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Article in *Biological Conservation* · November 2010

DOI: 10.1016/j.biocon.2010.07.005

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Do fences create an edge-effect on the movement patterns of a highly mobile mega-herbivore?

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ARTICLE INFO

Article history:

Received 12 January 2010

Received in revised form 13 May 2010

Accepted 7 July 2010

Available online 31 July 2010

Keywords:

Barriers

Movement metrics

Ecosystem engineer

Habitat selection

African elephant

Loxodonta africana

ABSTRACT

Physical barriers, such as rivers and roads, constrain the movement of animals, usually by preventing access to adjacent habitats and impeding dispersal. Fences are artificial barriers that are commonly used as a conservation tool to intentionally restrict movements of animals to within protected reserves. However, the potential edge-effect of fences on the behaviour of animals within reserves is poorly understood. We examined the effect of fences on the movement patterns of African elephant (*Loxodonta africana*), an ecosystem modifier, in Pilanesberg National Park, South Africa. We used linear and non-linear models to determine the relationship between minimum distance from fence and seasonal daily net displacement of six GPS-collared female elephant. Elephant movement patterns were best explained by a piecewise regression that showed a strong negative relationship between minimum distance from fence and daily net displacement up to a “breakpoint” distance of 2551 m in the dry season and 3829 m in the wet season. The effect of the fence dissipated beyond this distance in both seasons. The increased tortuosity in movement patterns of elephant in the central area of the reserve suggested that they used this area more intensively for foraging compared to the peripheral area, as confirmed by differences in habitat selection. This occurs despite there being no difference in habitat composition between these areas. The decreased use of areas near the fence and more intensive foraging in the central areas constitute an important edge-effect of fences. Since elephant are ecosystem engineers, such edge-effects could potentially cascade throughout the reserve, adversely altering ecologically processes, particularly in reserves with a high edge-to-area ratio.

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1. Introduction

Natural and artificial landscape barriers can have large effects on animal movements (McDonald and St. Clair, 2004), foraging routes (Crist et al., 1992; Johnson et al., 2002), and home range use (Bailey et al., 1996). Barriers not only impede dispersing animals and restrict movements between patches, but can also create more complex movement paths in daily or seasonal behavioural patterns (Stamps et al., 1987). The effects of natural barriers, such as rivers and habitat boundaries, are well understood (Gobeil and Villard, 2002; Haddad and Kingsolver, 1999; Sieving et al., 1996), but the potential impact of artificial barriers, such as roads and fences, is of major conservation concern especially because they fragment habitats (Forman and Alexander, 1998; Hayward and Kerley, 2009). The effects of roads on the movement patterns of animals have been studied extensively (Benítez-López et al., 2010; Blake et al., 2008; Coffin, 2007; Dyer et al., 2002; Forman, 2003; Forman and Alexander, 1998; Trombulak and Frissell,

2000), but there is a surprising paucity on the effects of fences on movement behaviour. Fences are impermeable barriers to movement (Bauman et al., 1999; Hayward and Kerley, 2009), but they may also create an edge-effect, which can have a cascading effect on the behaviour of animals within their boundaries.

Fences provide both positive as well as negative contributions to conservation (see Hayward and Kerley (2009) for a review). Fences erected to prevent the spread of disease from wildlife to livestock, such as Botswana's veterinary fences, have resulted in mass-mortality of migrating ungulates (Hayward and Kerley, 2009; Williamson and Williamson, 2009). Similarly, Australia's dingo exclusion fence has resulted in mesopredator release of non-native foxes and cats (Dickman et al., 2009; Hayward and Kerley, 2009; Williamson and Williamson, 2009). By contrast, fences play a large positive role in the conservation efforts in southern Africa as many reserves with large mammals are fenced, which successfully protects them and reduces human-animal conflict (Grant et al., 2008). Unfortunately, this situation is also a cause for concern, especially for managers of small (<1000 km²) fenced reserves that include top predators that require large areas, such as lion *Panthera leo* (Kettles and Slotow, 2009), or highly mobile

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mega-herbivores, such as giraffe *Giraffa camelopardus* (Bond and Loffell, 2001) and African elephant *Loxodonta africana* (Kerley et al., 2008).

Elephant are ecosystem engineers or modifiers (Jones et al., 1994; Wright and Jones, 2006) and thus, their movement behaviour and distribution in the landscape have the potential to affect many ecological processes (Kareiva, 1990; Turchin, 1998). Within fenced reserves, elephant can drastically and irreversibly alter the environment by killing trees (Shannon et al., 2008a), changing woody communities (e.g. Wiseman et al., 2004), and possibly decreasing biological diversity (Cumming et al., 1997; Grant, 2005; Owen-Smith et al., 2006). However fences, as impermeable barriers, may also alter movement patterns of elephant within their boundaries by creating an edge-effect whereby the degree of impact on the environment (via elephant) can be spatially non-uniform. For example, in some reserves in South Africa, elephant are “habituated” to electrified fences before introduction (Garai and Carr, 2001; Garai et al., 2004) which results in an avoidance of fences. The success of this aversive conditioning is supported by the observation that elephant herds are cautious when exploring new areas after fences are removed (Druce et al., 2008). Where elephant are not habituated to electrified fences (e.g. free ranging populations), areas near fences can be disproportionately utilised (Loarie et al., 2009b). In Namibia, Loarie et al., (2009a,b) have shown that fences constrain the movements of elephant, especially during the wet season when home ranges typically expand, causing them to revisit the fence more often. This shift in movement pattern is hypothesised to result in an overutilization of vegetation near the fence.

Thus, whether elephant avoid fences or increase utilization of areas closer to fence lines, these expressions of the edge-effect could potentially have a deleterious effect on vegetation structure within reserves (Grant et al., 2008; Van Aarde and Jackson, 2007). Furthermore, elephant could frequently include areas near fences within their home ranges, yet utilize and move within those areas differently, which could still result in spatially non-uniform effects on the vegetation. This heterogeneous effect would be most pronounced in the dry season when home ranges typically are smaller (Shannon et al., in press) or in small reserves with large elephant populations (Shannon et al., 2006a).

In this study, we examined the effect of the impermeable boundary fence on the movement patterns and habitat use of female elephant in the Pilanesberg National Park (PNP), South Africa. We hypothesised that the presence of the fence will affect the movement behaviour of elephant in PNP, possibly due to the habituation at the time of introduction and/or the human disturbance outside the reserve. We expected this behavioural alteration to manifest as an increase in daily net displacement closer to the fence, which would be marked in the dry season, due to smaller home range sizes and limited availability of forage (Leggett, 2006; Loarie et al., 2009a). Differences in movement patterns of elephant may ultimately be driven by their selection of habitats within the reserve, and thus we also examined habitat selection in relation to the fence.

2. Material and methods

2.1. Study area

Pilanesberg National Park (PNP; 25°8–25°22'S, 26°57–27°13'E; 570 km²), Northwest Province, South Africa, is located within the transition zone of Kalahari Thornveld in the west and Bushveld in the east. The region has summer rainfall of approximately 630 mm p.a. and has two main seasons, a wet season between November and April, and a dry season from May to October. Geo-

logically, PNP is an extinct volcanic crater formed over 1200 million years ago and is an example of an alkaline ring complex. The habitat consists mainly of savanna ranging from broadleaf/*Acacia* thickets to open grassland. We assigned habitats based on a vegetation map prepared by the PNP management (Brockett, 1993) and categorised PNP into six major vegetation types: *Acacia caffra* woodland, *A. karoo* woodland, *A. mellifera* woodland, *Combretum* woodland, *Mixed Acacia* woodland and grassland.

Elephant were introduced to PNP between 1981 and 1998. The total population in 2004 was 158, comprising 34 adult males and 124 females and juveniles in 16 family groups (mean group size 8 ± 3 SD) (Shannon et al., 2008b). GPS-collars (Africa Wildlife Tracking, Pretoria, SA) were fitted to six elephant cows, belonging to different breeding herds within the PNP population (between October 2004 and February 2005). Elephant cow herds, known as family units, consist of a matriarch with her daughters and their offspring. The individuals in a family unit are always in close proximity to each other and consequently move about the landscape in a cohesive unit. Thus, the movement of these elephants (ID: CE03, CE13, CE32, CE61, CE81 and CE88) was assumed to represent the movement behaviour of the breeding herd to which they belonged. We do not have similar data on adult bull elephants, whose behaviour is substantially different from that of females, and may be considered as a different “ecological species” (Shannon et al., 2006b). Thus, in this paper, elephant refers to mixed-sex family units. Positional fixes were obtained every 4–6 h. Error associated with the fixes were expected to be comparable to that of Loarie et al., (2009a; error SD ± 50 m of estimated location), as they used similar GPS collars from the same manufacturer and habitat conditions are similar (positional dilution of precision was not available for our collars). All elephant handling procedures were approved by the Animal Ethics Committee of the University of KwaZulu-Natal.

2.2. Analysis of movement patterns

We computed daily net displacement as a function of step length and turning angle for each elephant using Hawth's Tools (Beyer, 2006) in ArcGIS 9.3 software (Environmental Systems Research Institute, Redlands, CA, USA). To meet assumptions of independence of data for parametric statistics, we subsampled the data by time to remove autocorrelation in step length. We estimated the Autocorrelation Function (ACF) for a set of daily net displacement values with a lag of up to three time steps. We used the Ljung-Box Q statistic to determine the minimum interval of time steps that were not autocorrelated. The resulting metrics from this sub-sampling regime are assumed to represent statistically independent data with regard to movement and habitat selection. For each point along the daily path, we extracted the distance to fence using ArcGIS 9.3 and used the minimum distance from the fence along the daily path as our predictor variable (Fig. 1). Minimum distance from the fence allowed us to test the prediction that close proximity to the fence at any point in the daily trajectory will influence elephant movement patterns.

We removed from the analysis all locations from 21 September 2005 to 20 September 2006 to remove the changes in movement (Woolley et al., 2008) and habitat use as a result of a fire that affected large areas of the park in September 2005. We also removed all location data for elephants ranging into the extension zone of PNP, an area of ~1660 ha that was added to the northwestern boundary in March 2004. Elephant movements within that new area should be interpreted as exploration (Druce et al., 2008), which would differ from their general movement decisions within the rest of the reserve. Despite truncating the data in this manner, we still capture the representative movement and space use patterns of elephant because of the large sample size of locations ($n = 790$ paths in the wet season, 1113 paths in the dry season).

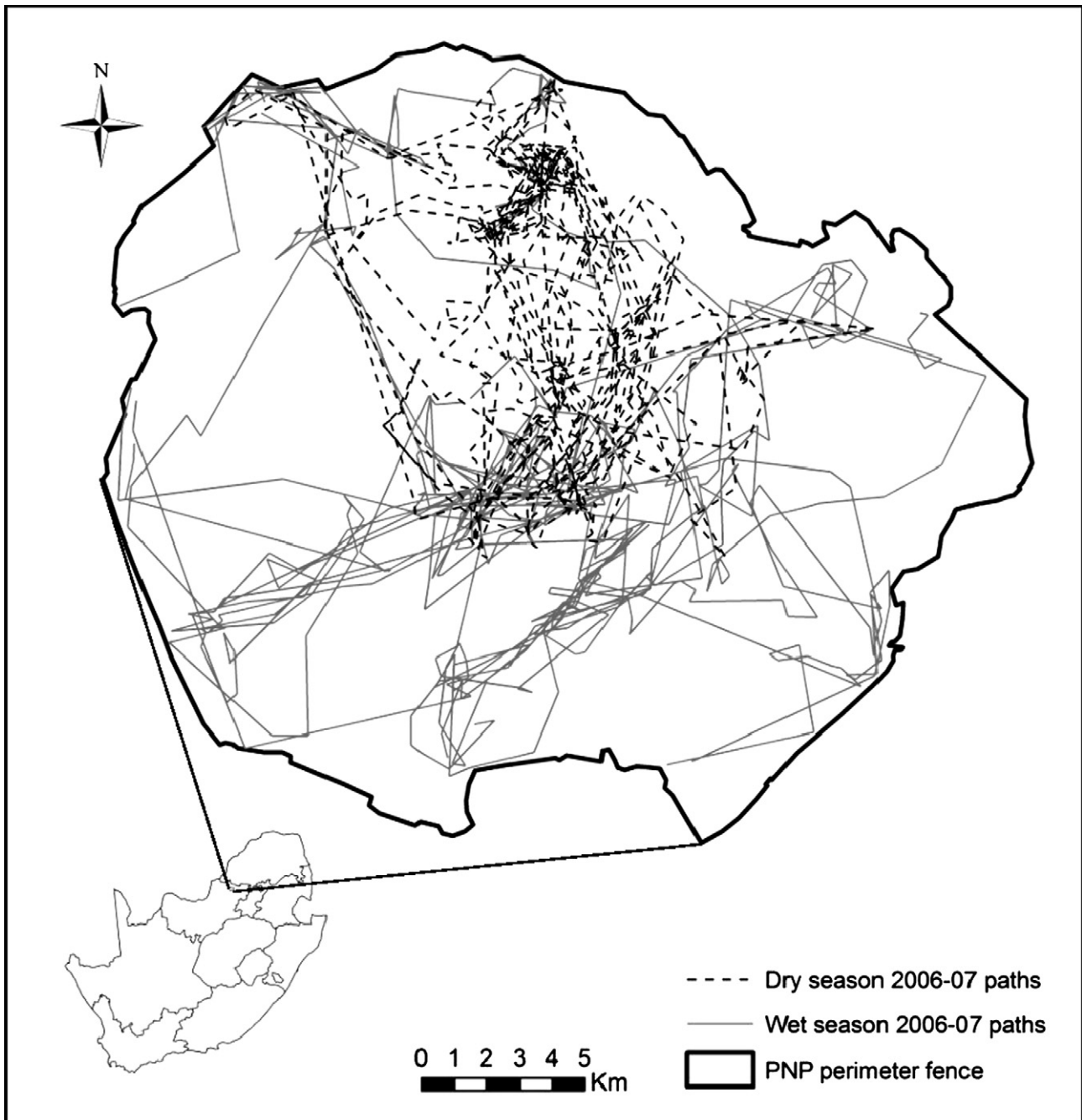


Fig. 1. Map of Pilanesberg National Park, South Africa, showing the perimeter fence and movement paths of CE 81 as an illustration of the use of the landscape by an elephant herd in the dry and wet seasons.

To determine the relationship between the minimum distance to the fence and daily net displacement of elephant in each season (wet and dry), we first fitted a Lowess smoothed and unsmoothed model (Cleveland, 1979) to each scatterplot of the data to check whether a non-linear relationship existed. Movement responses across distance gradients tended to follow a sigmoid curve, but our Lowess fitting suggested threshold changes with a single breakpoint. Evidence for a threshold in the changes in movement patterns along the distance from fence gradient was examined by comparing three regression models: linear model, sigmoid model of the form $[Y = a + bx + bx^2 + bx^3]$ and piecewise regression model with one breakpoint (Muggeo, 2003; Toms and Lesperance, 2008) of the form: $[Y = a + bx \text{ if } D \leq \text{breakpoint } T; Y = a + bx + (b + e)(D - T) \text{ where } D > \text{breakpoint } T]$, where Y is daily net displacement, a is the

intercept, x is the minimum distance from fence, b is the slope for distance to fence to the left of the breakpoint (T), and $e = \text{“difference in slope parameter”}$ so that $b + e$ is the slope of the line segment to the right of the breakpoint. We used ranges of initial estimates of the breakpoint at 500 m intervals based on visual inspection of the Lowess smoothing function (Eigenbrod et al., 2009; Toms and Lesperance, 2008).

To quantify the extent of the edge-effect of the fence on the daily net displacement of elephant, we compared Akaike's Information Criterion (AIC) values of the simple linear model, the sigmoidal model and the piecewise regression model (Burnham and Anderson, 2002). Strong evidence for a threshold response, indicating a change in response pattern, requires that the piecewise regression model (Radford et al., 2005) or the sigmoidal

model (e.g. Fahrig, 2002) provide a better fit to the data than the simple regression model. We report Akaike weights (w_i), as a measure of relative support for each model, and parameter estimates for the effect of the fence in each model. We also calculated the bootstrapped 95% confidence intervals for the breakpoint in the piecewise regression model. Statistical analyses were conducted in SPSS 15.0 and R 2.10.

2.3. Analysis of habitat use

To determine whether the patterns in movement metrics were independent of habitat and space use by elephants, we divided the reserve into two zones based on the threshold limit (of minimum distance from the fence) obtained from the piecewise regression analysis for each season. We determined whether the proportion of habitat types differed across the two zones using a chi-square contingency test. We also determined whether elephant selected the habitats differently within these zones using compositional analysis (Aebischer et al., 1993) by comparing the percentage of individual elephant locations within each zone to the proportions of the habitats in that zone. We used all locations, collected over equal time intervals, for the compositional analysis as it is robust to autocorrelation (Aebischer et al., 1993). We used the *Compana* function (ADEHABITAT package; Calenge, 2006) in the statistical software R 2.10 to conduct the compositional analysis. We used Mixed *Acacia* Woodland as a denominator habitat for the log-ratios and χ^2 tests with $\alpha = 0.05$ for significance tests. Habitats with zero use values were substituted with 0.01 (Aebischer et al., 1993). Because we are interested in the effects of proximity to the fence on habitat selection, we do not discuss results of specific habitat selection by elephant, but only differences in degree of selection between the zones.

3. Results

3.1. Analysis of movement patterns

We obtained 3806 daily pathways for the six female herds across 3 years. Based on the autocorrelation function, we determined that a sampling interval gap of 24 h yielded spatially independent movement paths (ACF = 0.019, $Q = 0.277$, $P = 0.6$). We thus resampled the data at ≥ 24 h intervals, and obtained 1113 daily paths for the dry season and 790 paths for the wet season (e.g. Fig. 1).

The scatterplots of the data fitted with a Lowess model indicated that a non-linear relationship existed between the minimum distance to fence and daily net displacement. Based on the AIC scores, the piecewise regression model for both dry and wet seasons provided a better fit to the data than the sigmoidal or linear regressions (Table 1 and Fig. 2). The piecewise regression identified a negative relationship between minimum distance from the fence and daily net displacement for the dry season ($b = -0.75$) with one breakpoint at a threshold value of 2551 m (± 397 m 95% CI) from the fence (Fig. 2a). In the wet season, daily net displacement was also negatively related to minimum distance from the fence ($b = -0.47$) with a breakpoint at 3829 m (± 1250 m 95% CI) from the fence (Fig. 2b). Beyond these breakpoints, minimum distance from the fence had a weak positive effect on the daily net displacement of elephant in the dry season ($b = 0.04$) and weak negative effect in the wet season ($b = -0.01$).

3.2. Analysis of habitat use

We found no significant difference in habitat composition on either side of the breakpoint for the wet season ($\chi^2_1 = 9.15$,

Table 1

Values of Akaike's Information Criterion (AIC) and weights (w) for the models used to identify the effect of distance to fence on daily net displacement of elephant in the wet and dry seasons in Pilanesberg National Park, South Africa.

Model	AIC	Δ AIC	w
<i>Dry season</i>			
Piecewise regression	19280.32	0	0.971
Sigmoidal function	19287.32	7.00	0.029
Linear regression	19364.90	84.58	0
<i>Wet season</i>			
Piecewise regression	13849.51	0	0.986
Sigmoidal function	13858.01	8.48	0.014
Linear regression	13882.76	33.25	0

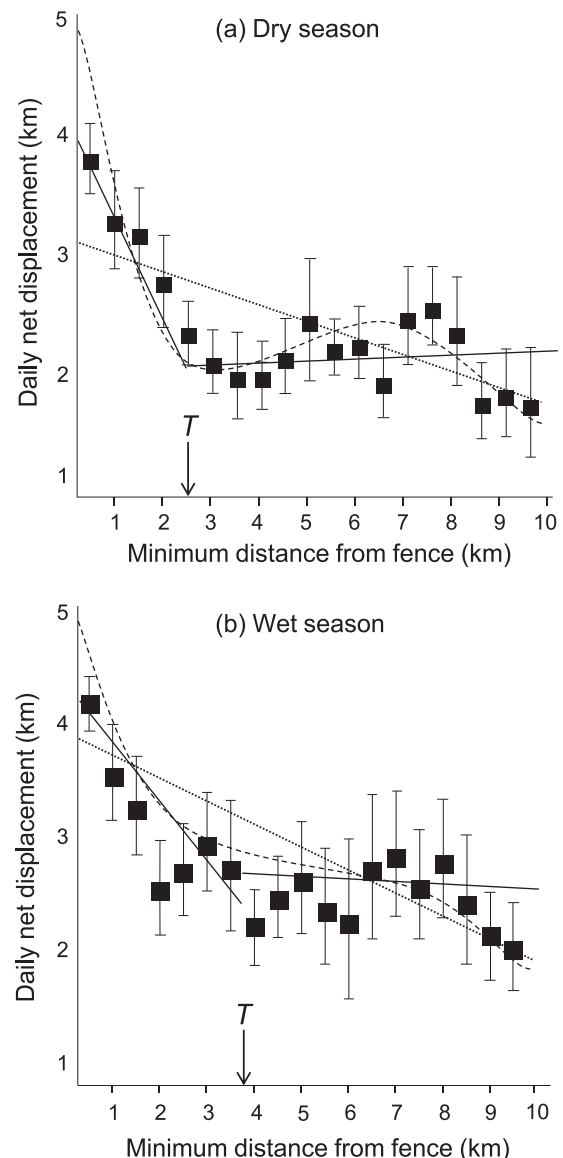


Fig. 2. The effect of the boundary fence on daily net displacement (means ± 1 SE at 500 m intervals) of six elephant herds in Pilanesberg National Park, South Africa in the (a) dry and (b) wet seasons. Shown are regressions fitting linear (dotted line), sigmoidal (dashed line), and piecewise responses (solid line). T denotes the breakpoint distance from fence for the piecewise regression model.

$P = 0.10$) or the dry season ($\chi^2_1 = 7.64$, $P = 0.18$). Compositional analysis of habitat selection by elephant ranked grasslands as the highest selected habitat in the central area of the reserve in both

seasons, but grasslands ranked low in the peripheral areas for both seasons (Table 2). Instead, *Acacia mellifera* woodland, which was ranked low in the central region in both seasons, was ranked highest in selection in the peripheral area. Selection of all other habitats differed between seasons and between areas on either side of the breakpoint (Table 2).

4. Discussion

The movement patterns of elephant in PNP were strongly influenced by the proximity of the impermeable perimeter fence. Daily net displacement was markedly higher when closer to the fence, and showed a strong linear decrease up to 2.6 km from the fence in the dry season and 3.8 km in the wet season. Beyond these threshold distances, displacement rate was lower and largely unaffected by the proximity to the fence. This pattern of elephant movement cannot be attributed to habitat composition, as we found no significant differences in habitat types on either side of the breakpoint. Elephant did differ in the selection of habitats, indicating differences in foraging behaviours between the two areas on either side of the threshold distance. Thus, by using movement metrics rather than just static patterns of animal distribution (Forrester et al., 2007), we were able to discriminate non-linear spatially-explicit behavioural differences related to the impermeable fence.

As expected, season also had a strong effect on the space use of elephant. The reduced availability of forage for elephant during the dry season results in smaller dry season home ranges (Leggett, 2006; Loarie et al., 2009a; Owen-Smith, 1988) that are concentrated around water and forage resources (Chamaillé-Jammes et al., 2007; Loarie et al., 2009b). The wider availability of resources in the wet season lifts this constraint, resulting in larger home range sizes and greater movement across the landscape (Loarie et al., 2009b; Owen-Smith, 1988; Shannon et al., in press). In PNP, we found that elephant had an overall lower daily net displacement during the dry season compared to the wet season,

and the effect of the fence also dissipated at a shorter distance. This restricted movement in the dry season is consistent with the expectation that there are ecological and energetic constraints on movement during that season. However, even in the dry season, there was a markedly higher net displacement close to the fence. This consistent and strong negative response to the fence implies a risk aversion behaviour that outweighs the ecological drivers of seasonal movement patterns. Such an edge-effect of fences could potentially cascade into other aspects of elephant behaviour across the reserve, especially in reserves where seasonally-limited resources may prevent them from overcoming the energetic cost.

Landscape level movement patterns can reflect foraging behaviour (Fortin, 2003; Johnson et al., 2002; Morales et al., 2004) and can be a response to habitat quality and landscape configuration (Forester et al., 2007; Fortin, 2003; Zollner and Lima, 1999). Lower net displacement is a measure of tortuosity in movement patterns, which is indicative of foraging and more intensive use of habitats (Johnson et al., 2002; Morales et al., 2004; Patterson et al., 2008). In PNP, elephant selected grassland, *A. caffra* woodland, and *Combretum* woodland habitats in the central areas, which contain the main forage plant species for elephant herds (Woolley, 2008). These habitats were not selected in the area closer to the fence in either season. Lower daily net displacement and differences in habitat selection imply that elephant utilised the central region of the reserve for foraging more intensively compared to the peripheral areas, even though there was no difference in the proportion of different vegetation types on either side of the threshold distance.

Travelling greater distances when closer to the fence may be a result of the aversive response to the electrified boundary as well as the negative effects of increased disturbance from human activity outside the fences. Elephant have been shown to display a “streaking” behaviour in response to human related disturbances, moving swiftly through travel corridors in unprotected areas (Douglas-Hamilton et al., 2005) or when crossing roads in unprotected areas (Blake et al., 2008). In PNP, the management roads along the perimeter fence are seldom used by tourists and thus

Table 2

Compositional analysis of habitat use by elephants on either side of the threshold distance from the fence in both the dry and wet season in Pilanesberg National Park, South Africa. Habitat types are listed in order of rank of selection with 5 being highest selection and 1 being lowest selection. + and – denote direction of selection and +++ and – – – denote significant differences at $P < 0.05$. The denominator habitat for the analysis is Mixed *Acacia* woodland.

	<i>A. caffra</i> woodland	<i>A. karoo</i> woodland	<i>A. mellifera</i> woodland	<i>Combretum</i> woodland	Grassland	Rank
<i>Dry season: area near the fence</i>						
<i>A. mellifera</i> woodland	+	+		+	+++	5
<i>Combretum</i> woodland	+	+++	–		+	4
<i>A. caffra</i> woodland		+++	–	–	+	3
Grassland	–	+	– – –	–		2
<i>A. karoo</i> woodland	– – –		–	– – –	–	1
<i>Dry season: central area</i>						
Grassland	+	+++	+	+++		5
<i>A. caffra</i> woodland	+	+++		+++	–	4
<i>A. mellifera</i> woodland		+	–	+	–	3
<i>Combretum</i> woodland	–	+	– – –		– – –	2
<i>A. karoo</i> woodland	–		– – –	–	– – –	1
<i>Wet season: area near the fence</i>						
<i>A. mellifera</i> woodland	+	+		+	+	5
<i>A. caffra</i> woodland		+	–	+	+	4
<i>Combretum</i> woodland	–	+	–		+	3
<i>A. karoo</i> woodland	–		–	–	+	2
Grassland	–	–	–	–		1
<i>Wet season: central area</i>						
Grassland	+++	+++	+++	+++		5
<i>Combretum</i> woodland	+++	+++	+++		– – –	4
<i>A. caffra</i> woodland		+++	+	– – –	– – –	3
<i>A. mellifera</i> woodland	–	+		– – –	– – –	2
<i>A. karoo</i> woodland	– – –		–	– – –	– – –	1

may provide easier travel paths, yet herds in PNP are rarely observed using these fence roads (S. Dell, Field Ecologist, PNP, personal communication). Thus, the negative association of the fence in PNP may be a better explanation for the behavioural change closer to fences than the ease of using management roads.

In PNP, the reduced foraging by elephant in the areas close to the fence may transfer foraging pressure into the interior areas of the reserve. Increasing foraging pressure by elephant has been linked to a deterioration in habitat quality and vegetation structure (Guldmond and Van Aarde, 2008; Kerley et al., 2008). Thus, as highly mobile ecosystem modifiers, elephant may be transmitting the edge-effect of fences to the central parts of the reserve. Large-scale extensions of edge-effects have been demonstrated for other species and ecosystems (Curran et al., 1999; Ewers and Didham, 2008; Laurance, 2000; Woodroffe and Ginsberg, 1998). For example, human hunting of large carnivores on the periphery of protected areas strongly reduces population persistence inside the protected area (Balme et al., 2010; Woodroffe and Ginsberg, 1998). In the roughly circular shaped PNP, even a conservative 500 m-wide zone of influence around the perimeter fence accounts for nearly 10% of the area of the reserve where elephant show lowered utilization activity. Indeed, we show an edge-effect on movement that extends up to 3.8 km inward from the fence, indicating that edge-effects on elephant movements can be great. In reserves with a high edge-to-area ratio [such as Phinda (Druce et al., 2008) and Phongola Game Reserves (Shannon et al., 2006a) in South Africa] these edge-effects may be further exacerbated as elephant will be exposed to a proportionally greater area that is influenced by a fence effect. Thus, small fenced reserves, especially those with a suboptimal reserve shape may also have to take the fence effect into account while estimating the reserve's carrying capacity for large herbivore population management. Given that the use of fences is increasing in the conservation efforts of several countries (Hayward and Kerley, 2009), the consolidation of small fenced reserves and removal of internal fences to create larger, optimally-shaped reserves (Soulé and Wilcox, 1980) can help mitigate edge-effects created by perimeter fences.

Acknowledgements

Funding was received from Amarula (Distell (Pty.) Ltd.), South Africa, PPC Cement, South Africa and National Research Foundation (GUN: 2053623 to RS), South Africa. ATV and MT were supported by University of Kwazulu-Natal post-doctoral fellowships. We thank Northwest Parks and Tourism Board for logistical and other support, in particular Gus van Dyk for his contribution to the elephant project at Pilanesberg. We thank L.A. Woolley for providing the base maps.

References

- Aebischer, N., Robertson, P., Kenward, R., 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74, 1313–1325.
- Bailey, D., Gross, J., Laca, E., Rittenhouse, L., Coughenour, M., Swift, D., Sims, P., 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management* 49, 386–400.
- Balme, G.A., Slotow, R., Hunter, L.T.B., 2010. Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda-Mkhuze complex, South Africa. *Animal Conservation*. doi:10.1111/j.1469-1795.2009.00342.x.
- Bauman, P., Jenks, J., Roddy, D., 1999. Evaluating techniques to monitor elk movement across fence lines. *Wildlife Society Bulletin* 27, 344–352.
- Benítez-López, A., Alkemade, R., Verweij, P.A., 2010. The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. *Biological Conservation* 143, 1307–1316.
- Beyer, H., 2006. Hawth's Analysis Tools for ArcGIS. <<http://www.spatial ecology.com/htools>>.
- Blake, S., Deem, S., Strindberg, S., Maisels, F., Momont, L., Isia, I., Douglas-Hamilton, I., Karesh, W., Kock, M., 2008. Roadless wilderness area determines forest elephant movements in the Congo Basin. *PLoS ONE* 3, e3546. doi:3510.1371/journal.pone.0003546.
- Bond, W., Loffell, D., 2001. Introduction of giraffe changes *Acacia* distribution in a South African savanna. *African Journal of Ecology* 39, 286–294.
- Brockett, B.H., 1993. Woody Vegetation States and Community Descriptions Reference Guide for Pilanesberg National Park. Bophuthatswana National Parks and Wildlife Management Board, South Africa Version 1.0.
- Burnham, K.P., Anderson, D.R., 2002. Model selection and inference. A Practical Information – Theoretic Approach. Springer, New York, USA.
- Calenge, C., 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197, 516–519.
- Chamaillé-Jammes, S., Valeix, M., Fritz, H., 2007. Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. *Journal of Applied Ecology* 44, 625–633.
- Cleveland, W.S., 1979. Robust locally weighted regression and smoothing scatterplots. *Journal of the American Statistical Association* 74, 829–836.
- Coffin, A., 2007. From roadkill to road ecology: a review of the ecological effects of roads. *Journal of Transport Geography* 15, 396–406.
- Crist, T., Guertin, D., Wiens, J., Milne, B., 1992. Animal movement in heterogeneous landscapes: an experiment with *Eleodes* beetles in shortgrass prairie. *Functional Ecology* 6, 536–544.
- Cumming, D.H.M., Fenton, M.B., Rautenbach, I.L., Taylor, R.D., Cumming, G.S., Cumming, M.S., Dunlop, J.M., Ford, A.G., Hovorka, M.D., Johnston, D.S., Kalcounis, M., Mahlangu, Z., Portfors, C.V.R., 1997. Elephants, woodlands and biodiversity in southern Africa. *South African Journal of Science* 93, 231–236.
- Curran, L., Caniogo, I., Paoli, G., Astianti, D., Kusneti, M., Leighton, M., Nirarita, C., Haeruman, H., 1999. Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science* 286, 2184–2188.
- Dickman, C., Glen, A., Letnic, M., 2009. Reintroducing the dingo: can Australia's conservation wastelands be restored? In: Hayward, M., Somers, M. (Eds.), *Reintroductions of Top-order Predators*, pp. 238–269.
- Douglas-Hamilton, I., Krink, T., Vollrath, F., 2005. Movements and corridors of African elephants in relation to protected areas. *Naturwissenschaften* 92, 158–163.
- Druce, L., 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.
- Dyer, S., O'Neill, J., Wasel, S., Boutin, S., 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. *Canadian Journal of Zoology* 80, 839–845.
- Eigenbrod, F., Hecnar, S., Fahrig, L., 2009. Quantifying the road-effect zone: threshold effects of a motorway on anuran populations in Ontario, Canada. *Ecology and Society* 14, e24.
- Ewers, R., Didham, R., 2008. Pervasive impact of large-scale edge effects on a beetle community. *Proceedings of the National Academy of Sciences* 105, 5426–5429.
- Fahrig, L., 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. *Ecological Applications* 12, 346–353.
- Forester, J., Ives, A., Turner, M., Anderson, D., Fortin, D., Beyer, H., Smith, D., Boyce, M., 2007. State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. *Ecological Monographs* 77, 285–299.
- Forman, R., 2003. *Road Ecology: Science and Solutions*. Island Press, Washington, DC, USA.
- Forman, R., Alexander, L., 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29, 207–231.
- Fortin, D., 2003. Searching behavior and use of sampling information by free-ranging bison (*Bos bison*). *Behavioral Ecology and Sociobiology* 54, 194–203.
- Garäi, M., Carr, R., 2001. Unsuccessful introductions of adult elephant bulls to confined areas in South Africa. *Pachyderm* 31, 52–57.
- Garäi, M., Slotow, R., Carr, R., Reilly, B., 2004. Elephant reintroductions to small fenced reserves in South Africa. *Pachyderm* 37, 28–36.
- Gobeil, J., Villard, M., 2002. Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. *Oikos* 98, 447–458.
- Grant, C., 2005. *Elephant Effects on Biodiversity: An Assessment of Current Knowledge and Understanding as a Basis for Elephant Management in SANParks*. Scientific Report 3.
- Grant, C.C., Bengis, R., Balfour, D., Peel, M., Davies-Mostert, W., Killian, H., Little, R., Smit, I., Garäi, M.E., Henley, M., Anthony, B., Hartley, P., 2008. Controlling the distribution of elephants. In: Scholes, R.J., Mennell, K.G. (Eds.), *Elephant Management: A Scientific Assessment for South Africa*. Wits University Press, Johannesburg, SA, pp. 329–369.
- Guldmond, R., Van Aarde, R., 2008. A meta-analysis of the impact of African elephants on savanna vegetation. *Journal of Wildlife Management* 72, 892–899.
- Haddad, N., Kingsolver, J., 1999. Corridor use predicted from behaviors at habitat boundaries. *The American Naturalist* 153, 215–227.
- Hayward, M., Kerley, G., 2009. Fencing for conservation: restriction of evolutionary potential or a riposte to threatening processes? *Biological Conservation* 142, 1–13.
- Johnson, C., Parker, K., Heard, D., Gillingham, M., 2002. Movement parameters of ungulates and scale-specific responses to the environment. *Journal of Animal Ecology* 71, 225–235.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.

- Kareiva, P., 1990. Population dynamics in spatially complex environments: theory and data. *Philosophical Transactions of the Royal Society of London B* 330, 175–190.
- Kerley, G., Landman, M., Kruger, L., Owen-Smith, N., Balfour, D., de Boer, W., Gaylard, A., Lindsay, K., Slotow, R., 2008. Effects of elephant on ecosystems and biodiversity. In: Scholes, R.J., Mennell, K.G. (Eds.), *Elephant Management: A Scientific Assessment for South Africa*. Wits University Press, Johannesburg, SA, pp. 101–147.
- Kettles, R., Slotow, R., 2009. Management of free-ranging lions on an enclosed game reserve. *South African Journal of Wildlife Research* 39, 23–33.
- Laurance, W., 2000. Do edge effects occur over large spatial scales? *Trends in Ecology & Evolution* 15, 134–135.
- Leggett, K., 2006. Home range and seasonal movement of elephants in the Kunene Region, northwestern Namibia. *African Zoology* 41, 17–36.
- Loarie, S., van Aarde, R., Pimm, S., 2009a. Elephant seasonal vegetation preferences across dry and wet savannas. *Biological Conservation* 142, 3099–3107.
- Loarie, S., van Aarde, R., Pimm, S., 2009b. Fences and artificial water affect African savannah elephant movement patterns. *Biological Conservation* 142, 3086–3098.
- McDonald, W., St Clair, C., 2004. The effects of artificial and natural barriers on the movement of small mammals in Banff National Park, Canada. *Oikos* 105, 397–407.
- Morales, J., Haydon, D., Frair, J., Holsinger, K., Fryxell, J., 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* 85, 2436–2445.
- Muggeo, V., 2003. Estimating regression models with unknown break-points. *Statistics in Medicine* 22, 3055–3071.
- 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.
- Owen-Smith, R., 1988. *Megaherbivores*. Cambridge University Press, Cambridge, UK.
- Patterson, T., Thomas, L., Wilcox, C., Ovaskainen, O., Matthiopoulos, J., 2008. State-space models of individual animal movement. *Trends in Ecology & Evolution* 23, 87–94.
- Radford, J., Bennett, A., Cheers, G., 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation* 124, 317–337.
- Shannon, G., Druce, D.J., Page, B.R., Eckhardt, H.C., Grant, R., Slotow, R., 2008a. The utilization of large savanna trees by elephant in southern Kruger National Park. *Journal of Tropical Ecology* 24, 281–289.
- Shannon, G., Page, B., Duffy, K., Slotow, R., in press. The ranging behaviour of a large sexually dimorphic herbivore in response to seasonal and annual environmental variation. *Austral Ecology*. doi:10.1111/j.1442-9993.2009.02080.x.
- Shannon, G., Page, B., Slotow, R., Duffy, K., 2006a. African elephant home range and habitat selection in Pongola Game Reserve, South Africa. *African Zoology* 41, 37–44.
- Shannon, G., Page, B.R., Duffy, K.J., Slotow, R., 2006b. The role of foraging behaviour in the sexual segregation of the African elephant. *Oecologia* 150, 344–354.
- Shannon, G., Page, B.R., Mackey, R.L., Duffy, K.J., Slotow, R., 2008b. Activity budgets and sexual segregation in African elephants (*Loxodonta africana*). *Journal of Mammalogy* 89, 467–476.
- Sieving, K., Willson, M., De Santo, T., 1996. Habitat barriers to movement of understory birds in fragmented south-temperate rainforest. *The Auk* 113, 944–949.
- Soulé, M., Wilcox, B., 1980. *Conservation Biology: An Evolutionary-Ecological Perspective*. Sinauer Associates Sunderland, MA.
- Stamps, J., Buechner, M., Krishnan, V., 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. *The American Naturalist* 129, 533–552.
- Toms, J., Lesperance, M., 2008. Piecewise regression: a tool for identifying ecological thresholds. *Ecology* 84, 2034–2041.
- Trombulak, S., Frissell, C., 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14, 18–30.
- Turchin, P., 1998. *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sinauer Associates, Sunderland, MA.
- Van Aarde, R., Jackson, T., 2007. Megaparks for metapopulations: addressing the causes of locally high elephant numbers in southern Africa. *Biological Conservation* 134, 289–297.
- Williamson, D., Williamson, J., 2009. Botswana's fences and the depletion of Kalahari wildlife. *Oryx* 18, 218–222.
- Wiseman, R., Page, B., O'Connor, T., 2004. Woody vegetation change in response to browsing in Ithala Game Reserve, South Africa. *South African Journal of Wildlife Research* 34, 25–37.
- Woodroffe, R., Ginsberg, J., 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280, 2126–2128.
- Woolley, L., Millspaugh, J., Woods, R., van Rensburg, S., Mackey, R., Page, B., Slotow, R., 2008. Population and individual elephant response to a catastrophic fire in Pilanesberg National Park. *PLoS ONE* 3, e3233. doi:10.1371/journal.pone.0003233.
- Woolley, L.A., 2008. *Environmental Stochasticity and African Elephant Population Dynamics: Investigating Limitation Through Juvenile Mortality*, Ph.D. Thesis. University of KwaZulu-Natal, Durban, South Africa, pp. 147.
- Wright, J., Jones, C., 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. *BioScience* 56, 203–209.
- Zollner, P., Lima, S., 1999. Search strategies for landscape-level interpatch movements. *Ecology* 80, 1019–1030.