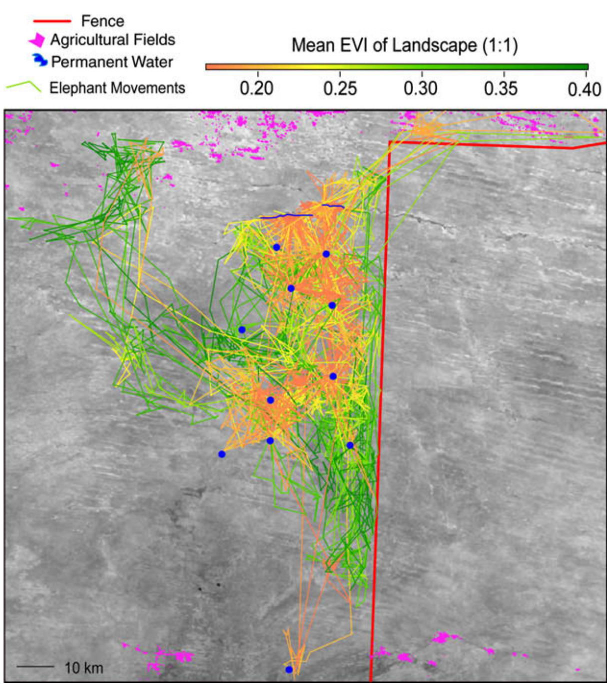

Fig. 11. Movement paths from six elephants at Khaudom Game Reserve over the course of the study. The blue broken line indicates a semi-permanent stream. The blue points indicate artificial water boreholes. Red lines are fences and pink features are agricultural fields. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

separately for fixes >15 km from a fence and those <15 km from a fence. For each elephant, the red points are counts near fences and the blue points are counts far from fences. The slope is significantly steeper ($p < 0.0001$ ANCOVA, F-value = 2004.54, $n = 29/34$ near/far, $df = 65$)) for the points closer to the fences indicating that elephant's wet season movements become denser when they are close to fences.

4. Discussion and conclusions

Elephant movements are complex and seasonally variable (De Beer and van Aarde, 2008; Young et al., 2009a,b; Cushman et al., 2005; Douglas-Hamilton et al., 2005; Leggett, 2006). Nonetheless, we find consistent patterns across a large gradient of environmental parameters.

Elephants consistently move more in a day (Fig. 4) and cover more area over 45 days (Fig. 5) in the wet season than in the dry season, and they make more visits to the same place in each dry season, than in each wet season (Fig. 12). From year-to-year, they are more faithful to their dry season ranges than their wet season ones (Fig. 6). Elephant activity is primarily crepuscular (Fig. 7). In the dry season in dry areas, they move more at night than midday. The converse is true in the wet season in wet areas.

There is a large precipitation gradient across this study from the arid west to the wetter east. In both seasons, elephants from drier savannahs move more and cover larger areas than individuals from wetter areas (Fig. 4). In wetter sites, the seasonal differences in area covered decrease (Fig. 5).

Other studies have noted seasonal differences in ranging patterns (Wittemyer et al., 2008) and that the formation of large herds often occurs during the wet season (Wittemyer 2001; Wittemyer et al., 2005). Interestingly, individual ranging patterns are decidedly more nomadic during this season and less consistent from year-to-year than dry season. We notice that during the dry season, elephants in dry savannahs move more than do those in wet savannahs. This is despite their need to be close to permanent water. The necessity to stay close to water is compromised by their search for scarce vegetation (Redfern et al., 2003; Western and Lindsay, 1984). When water is scarce, elephants spend much of their time travelling large distances between water and vegetation. Other studies report significant differences in the ranging patterns of male and female elephants (De Villiers and Kok, 1997; Shannon et al., 2006; Stokke and du Toit, 2002). While we did not explicitly compare male and female elephants due to the small number of males, we note that excluding males did not alter our results.

Human actions modify these general patterns. First, the erection of fences acts on wet season range in two ways. Fences act as barriers to movement and so might shrink wet season ranges. Whether they do so remains unclear in the absence of carefully controlled experiments. Moreover, in the wet season, fences cause elephants to revisit the same places more often — their daily movements ‘‘bunch up” near fences (Fig. 12).

Second, artificial water holes increase the dry season range available to an elephant (Fig. 11). The influence of artificial water holes on dry season ranging patterns is profound (De Beer and van Aarde, 2008; Smit et al., 2007a,b; Thomas et al., 2008; Viljoen, 1989). *Inter*

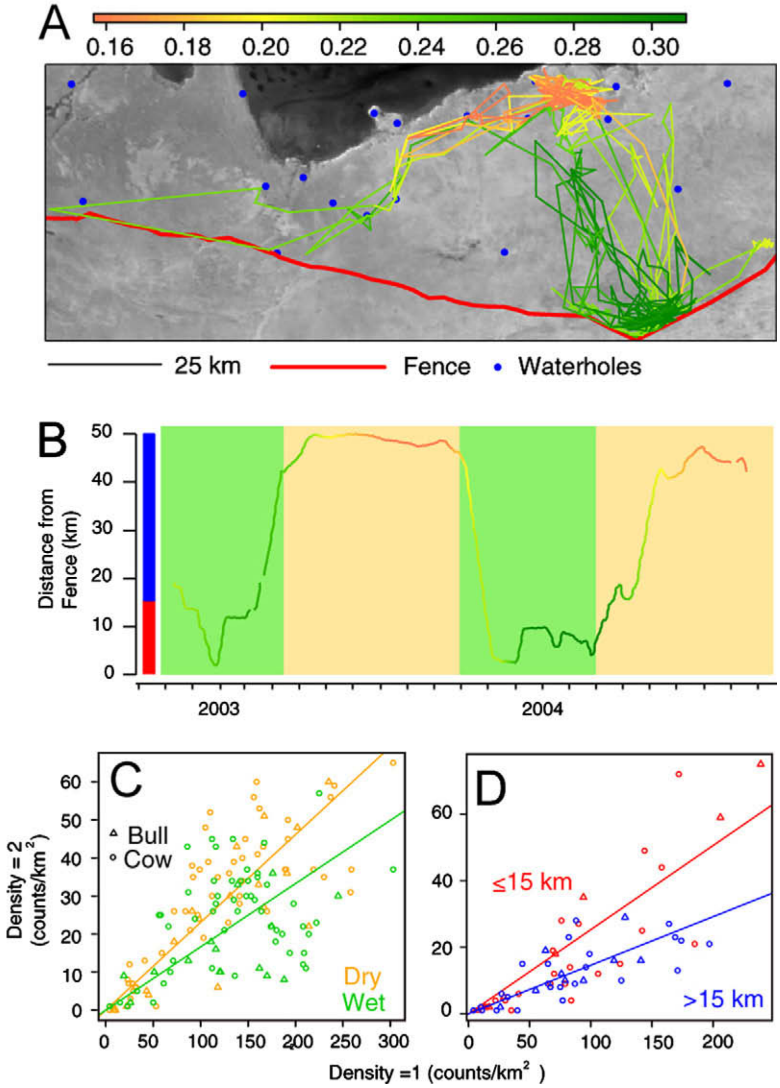

Fig. 12. (A) The path of a female elephant from Etosha National Park. The colour of the line indicates the mean EVI of the landscape when the movement occurred (see Fig. 3.) The red line is the Etosha National Park boundary fence. (B) The path of the same elephant over time. The *y*-axis is distance from the fence. The red bar indicates distances <15 km the blue bar indicates distances >15 km. (C) A plot of the 1-to-2 count quotient for wet season (green) and dry season (orange) for each elephant ($n = 68$) across all study sites (see text for details). Path densities are greater when the quotient is higher (slope is steeper). R^2 values are 0.57 and 0.54 for Dry and Wet, respectively. (D) The 1-to-2 count quotient for <15 km from a fence (red) and >15 km from a fence (blue) for each elephant during the wet season across all study sites ($n = 29/34$ near/far from fences). Triangles indicate bull elephants. R^2 values are 0.65 and 0.61 for <15 km and >15 km, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

alia, it makes elephants more vulnerable to predation and diseases (Dudley et al., 2001; Loveridge et al., 2006; Ottichilo, 1987; Walker et al., 1987). Our results show that water holes also strongly modify elephant movements by allowing elephants to range into formerly inaccessible areas. Khaudom Game Reserve in Namibia probably originally lacked enough permanent water to support elephants during the dry season (Wanke and Wanke, 2007). Elephants would have wandered into Khaudom during the wet season or, during wet years, occasionally over wintered on the Ncamasere and Cwiba rivers. Since then, artificial water holes have made extensive dry season ranging possible. Because elephants are more faithful to their dry season range than their wet season range (Fig. 6), this dry season presence has a more consistent footprint on the land than the more nomadic wet season footprint does.

4.1. Management and conservation implications

By design, our analyses seek to find general patterns of elephant movements — something that one can achieve only across a large range of locations and ecological conditions — in order to understand the impact of human interventions. The concern is to what extent artificial water sources and fences increase local elephant densities, Artificial water sources allow more extensive dry season ranging, allowing elephants to use — and potentially overexploit — vegetation in areas that would have be otherwise inaccessible to them except in the wet season. Fences cause elephants to "bunch-up" against them during the wet season, again locally increasing the pressure elephants put on their resources. Together, artificial water and fences decrease the differences between dry and wet season ranging patterns. Because these human modifications are more prevalent in the drier landscapes explored here — both artificial water holes and fences — elephant behavior in these dry landscapes is becoming increasingly similar to the behavior of wet savannah elephants. As it were, human interventions allow elephants to be almost everywhere in dry savannahs and at all times of year. The natural situations involved considerably more seasonality. Without that natural seasonality, elephants may well have negative impacts

upon the vegetation they utilize — and other animal species as a consequence.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.08.008.

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