Diversity and Distributions, (Diversity Distrib.) (2009) **15**, 776–783

BIODIVERSITY RESEARCH

The affects of artificial water availability on large herbivore ranging patterns in savanna habitats: a new approach based on modelling elephant path distributions

Graeme Shannon[1,2]*, Wayne S. Matthews[3], Bruce R. Page[2], Guy E. Parker[1,4] and Robert J. Smith[1]

[1]*Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, Kent CT2 7NR, UK,* [2]*School of Biological and Conservation Sciences, University of KwaZulu-Natal, Westville Campus, Private Bag X54001, Durban 4000, South Africa,* [3]*Tembe Elephant Park, Ezemvelo KwaZulu-Natal Wildlife, Private Bag 356, Kwangwanase 3973, South Africa,* [4]*Marwell Preservation Trust, Colden Common, Winchester SO21 1JH, UK*

*Correspondence: Graeme Shannon, School of Biological and Conservation Sciences, University of KwaZulu-Natal, Westville Campus, Private Bag X54001, Durban 4000, South Africa.
E-mail: shannongraeme@gmail.com

ABSTRACT

Aim Artificial water points are often used in protected savanna ecosystems to maintain populations of large herbivores. However, these interventions lead to increased ranging and foraging pressure and can negatively impact important habitats and species. This study investigated the influence of artificial water provision on the foraging and movement paths of an African elephant population and modelled the impact of changing water availability on sensitive habitat types.

Location Tembe Elephant Park (TEP), KwaZulu-Natal, South Africa.

Methods We mapped and classified 414 km of elephant movement and foraging paths in a 300-km^2 fenced protected area. The data were analysed to determine the relationship between path size, distribution and distance to water. We also used a logistic modelling approach to explore the predicted effects of removing artificial water points on path distribution.

Results Elephant paths were unevenly distributed throughout the habitats of TEP and the most established and heavily used paths were found closest to water. We also discovered a number of elephant ‘rest areas’ along the paths, which were distinct clearings that tended to be close to water and in sand forest habitat. Our model predicted that the removal of artificial water points would reduce the area crossed by elephant paths by 79%, leading to an 89% reduction in the presence of elephant paths in sand forest.

Main conclusions Our study provides further evidence that manipulating surface water availability can be a useful tool for managing large herbivore impacts on vegetation and acts as the basis for further research on the trade-offs between conservation objectives.

Keywords

Herbivore, *Loxodonta africana*, savanna, surface water, Tembe Elephant Park, vegetation impacts, wildlife management.

INTRODUCTION

Large herbivore species are increasingly restricted to protected areas (PAs) because of habitat loss and overharvesting (Caro & Scholte, 2007), a situation that limits their opportunities for dispersal and their access to natural water sources (Western, 1975; Redfern *et al.*, 2003, 2005; Chamaillé-Jammes *et al.*, 2007a). In response, wildlife managers often set up permanent water supplies by creating artificial water points or augmenting existing seasonal sources (see Smit *et al.*, 2007). However, this can lead to increased and continuous use of areas that were previously only accessed during periods of high rainfall (Owen-Smith, 1996). The ensuing increase in large herbivore densities around these permanent water points, results in neighbouring vegetation being heavily impacted by trampling and foraging, especially when they are placed in sensitive habitat types (Owen-Smith, 1996; Thrash & Derry, 1999). Moreover, providing relatively high densities of artificial water points can lead to ecosystem instability, a loss in landscape heterogeneity and the collapse of key herbivore populations (Owen-Smith, 1996; Gaylard *et al.*, 2003).

DOI:10.1111/j.1472-4642.2009.00581.x
www.blackwellpublishing.com/ddi

The issues discussed above are particularly pertinent in the debate over the management and conservation of the African elephant (*Loxodonta africana*) (Owen-Smith *et al.*, 2006), as a significant number of populations are restricted to PAs through habitat loss, human–elephant conflict, poaching and/or fencing (Blanc *et al.*, 2007). In addition, elephants are very large, water-dependent herbivores, which are capable of driving changes in habitat structure and impacting sensitive plant species when at high densities (Owen-Smith, 1992; Johnson *et al.*, 1999; O'Connor *et al.*, 2007; Shannon *et al.*, 2008a). Therefore, the provision of artificial water points in PAs containing elephants is likely to have significant impacts on vegetation utilization (Owen-Smith, 1996; Thrash, 1998; Grainger *et al.*, 2005; de Beer & van Aarde, 2008). Despite this, artificial water points are important in ensuring year round availability of water, especially in fenced or spatially restricted PAs, which often have no naturally occurring permanent supplies (Boone & Hobbs, 2004). They also act as focal points for visitors who want to see large and charismatic mammal species. Therefore, there is a need to understand the consequences of manipulating water availability on the ranging behaviour of elephants, allowing informed decisions that balance the needs of biodiversity conservation, elephant population management and tourist revenue generation.

Previous studies on the influence of water availability on elephant distribution and ranging patterns have either used data from a small number of radio- or GPS-collared individuals or census data (Lindeque & Lindeque, 1991; Stokke & du Toit, 2002; Grainger *et al.*, 2005; Chamaillé-Jammes *et al.*, 2007a; Smit *et al.*, 2007; de Beer & van Aarde, 2008). Here we use a complementary approach that focuses on mapping elephant pathways. The position of these pathways reflects long-term movement and feeding patterns of the whole population (Agnew, 1966). Our research was based in Tembe Elephant Park (TEP), a fenced reserve in the savanna region of South Africa that contains three artificial water points, together with dense vegetation on a sandy substrate. TEP also contains a number of key habitat types that are impacted by elephant feeding patterns. The most important of these is sand forest, a slow growing habitat type that contains many endemic species and responds poorly to browsing pressure (Matthews *et al.*, 2001). Therefore, in this study, we mapped the elephant paths and determined their spatial extent and characteristics. We also used logistic regression modelling to predict the potential impacts of changing the pattern of water provision on the spatial pattern of the pathway system and its impacts on sand forest.

METHODS

Study area

Tembe Elephant Park is a 300-km^2 fully fenced PA, situated in northern KwaZulu-Natal on the border with Mozambique (Fig. 1). It falls within the Maputaland Centre of Endemism and contains a number of threatened and endemic species

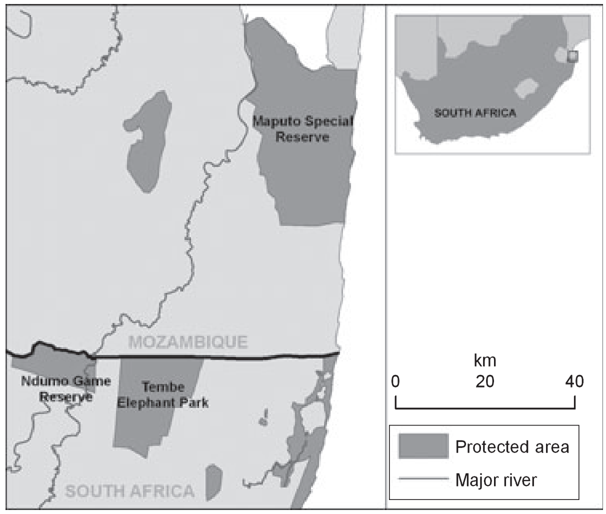

Figure 1 A map showing the position of TEP and neighbouring protected areas in South Africa and Mozambique.

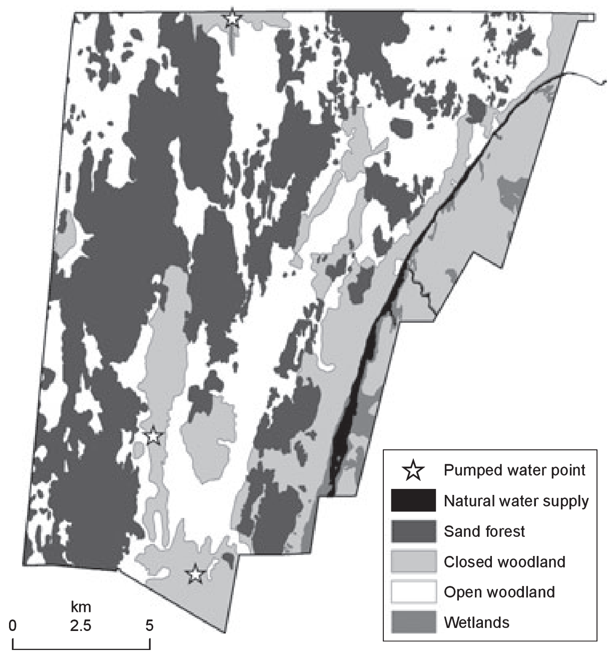

Figure 2 Tembe Elephant Park habitat types and water availability map.

(Matthews *et al.*, 2001; Smith *et al.*, 2008). The average rainfall is 700 mm per annum with a range of 250–1400 mm (Matthews, unpublished data). Water availability in TEP includes a permanent wetland (the Muzi swamp) in the west and a number of ephemeral pans throughout the reserve, three of which are pumped with groundwater to provide additional permanent water points (Fig. 2). TEP currently contains a population of *c.* 180 elephants, which historically ranged between the woodland and forest of the reserve and the grasslands of Mozambique to the north (Morley & van Aarde, 2007). However, the reserve was fully fenced in 1989 to protect the elephant population from poaching events linked to the civil war in Mozambique. There are now plans to link TEP with the Maputo Special Reserve (MSR) in Mozambique (Fig. 1) as part of the Lubombo Transfrontier Conservation Area (TFCA) initiative (Smith *et al.*, 2008).

Mapping and analysing the path and rest area data

Each elephant path in TEP was mapped by walking its entire extent and using a GPS unit to record the location every 25 s (Fig. 3). We also gave a use intensity score to each path of 1, 2 or 3 based on a system described in Table 1. During the study, we discovered that the elephant paths were associated with discrete rest areas that were created by elephant activity. They were characterized by the presence of trees used as rubbing posts at 1–4 m above the ground, as well as spoor, aggregations of dung piles, and the uprooting of saplings. The location of each rest area was recorded using a GPS unit and their size and degree of use were classified as one of two types (Table 1). The GPS data on paths were imported into the ArcView v3.3 GIS software package (ESRI, Redlands, CA, USA) and converted from points to lines. The GIS also contained a habitat map of TEP that had been produced from vegetation transects, satellite imagery and aerial photographs (Matthews *et al.*, 2001). The original map contained 13 vegetation types, which were grouped into four habitat categories based on structure and species composition: (1) sand forest, (2) closed woodland, (3) open woodland, and (4) wetlands. Water availability was mapped using aerial photographs and recording the exact location of permanent (Muzi swamp), ephemeral and artificial water points (maintained through pumping).

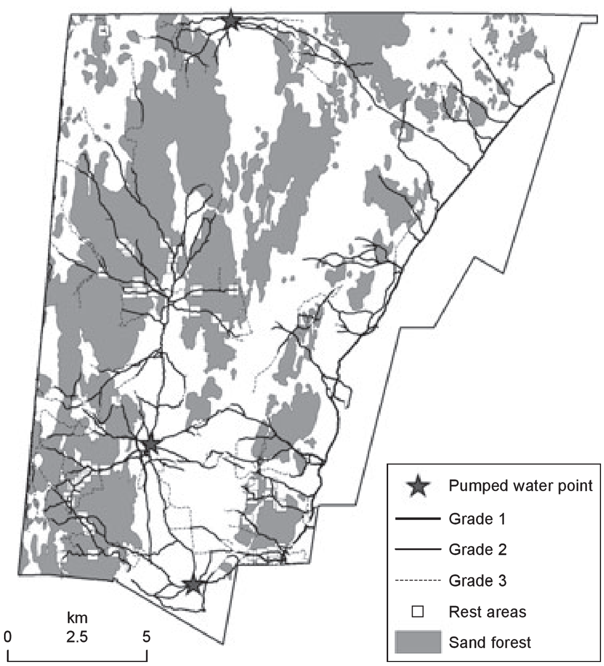

Figure 3 Elephant paths and rest areas in Tembe Elephant Park (grade 1 = most heavily used).

The data were initially analysed to test whether elephant paths were associated with particular habitat types. The GIS was used to select 150 points that fell along the paths and determine the habitat type at each location. These points were selected at random, other than the constraint that they had to be at least 2 km apart to reduce the influence of spatial autocorrelation. A chi-square test was used to determine whether the number of sample points found in each habitat type differed from expected, where the expected number was calculated as the proportion of each habitat type within TEP multiplied by 150. The second analysis aimed to establish whether the distribution of elephant paths was related to distance to water. This adopted a similar sampling strategy to that used for the habitat association analysis, with 50 points being selected at random in each of the three path types (the 2-km separation constraint was used). The distance was then measured from each of these points to the nearest water point (either natural or artificial) to establish whether the path types

Table 1 Details of the elephant path and rest area classification system.

	Extent	Direct signs of elephant presence	Description
Path grade			
1	Width of 0.6–1.0 m	Dung piles every 10–50 m	Eroded well below the surrounding surface with no vegetation growing on or immediately around the path
2	Width of 0.3–0.7 m	Dung piles > 50 m, although often aggregated	No growth of vegetation on the path. Slightly lower than the surrounding surface with overhanging vegetation in the denser habitats
3	Width of 0.15 m	Fresh dung piles rarely sighted	Vegetation present but thinned so that the path was still visible with the sand being exposed. These narrower paths branched off from the larger grade 1 and 2 paths
Rest area grade			
1	Approximately circular and at least 20 m in diameter	More than 10 dung piles	Large clearing with a broad sandy base. All the vegetation removed except the largest tree(s) in the centre
2	Less than 20 m in diameter	Scattered spoor and dung piles	Some understorey vegetation remaining in clumps around the periphery

differed in their distance to water. The same procedure (as described above) was used to test whether the elephant rest areas (grade 1 & 2 combined) were associated with particular vegetation types. The GIS was also used to measure the distance from the two types of rest area (grade 1 or 2) to the nearest water point. A Mann–Whitney *U*-test was used to determine if the larger grade 1 rest areas were closer to water than the smaller grade 2 rest areas.

Modelling the impact of water management on elephant path location

The potential impact of a changed water management regime was modelled by first using the GIS to divide TEP into a series of 25-ha grid squares. We then identified whether each grid square contained an elephant path and calculated the area of each habitat type it contained. The actual grade of paths was not used in the analysis, as this was strongly dependent on their configuration, i.e. a path 2 type was only likely to lead off a larger path 1 type. The geometric centre of each square was identified and the distance calculated to the nearest permanent water point (natural or artificial), as well as its geographical coordinates. These data were imported into the SPSS (Chicago, IL, USA) statistical package and 50 grid squares were selected at random from the 622 squares that contained no elephant paths and 50 grid squares were selected at random from the 672 squares that contained elephant paths. Reducing our sample in this way minimized the effects of spatial autocorrelation on our subsequent analyses.

The data were then analysed using stepwise logistic regression modelling to identify whether distance to permanent water, area of each broad habitat type, latitude or longitude best determined whether a grid square was crossed by an elephant path. Longitude and latitude were included in the model to investigate the continued use of elephant paths that were established prior to the complete fencing of TEP in 1989. These paths would have linked TEP with key habitats such as the Futi flood plain to the north and the nearby Ndumo Game Reserve (NGR) to the west (Klingelhoeffer, 1987).

We tested whether the resultant model was affected by spatial autocorrelation by using the Crime-Stat software package (version 3.1; Levine and Associates, Annadale, VA, USA) to undertake a Moran's *I*-test on the standardized residuals. The model in conjunction with the GIS was used to predict where pathways would be found in the future based on a scenario where water was no longer pumped to the three artificial water points. We did this by using the GIS to calculate the distance of each grid square from naturally occurring permanent water (the Muzi swamp) only and then using the model to determine the probability of a path being found in each grid square, given the change in water availability. A cut-off probability – above which we assumed that a path would be present – was determined by using the data from the 50 grid squares used in the original analysis. The 95% confidence intervals were calculated for the modelled probability value for each square and the cut-off was set as the upper confidence interval.

RESULTS

Paths and rest areas

The total length of paths mapped in TEP was 414 km, which consisted of 15 km (4%) of grade 1 paths, 272 km (66%) of grade 2 paths and 127 km (30%) of grade 3 paths. The paths were not randomly distributed throughout the reserve, with closed woodland containing more, and open woodland and sand forest containing less path length than expected from the total area of these vegetation types (d.f. = 3, $\chi^2 = 9.43$, $P = 0.024$). There were significant differences between the distance of the three path types from water ($n = 150$, $\chi^2 = 41.55$, $P < 0.001$), with large paths being the closest, and small paths being furthest away (Fig. 4). For example, all of the grade 1 paths occurred within 1.5 km of water.

We identified 74 rest areas, of which 26 were categorized as grade 1 and 52 as grade 2. These were also not randomly distributed throughout the vegetation types (d.f. = 3, $\chi^2 = 88.23$, $P < 0.001$), with the majority (93%) being found in sand forest (Fig. 3). The median distance to water of large refuges rest areas was 1.20 km and for small rest areas it was 1.92 km ($n = 74$, $U = 358.5$, $P = 0.005$).

Modelling the impact of water management on elephant path location

The probability of a grid square containing part of an elephant path was related to its latitudinal position (Wald = 20.47, $P < 0.001$) and its distance to permanent water (Wald = 15.32, $P < 0.001$), with squares in the East of TEP that were closest to water being the most likely to be crossed by a path (Fig. 5). The model was not affected by spatial autocorrelation (Moran's $I = 0.006$, $P = 0.5$) and the area under the curve value of the receiver operating characteristics plot was 0.825, indicating a very good model fit (Swets, 1988).

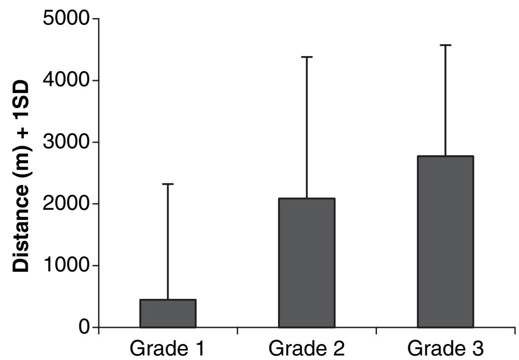

Figure 4 Median distance to water of the different grades of elephant path.

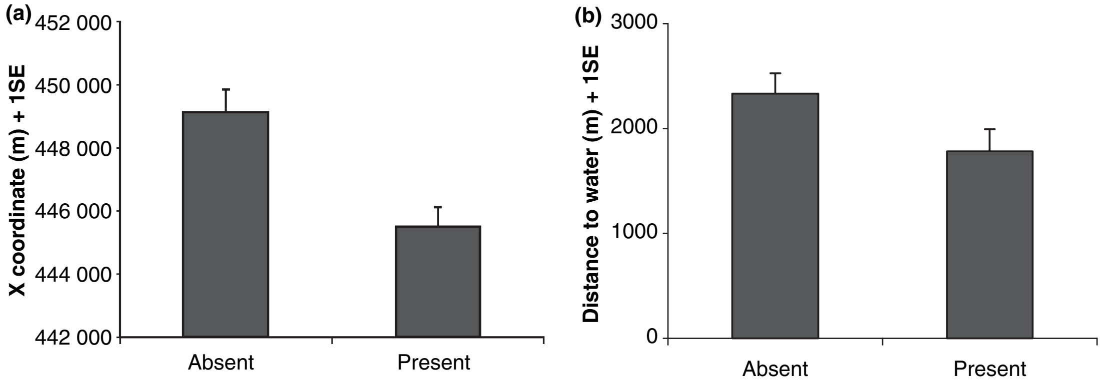

Figure 5 Mean difference between sample grid squares containing pathways and grid squares not containing pathways for the factors used in the pathway presence model. (a) Latitude (x coordinate in UTM 36s) and (b) distance to water.

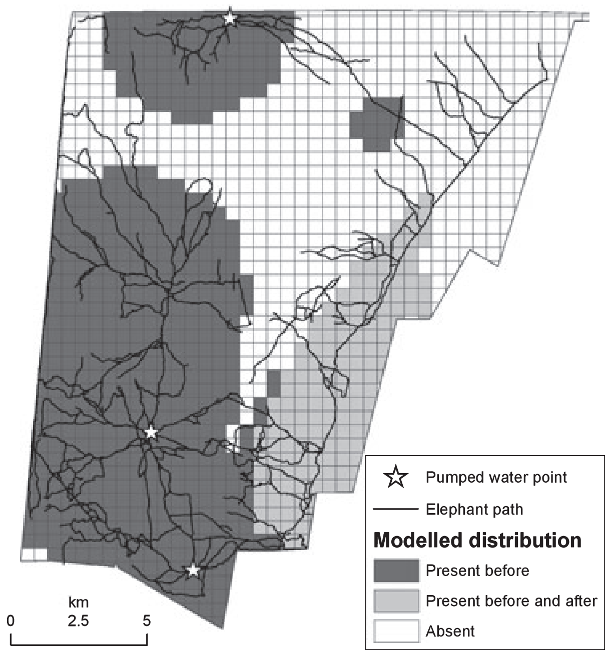

Figure 6 A map of the results of the pathway modelling process. Based on the model, grid squares shown in dark grey would only be expected to contain paths before pumping to the artificial water points was terminated. Grid squares shown in light grey would contain pathways irrespective of the availability of artificial water points.

The GIS maps show that 622 grid squares contain paths and the model based on current water availability predicted 453, or 72.8%, of these correctly. Overall, the model predicted that 748 squares should contain paths, so 60.6% (453) of those were correctly classified (Fig. 6). Furthermore, the number of squares containing paths in the future, based on the artificial water points no longer being pumped, fell by 78.6% from 748 to 160, while the amount of squares containing paths in sand forest would fall by 89.2% from 7388 to 800 ha (Fig. 6). However, it is important to note that the actual area of sand forest in squares crossed by paths was 5609 ha, 24% less than that predicted by the model.

DISCUSSION

Protected area managers often need to balance conservation and tourism objectives and these issues are particularly relevant when developing water-provisioning plans in savanna ecosystems. This study investigated these issues and focused on the African elephant because this species is of a conservation priority, yet can have negative impacts on habitats and associated species (O'Connor *et al.*, 2007).

Another advantage of focusing on elephants is the relative ease with which their movements can be studied and in this project, we took advantage of the conditions in TEP to map the precise location of elephant paths. It is important to remember when studying these paths that their locations are partly context specific, so that a path may develop only to link other paths (Vanleeuwe & Gautier-Hion, 1998). This can make it more difficult to determine the underlying factors that influence path location, such as water availability. However, this technique also has advantages because the distribution of paths reflects long-term movement patterns of the entire elephant population. In this section, we first discuss the characteristics of the elephant paths and resting places, before discussing the results of the modelling process and the influence of the factors that best predicted where paths were located. Finally, we consider the broader relevance of this research for managing water availability in savanna ecosystems.

The distribution and characteristics of the elephant paths and rest areas

The elephant paths in TEP form a network that covers much of the reserve. The grade 1 paths, which were the widest and most heavily used, formed short sections that generally merged into the more widespread grade 2 paths. These grade 2 paths seem to act as important routes for the elephants to reach favoured areas, and prior to the fencing of the reserve, many of them are believed to have provided dispersal routes into Mozambique (Klingelhoeffer, 1987). Similar results have been recorded in

Odzala National Park, Congo, where elephant 'boulevards', which are similar to grade 2 paths in TEP, were well defined, relatively straight and long and linked favoured sites (Vanleeuwe & Gautier-Hion, 1998).

Elephant paths were found throughout TEP but they tended to be found close to the Muzi swamp and other, smaller water points. The importance of distance to water was expected, given that elephants are known to be water dependent (Western, 1975; Redfern *et al.*, 2003; Grainger *et al.*, 2005). However, it is worth noting that the maximum distance from water is 8 km, well within the daily range of an elephant (Owen-Smith, 1992). Nevertheless, strong water dependence appears to influence the foraging behaviour of elephant in TEP (Viljoen, 1989; Stokke & du Toit, 2002; Shannon *et al.*, 2008a), as distance to water was a key variable in predicting the frequency of path use.

Elephants are known to demonstrate clear habitat preferences, despite their body size and generalist foraging approach (Shannon *et al.*, 2006) and we found that elephant path density in TEP tended to vary with habitat, with higher densities in closed woodland. However, this factor was not identified as important in the regression modelling process, suggesting that this habitat association was largely driven by closed woodland habitats being in greater proximity to water. Previous work from TEP has shown that the majority of browsing species prefer feeding in open woodland, probably in part because of the relative abundance of forage species (Matthews, 2005). However, elephants can move freely through open woodland, and so paths are less likely to develop. Therefore, our model may underestimate the role of vegetation composition in determining where elephants feed in TEP. The importance of longitude may provide a clearer explanation of elephant feeding preferences because the western boundary of TEP is within 5 km of the NGR, which contains a number of habitat types favoured by elephants. This may explain why there is a grade 2 elephant path that follows the western TEP fence line (Fig. 3), as elephants may be seeking access to preferred resources that were used prior to the fencing of TEP (Klingelhoeffer, 1987). In contrast, latitude was not important even though it is believed that elephants traditionally dispersed northwards through the Futi floodplains of Mozambique.

The elephant rest areas were found in a much smaller section of TEP making more complex analysis of their spatial patterns difficult. Nonetheless, we found that their location was correlated with distance to water and they were predominantly found in the sand forest habitat, probably as a result of the closed canopy and dense understorey that typifies this habitat type. Once again, this illustrates the impact of the artificial water points in TEP, as none of the natural (permanent) water points are close to the sand forest. The importance of sand forest is probably twofold. First, elephants tend to reduce their levels of activity during the hottest period of the day (Shannon *et al.*, 2008b), commonly seeking shade in the densest available habitat (Owen-Smith, 1992; Kinahan *et al.*, 2007). The resultant trampling is likely to create clearings (Höft & Höft, 1995), which would be especially pronounced in a dense and sensitive vegetation type such as sand forest (Matthews *et al.*, 2001). Second, this may also be a behavioural response to poaching and human disturbance. This was previously noted in the MSR during the civil war, where elephants changed their habitat preference from open grasslands to forest patches (de Boer *et al.*, 2000).

Implications for elephant management and conservation

Maputaland's elephants often seek refuge in thick vegetation but this has created conservation problems in TEP because most of the dense vegetation consists of the rare endemic sand forest, which due to its unique biology is susceptible to elephant browsing, even at comparably moderate levels (Matthews *et al.*, 2001). Moreover, the provision of artificial water points in the central and eastern sections of TEP has encouraged elephants and other large herbivores to feed more extensively in these fragile habitats, which may result in habitat degradation and the loss of biodiversity. The reserve's managers recognize this problem and have considered a number of potential solutions. Our research investigated one strategy that would involve discontinuing water pumping, so that permanent water would only be found in the east of the reserve. The logistic regression model predicted that changing water availability in this way would reduce the area containing elephant paths by nearly 80%, also reducing the amount of sand forest in grid squares containing paths by nearly 90%.

The modelling techniques used in our analysis were the first to predict the impact of changing water availability on elephant path distribution, but the relevance of the results depends on two assumptions. First, we assume that the path system partly developed through elephant browsing and trampling vegetation lying close to water points, with paths both joining favoured resources and allowing opportunistic feeding on adjoining vegetation. In such a situation, reducing the number of permanent water points would have a double impact on browsing pressure. Second, we assume that browsing will be limited in the future to those areas predicted from the model. This is more problematic because changing the water supply would not reduce the number of feeding elephants, so it is likely that some animals would move further from water to feed. Nonetheless, we would expect this browsing to be less focused and less likely to impact the sand forest.

It should also be noted that the model only correctly predicted the presence of the current path system for 73% of the grid squares, partly because a number of the path sections are located relatively far from permanent water and provide a link between water points in different parts of the reserve as well as key foraging resources (Vanleeuwe & Gautier-Hion, 1998). Furthermore, there are several temporary water points in the centre of the reserve that provide water for an extended period because they are located on clay soils. These have encouraged the development of a network of paths around them (see Fig. 3), which also impacted the overall accuracy of the model. Despite these concerns, the model was still effective at explaining much of the observed variation and provides important insights into how reducing the number of permanent water points in TEP would limit pressure on sensitive habitat types.

One could argue, therefore, that permanent water availability should be reduced in TEP but this does not allow for other constraints. One of the main revenue generators in TEP is ecotourism and reducing permanent water availability would reduce the number and visibility of most of the large mammals found in the reserve. In addition, there are only three artificial water points in TEP, so even closing one would have a large impact on game viewing opportunities. The advantage of our research is that it provides a clear picture of the trade-offs involved in such a decision and allows comparisons with other strategies. Fortunately, in the case of TEP, there are alternative options as there are plans in the medium term to join the reserve with NGR in the west and MSR in the north through the Usuthu–Tembe–Futi corridor initiative of the Lubombo TFCA. A strategy, which could eventually lead to reduced elephant feeding levels in the most sensitive habitat types (Druce *et al.*, 2008). MSR already contains a population of elephants (estimated at 330 in 2006; Matthews & Nemane, 2006), but the combined elephant population in the Lubombo TFCA zone would be relatively small. Currently TEP management are implementing a contraceptive programme to reduce population growth in the short term (see Delsink *et al.*, 2006) until the park is linked with the other two reserves.

Throughout Africa, there are a number of other PAs where elephant feeding pressure is seen as having a negative impact on habitat structure and biodiversity (Owen-Smith *et al.*, 2006). Some of these PAs contain large numbers of artificial water points, many of which could be closed without having dramatic impacts on tourism potential (Gaylard *et al.*, 2003; Chamaillé-Jammes *et al.*, 2007b). The results from our study further demonstrate that surface water availability has a strong influence on elephant movements at the habitat and landscape scale. Moreover, our work presents further support for strategies that seek to reduce and manage large herbivore driven impacts, while also providing a methodology that could be expanded to include data on game viewing impacts and subsequent tourist satisfaction levels, which would help inform future management decisions.

ACKNOWLEDGEMENTS

We would like to thank Ezemvelo KwaZulu-Natal Wildlife for logistical support and access to the study site. Field ranger *N. Nthombeni* is thanked for his assistance with the data collection, providing expertise in locating and mapping the elephant paths. We are also very grateful to *N. Leader-Williams* for his comments on earlier drafts of the manuscript.

REFERENCES

Agnew, A.D.G. (1966) The use of game trails as a possible measure of habitat utilisation by large mammals. *East African Wildlife Journal*, **4**, 38–46.

de Beer, Y. & van Aarde, R.J. (2008) Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas? *Journal of Arid Environments*, **72**, 2017–2025.

Blanc, J.J., Barnes, R.F.W., Craig, G.C., Dublin, H.T., Thouless, C.R., Douglas-Hamilton, I. & Hart, J.A. (2007) *African elephant status report: an update from the African Elephant Database*. IUCN, Gland.

de Boer, W.F., Ntumi, C.P., Correia, A.U. & Mafuca, J.M. (2000) Diet and distribution of elephant in the Maputo Elephant Reserve, Mozambique. *African Journal of Ecology*, **38**, 188–201.

Boone, R.B. & Hobbs, N.T. (2004) Lines and fragments: effects of fencing on large herbivores. *African Journal of Range & Forage Science*, **21**, 147–158.

Caro, T. & Scholte, P. (2007) When protection falters. *African Journal of Ecology*, **45**, 233–235.

Chamaillé-Jammes, S., Valeix, M. & Fritz, H. (2007a) Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. *Journal of Applied Ecology*, **44**, 625–633.

Chamaillé-Jammes, S., Fritz, H. & Murindagomo, F. (2007b) Climate-driven fluctuations in surface-water availability and the buffering role of artificial pumping in an African savanna: potential implications for herbivore dynamics. *Austral Ecology*, **32**, 740–748.

Delsink, A.K., van Altena, J.J., Grobler, D., Bertyschinger, H., Kirkpatrick, J. & Slotow, R. (2006) Regulation of a small, discrete African elephant population through immunocontraception in the Makalali Conservancy, Limpopo, South Africa. *South African Journal of Science*, **102**, 403–405.

Druce, H.C., Pretorius, K. & Slotow, R. (2008) The response of an elephant population to conservation area expansion: Phinda Private Game Reserve, South Africa. *Biological Conservation*, **141**, 3127–3138.

Gaylard, A., Owen-Smith, N. & Redfern, J. (2003) Surface water availability: implications for heterogeneity and ecosystem process. *The Kruger experience* (ed. by J.T. du Toit, K.H. Rogers and H.C. Biggs), pp. 332–348. Island Press, Washington, USA.

Grainger, M., van Aarde, R. & Whyte, I. (2005) Landscape heterogeneity and the use of space by elephants in the Kruger National Park, South Africa. *African Journal of Ecology*, **43**, 369–375.

Höft, R. & Höft, M. (1995) The differential effects of elephants on rainforest communities in the Shimba Hills, Kenya. *Biological Conservation*, **73**, 67–79.

Johnson, C.F., Cowling, R.M. & Philipson, P.B. (1999) The flora of the Addo Elephant National Park, South Africa: Are threatened species vulnerable to elephant damage? *Biodiversity & Conservation*, **8**, 1447–1456.

Kinahan, A.A., Pimm, S.L. & van Aarde, R.J. (2007) Ambient temperature as a determinant of landscape use in the African elephant *Loxodonta africana*. *Journal of Thermal Biology*, **32**, 47–58.

Klingelhoeffer, E.W. (1987) *Aspects of the ecology of the elephant Loxodonta africana, and a management plan for the Tembe Elephant Reserve in Tongaland, KwaZulu*. MSc Thesis, University of Pretoria, Pretoria, South Africa.

Lindeque, M. & Lindeque, P.M. (1991) Satellite tracking of elephants in northwestern Namibia. *African Journal of Ecology*, **29**, 196–206.

Matthews, W.S. (2005) *Contributions to the ecology of Maputaland, southern Africa, with emphasis on Sand Forest*. PhD Thesis, Department of Botany, University of Pretoria, Pretoria, South Africa.

Matthews, W.S. & Nemane, M. (2006) *Aerial survey report for Maputo Special Reserve, Mozambique. November 2006*. Internal Reports for Usuthu–Tembe–Futi TFCA Project and KwaZulu-Natal Nature Conservation Service, Pietermaritzburg, South Africa.

Matthews, W.S., van Wyk, A.E., van Rooyen, N. & Botha, G.A. (2001) Vegetation of the Tembe Elephant Park, Maputaland, South Africa. *South African Journal of Botany*, **67**, 573–594.

Morley, R.C. & van Aarde, R.J. (2007) Estimating the abundance for a savanna elephant population using mark–resight methods: a case study for the Tembe Elephant Park, South Africa. *Journal of Zoology (London)*, **271**, 418–427.

O'Connor, T., Goodman, P.S. & Clegg, B. (2007) A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. *Biological Conservation*, **136**, 329–345.

Owen-Smith, R.N. (1992) *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press, Cambridge, UK.

Owen-Smith, R.N. (1996) Ecological guidelines for waterpoints in extensive protected areas. *South African Journal of Wildlife Research*, **26**, 107–112.

Owen-Smith, N., Kerley, G.I.H., Page, B., Slotow, R. & van Aarde, R.J. (2006) A scientific perspective on the management of elephants in the Kruger National Park and elsewhere. *South African Journal of Science*, **102**, 389–394.

Redfern, J.V., Grant, R., Biggs, H. & Getz, W.M. (2003) Surface water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology*, **84**, 2092–2107.

Redfern, J.V., Grant, C.C., Gaylard, A. & Getz, W.M. (2005) Surface water availability and the management of herbivore distributions in an African savanna ecosystem. *Journal of Arid Environments*, **63**, 406–424.

Shannon, G., Page, B., Duffy, K. & Slotow, R. (2006) African elephant home range and habitat selection in Pongola Game Reserve, South Africa. *African Zoology*, **41**, 37–44.

Shannon, G., Druce, D.J., Page, B.R., Eckhardt, H.C., Grant, R. & Slotow, R. (2008a) The utilisation of large savanna trees by elephant in southern Kruger National Park. *Journal of Tropical Ecology*, **24**, 281–289.

Shannon, G., Page, B., Mackey, R., Duffy, K. & Slotow, R. (2008b) Activity budgets and sexual segregation in the African elephant (*Loxodonta africana*). *Journal of Mammalogy*, **89**, 467–476.

Smit, I.P.J., Grant, C.C. & Devereux, B.J. (2007) Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation*, **136**, 85–99.

Smith, R.J., Easton, J., Nhancale, B.A., Armstrong, A.J., Culverwell, J., Dlamini, S., Goodman, P.S., Loffler, L., Matthews, W.S., Monadjem, A., Mulqueeny, C.M., Ngwenya, P., Ntumi, C.P., Soto, B. & Leader-Williams, N. (2008) Designing a transfrontier conservation landscape for the Maputaland centre of endemism using biodiversity, economic and threat data. *Biological Conservation*, **141**, 2127–2138.

Stokke, S. & du Toit, J. (2002) Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. *African Journal of Ecology*, **40**, 360–371.

Swets, J.A. (1988) Measuring the accuracy of diagnostic systems. *Science*, **240**, 1285–1292.

Thrash, I. (1998) Impact of water provision on herbaceous vegetation in Kruger National Park, South Africa. *Journal of Arid Environments*, **38**, 437–450.

Thrash, I. & Derry, J.F. (1999) The nature and modelling of piospheres: a review. *Koedoe*, **42**, 73–94.

Vanleeuwe, H. & Gautier-Hion, A. (1998) Forest elephant paths and movements at the Odzala National Park, Congo: the role of clearings and Marantacea forests. *African Journal of Ecology*, **36**, 174–182.

Viljoen, P.J. (1989) Habitat selection and preferred food plants of a desert dwelling elephant population in the northern Namib Desert. South West Africa/Namibia. *African Jouranl of Ecology*, **27**, 227–240.

Western, D. (1975) Water availability and its influence on the structure and dynamics of a savannah large mammal community. *East African Wildlife Journal*, **13**, 265–288.

Editor: Graeme Cumming