Chapter 19
Mapping Landscape Resistance to Identify Corridors and Barriers for Elephant Movement in Southern Africa

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19.1 Introduction

One of Africa's greatest conservation successes is the recovery of elephant (*Loxodonta africana*) populations within protected areas (e.g. Aleper and Moe 2006), such as those in northern Botswana. This recovery poses several challenges, however. First, habitat within protected areas is becoming degraded from high intensity elephant browsing. Second, the increasing elephant and human populations in the region have led to large increases in human–elephant conflict along the periphery of protected areas (Sitati et al. 2005; Lee and Graham 2006). Management options include facilitating natural dispersal, active relocation, and culling. Relocation is prohibitively expensive as a population-level solution given the high per capita cost. Culling is politically unpopular given Botswana's booming wildlife tourist industry. Simultaneously, large areas of the neighboring countries of Namibia, Zambia and Angola have low elephant densities. Some of these governments desire to increase elephant populations within their protected areas to promote the growth of wildlife tourism. Thus, facilitated dispersal of elephants from high density areas of northern Botswana to protected areas in other countries with low elephant densities is an attractive potential solution.

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S.A. Cushman and F. Huettmann (eds.), *Spatial Complexity, Informatics, and Wildlife Conservation*
DOI 10.1007/978-4-431-87771-4_19, © Springer 2010

Recently, several approaches have been shown to be effective in developing rigorous, species specific landscape resistance maps, which represent the resistance to organism movement as functions of multiple variables from a variety of spatial scales. Such resistance maps, if reflective of the factors and scales at which organisms respond to environmental conditions in their movement behaviour, provide a key foundation for a variety of applied analyses of landscape connectivity, including identification of factors that influence landscape connectivity and mapping of movement corridors. Cushman et al. (2006) developed landscape resistance maps using molecular genetic data and least cost path modelling. Such landscape genetic approaches hold tremendous promise for evaluating the factors that affect gene flow over time scales of several to many generations. However, many of the issues of most conservation importance are incipient in time such that they have not yet left a genetic signature in the population. In addition, for some conservation questions it is the movement of organisms rather than of genes that is the critical parameter.

To address the factors that affect organism movement directly on time scales of less than the life span of individual organisms, landscape resistance modelling with telemetry data perhaps holds the greatest promise (e.g. Osborn and Parker 2003). GPS telemetry data can provide spatially precise records of the movement paths of individual animals at a temporal sampling rate that allows direct assessment of the influences of landscape features on movement path selection. This enables the development of species-specific landscape resistance models in which the resistance of any location, or pixel, in a landscape is a function of multiple landscape features measured at one or several scales.

Cushman et al. (2005) investigated the pattern of temporal autocorrelation of elephant movements monitored thorough satellite telemetry in Botswana. They found that autocorrelation of elephant movements is long-term, complex and seasonally related. During much of the year, locations as much as 30 days apart were significantly autocorrelated. This autocorrelation presents a problem for traditional analyses that treat individual locations as statistically independent replicates for statistical analysis. Some researchers have advocated subsampling these autocorrelated movement data streams to achieve statistical independence. However, this approach does not in fact remove spatial dependence (Fortin and Dale 2005) and results in unacceptable information loss (Cushman et al. 2005). In addition, the spatial patterns of movement that create autocorrelation are the biological signal that should be investigated. Thus, alternative methods that do not depend on statistically independent individual locations are essential.

In this study, we use a path-level spatial randomization method to assess the effects of multiple landscape features on elephant movement in the transboundary region of Botswana, Namibia and Zambia. The first goal of this study was to evaluate the influences of water sources, roads, wildlife fences and human settlements on elephant movements, and use this information to produce a map of landscape resistance to elephant movements.

Movement resistance models are essential foundations for applied analyses of population connectivity. However, resistance maps are not in themselves sufficient to answer many questions of greatest concern. For example, pixel level resistance to movement does not in itself provide sufficient information to evaluate the existence, strength and location of barriers and corridors. Where resistance maps are point specific, connectivity is route specific. Connectivity must be evaluated as the path and cost of moving across a landscape resistance model from a source to a destination. The resistance model is the foundation for these analyses, but it is explicit consideration of movement paths across the resistance surface that provides the key information for conservation and management.

By adding source-destination least cost path analysis to species-specific landscape resistance mapping, it is possible to comprehensively analyze the effects of landscape structure on animal movement such that the strength and location of movement corridors and barriers can be rigorously evaluated (Cushman et al. 2009). The second goal of this paper is to map potential movement corridors and barriers between northern Botswana and Sioma National Park in Zambia, and evaluate the relative impact of water sources, wildlife fences and human settlements on elephant movement routes and degree of habitat isolation.

19.2 Materials and Methods

19.2.1 Movement Data

This study used GPS location data from four elephant herds and landscape maps of rivers, roads, fences and settlements to identify corridors, barriers and to produce a map of landscape resistance to elephant movement. The GPS data consist of fixes acquired at 8 hour intervals (Fig. 19.1). Elephant 1 was monitored from July 14, 2005 to September 18, 2006, elephant 2 from August 9, 2003 to December 3, 2004, elephant 3 from June 26, 2005 to September 18, 2006, and elephant 4 from August 19, 2003 to April 30, 2005.

19.2.2 Path Randomization and Landscape Resistance Hypotheses

Our analysis tests alternative hypotheses of landscape resistance against the movement paths selected by individual elephants. Elephant movements may be influenced by landscape features (Sitati et al. 2003, Murwira and Skidmore 2005). A priori, we proposed six landscape features that we believe may influence elephant movements, including distance to water (Chamaille-Jammes 2006), roads, wildlife fences, towns, villages and subsistence huts (Lee and Graham 2006). These features can be combined to create many alternative models of possible landscape resistance to movement.

To determine relative support among the many possible alternative models of landscape resistance, we compared utilized paths to available paths in a two-step

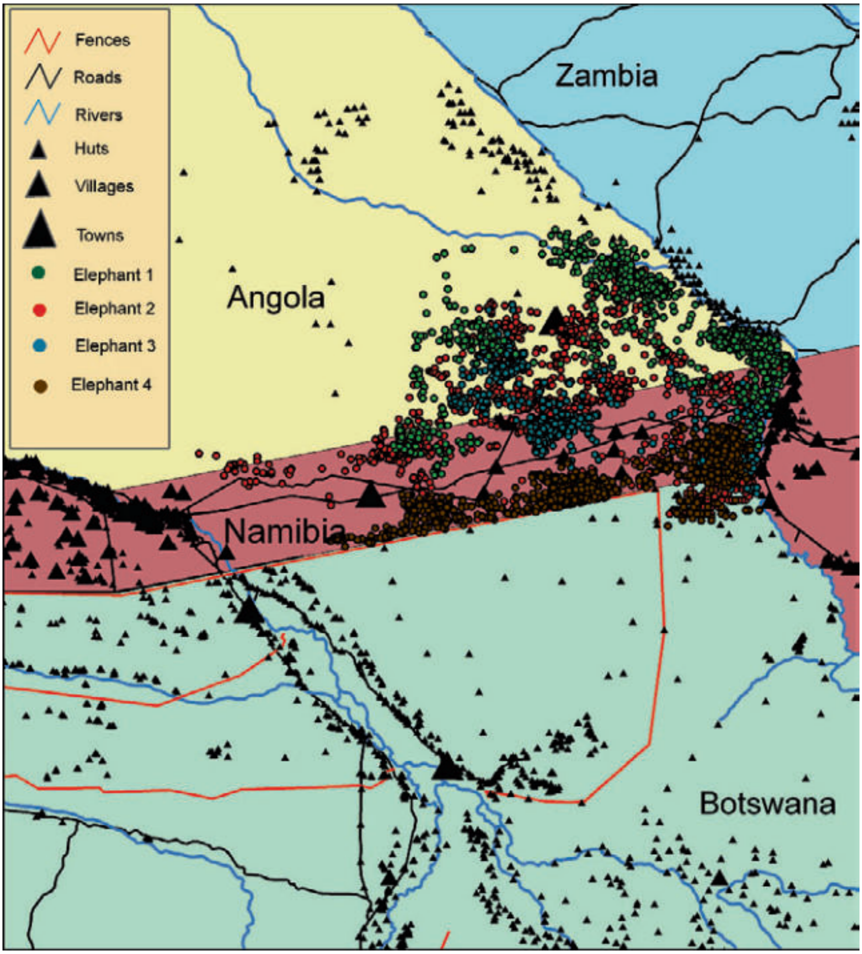

Fig. 19.1 Map showing the study area, landscape features used in the resistance hypotheses (fences, roads, rivers and settlements) and the locational data for each of the four elephants included in the analyses

process. First, the utilized path was created by converting the series of sequential point locations for each elephant into a line in ArcInfo workstation (ESRI 2005). Second, 199 available paths with identical topology were created by randomly shifting and rotating this utilized path. The available paths were randomly shifted a distance between 0 and 30 km in x and y, and randomly rotated between 0° and 360°. This resulted in a population of 199 available paths with identical spatial topology for each utilized path (Fig. 19.2). The statistical support for the resistance model is determined by calculating the number of standard errors the cumulative cost for the utilized path is from the distribution of costs of the randomized sample of 199 available paths.

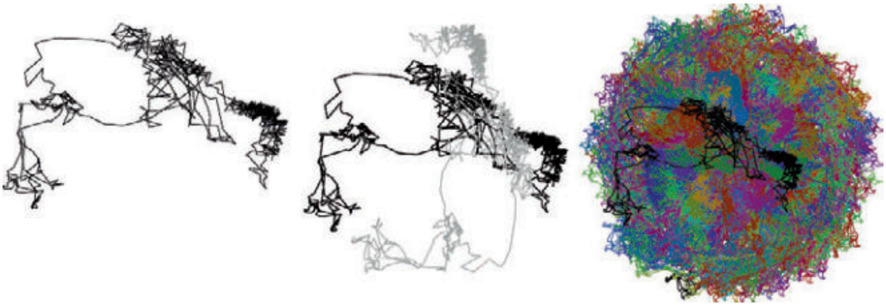

Fig. 19.2 Utilized path and random paths for elephant 1. The utilized path is shown on the left, a single random path overlaid in the middle, and the full set of 199 random paths on the right

19.2.3 Scaling of Landscape Resistance Factors

It is important to determine the spatial scale at which each landscape feature maximally influences elephant movement (Wiens 1989). We conducted a scaling analysis for each landscape feature independently by computing the standard errors of the utilized path from the distribution of available paths for each factor for multiple scales. We investigated scaling relationships of towns, villages and huts at five scales. These scales were created by placing a unimodal resistant kernel (e.g. Compton et al. 2007) of varying width over each town, village or hut and summing the kernels into a resistance surface. The five scales we compared corresponded to kernel widths of 1, 5, 10, 20, and 40. Similarly, we conducted a scaling analysis for distance to water. We compared resistance scaled as linear distance, square root of distance and the square of the distance to water. Roads and fences were analyzed at a single scale. We treated these as potential barriers, such that resistance only accumulated in crossing these features, and not as functions of their proximity.

19.2.4 Factorial Weighting Analysis

In addition to scaling, we also conducted factorial weighting analyses to determine the most supported combination of weights among the resistance factors for each individual elephant. A priori, we specified three levels of relative weight, 1, 5 and 10. A factor given a weight of five has five times the maximum resistance value of a factor given weight 1, and ½ the maximum resistance value of a factor given weight 10. The analysis then proceeds by computing combined resistance values for each cell in the landscape based on the sum of resistances due to the different landscape features. This was conducted across a factorial combination of the three relative weights given to each landscape feature.

19.2.5 Monte Carlo Randomization to Assess Support

We used a Monte Carlo permutation procedure to test for global support. When hypotheses are constructed across a quantitative range of values for a parameter, it is possible to evaluate the degree to which the analysis indicates a unimodal peak of support for a global best model. This is done by computing the differences in support (in our case standard errors from mean of the distribution of available paths) among all neighbouring cells in the hypothesis cube and comparing the sum of those differences to the distribution of the sum of differences from a large number of randomizations of the hypothesis cube.

In our case, we have two 3 × 3 × 3 hypothesis cubes for each elephant, totalling 27 cells per cube. We computed the sum of the differences in the standard errors from the mean of the available path distribution between each pair of neighbouring hypotheses in the 27 cell hypothesis cube. We then randomized the locations of each value of the standard error within the 27 cell cube 99,999 times, recalculating the sum of the differences in standard errors each time. The test evaluates the significance of a unimodal peak of support for the best model in the hypothesis cube.

19.2.6 Model Averaging

The scaling and weighting analyses identified a best resistance model for each elephant. We produced a global model across elephants by averaging the four individual resistance models on a cell-by-cell basis. This produced a single, average resistance model which was used for all subsequent analyses.

19.2.7 Least Cost Path Analysis

We mapped movement corridors and identified potential barriers by computing the density of least cost paths across the resistance map between 1,183 points in northern Botswana and the geographical center of Sioma National Park. The 1,183 points were selected systematically to provide source points at 5 km spacing throughout northern Botswana, to give a comprehensive view of movement routes from all of northern Botswana to Sioma national Park.

First, we computed the cost distance from Sioma National Park to all points in the study area, using the COSTDISTANCE function in ArcInfo Workstation (ESRI 2005). This provided a measure of isolation of each location in northern Botswana from Sioma National Park, based on the resistance map. Next, we calculated the difference in cost distance between the current landscape and the predicted resistance for the same landscape in the absence of fences, roads and human settlements, to provide a measure of the effects of human development on population isolation across the study area.

Then, we computed least cost paths between each of the 1,183 source pixels and the destination pixel using the COSTPATH function in ArcInfo Workstation (ESRI 2005). These least cost paths are single pixel in width, and record the route of a least cost path from the source to the destination pixel. We smoothed these lease cost paths by applying a parabolic kernel with a 3000 m radius, on the belief that actual paths taken will imperfectly follow least cost routes due to stochastic behavioural choices of individual animals. The kernel smoothed least cost paths were then summed to provide maps of the density of least cost routes from northern Botswana to Sioma. We computed these summed least cost path maps for two resistance models: (1) the full landscape resistance model, (2) landscape resistance predicted in the absence of settlements, fences and roads. The comparison of these two enables us to identify both the areas of highest importance for connectivity in the current landscape, and to evaluate the effects of anthropogenic barriers in blocking historical movement corridors.

19.3 Results

19.3.1 Scaling Analyses

There was high consistency among elephants in the scales at which each factor was most strongly related to movement path selection. All four elephants showed strong avoidance of towns, with three of the four showing strongest avoidance at a kernel width of 5 km (Table 19.1). Similarly, all four elephants showed significant avoidance of villages and huts, with three of four showing strongest avoidance at a kernel width of 1 km, in both cases (Tables 19.2 and 19.3). These results show that the movements of these four elephants are negatively related to the presence of human settlements on the landscape, with strong avoidance of towns at distances of up to 5 km, and avoidance of villages and huts at a finer spatial scale of up to 1 km.

Interestingly, there is an apparent positive relationship between elephant movements and the presence of huts and villages at scales of over 20 km and with towns at scales of over 40 km. This is a result of spatial covariation between the

Table 19.1 Scaling results showing avoidance of towns by elephants across scales from 1 to 40 km. Numbers in the table refer to the number of standard errors from the mean of the distribution of available paths that the utilized path fell in terms of cumulative resistance due to towns, at each of the five spatial scales. The table indicates that all four elephants significantly avoided towns, with three of the four most strongly avoiding towns at a scale of 5 km

	1 km	5 km	10 km	20 km	40 km
Elephant 1	–26.42	–38.71	–34.16	–15.28	67.13
Elephant 2	–51.02	–35.63	–13.46	27.34	30.63
Elephant 3	–4.8	–6.69	–4.68	0.76	13.91
Elephant 4	–51.02	–52.41	–52.41	–52.07	–10.5

Table 19.2 Scaling results for villages across scales from 1 to 40 km. The table indicates that all four elephants significantly avoided villages, with three of the four showing strongest avoidance at a scale of 1 km

	1 km	5 km	10 km	20 km	40 km
Elephant 1	−2.8	−3.63	2.2	11.67	9.08
Elephant 2	−48.2	−41	−23.8	0.47	12.63
Elephant 3	−6.35	−5.72	4.86	15.48	18.85
Elephant 4	−51.02	−29.45	−24.28	−12.8	−7.91

Table 19.3 Scaling results for huts across scales from 1 to 40 km. The table indicates that all four elephants significantly avoided huts, with three of the four showing strongest avoidance at a scale of 1 km

	1 km	5 km	10 km	20 km	40 km
Elephant 1	−68.9	−50.65	−2.57	51.28	76.67
Elephant 2	−33.52	−34.62	−19.09	10.05	30.54
Elephant 3	−86.36	−64.77	3.55	64.1	57
Elephant 4	−41.75	−38.82	−17.79	60.4	103.05

Table 19.4 Scaling results for distance to water. Sqrt D – Square root distance to water, D – Euclidean distance to water, Dsq – Square of the distance to water. The table indicates that all three elephants significantly selected movement paths near water. Two of the four elephants had highest support for a model where resistance increases as the square root of distance to water. Elephant 4 had statistically equal support for SqrtD and D, while elephant 2 had statistically equal support for D and Dsq

	SqrtD	D	Dsq
Elephant 1	−15.24	−12.41	−5.04
Elephant 2	−14.44	−15.8	−15.9
Elephant 3	−11.34	−5.87	−2.18
Elephant 4	−17.61	−17.83	−10.93

location of human settlements and water (Fig. 19.1). Human settlements tend to be located near permanent rivers. As shown below, elephants select areas near rivers preferentially for movement. This results in an apparent positive relationship between settlements and elephant movements at large spatial scales, but is an artefact of elephants selecting routes near water but that avoid coming into close proximity to human settlements.

Movements of all four elephants were strongly related to distance to water, with strong selection for movement paths relatively close to permanent rivers (Table 19.4). Two of the four elephants showed significantly stronger relationships with the square root of distance to water than to Euclidean distance or distance squared. Elephant 4 showed marginally more support for Euclidean distance, but it was not significantly more supported than the square root of distance to water. Elephant 2, however, had statistically equal support for selection of movement paths based on proximity to water as measured by Euclidean distance or the square of Euclidean distance.

Table 19.5 Avoidance of crossing fences and roads. All four elephants showed significant avoidance of crossing wildlife fences, with elephant 4 showing very strong avoidance. In contrast, only elephant 1 showed significant avoidance of crossing roads. This suggests that fences are a much stronger barrier to elephant movements in the study area than are roads

	Fence	Road
Elephant 1	–6.8	–10.65
Elephant 2	–25.4	–0.236
Elephant 3	–15.1	0.512
Elephant 4	–95.1	–0.621

All four elephants showed significant avoidance of crossing fences (Table 19.5), with elephant 4 showing much stronger avoidance than the others. In contrast, only elephant one showed a significant avoidance of crossing roads (Table 19.5).

19.3.2 Weighting Analyses

19.3.2.1 Towns–Villages–Huts

We conducted a weighting analysis for resistance due to settlements across a full factorial of three levels of relative weighting (1, 5, 10). The factorial of three levels of resistance for each of towns, villages and huts is represented as a 3 × 3 × 3 hypothesis cube. Elephants 1 and 3 had identical models receiving highest support. For these elephants, the relative influence of huts appears to be ten times that of villages or towns. In contrast, the most supported weighting hypothesis for elephant 2 suggests that the relative influence of villages is twice that of towns and ten times that of huts. Finally, the most supported weighting hypothesis for elephant 4 suggests that villages have twice the influence of huts and ten times the influence of towns.

19.3.2.2 Water–Fences–Settlements

We conducted a factorial weighting analysis to determine the relative importance of settlements, water and fences to elephant movement path selection for each of the four elephants, incorporating the optimal scaling for each elephant from the scaling analysis across a full factorial of three levels of relative weighting (1, 5, 10). The factorial of three levels of resistance for each factor is represented as a 3 × 3 × 3 hypothesis cube. Elephants 1, 2 and 3 had identical models receiving highest support. For these elephants, the relative influence of settlements and fences are equal, and ten times that of distance to rivers. Finally, the most supported weighting hypothesis for elephant 4 suggests that the relative influence of fences is five times that of settlements or water.

19.3.2.3 Roads

Only one elephant (Elephant 1) showed significant relationships with roads. We combined the optimal water–fences–settlements hypothesis for elephant 1 with the three possible levels of roads (1, 5, 10). The most supported combined model for Elephant 1 indicated that maximum road and water effects are approximately equal and much weaker than the effects of settlements or fences.

19.3.3 Monte Carlo Randomization Tests

19.3.3.1 Towns–Villages–Huts Factorial

We compared the actual sum of differences between adjacent cells in the Towns–Villages–Huts hypothesis cubes for each elephant with the distribution of summed differences from 99,999 random permutations of the hypothesis cubes (Table 19.6). For each elephant, the actual sum of differences of adjacent cells in the hypothesis cube is lower than any of those obtained in permuting the adjacencies randomly. For all elephants, there is a very strong and highly significant unimodal peak of support. This suggests a unimodal peak of support within the tested model space.

19.3.3.2 Settlements–Water–Fences Factorial

The comparison of the differences between adjacent cells in the Settlements–Water–Fences hypothesis cubes with the distribution of summed differences from 99,999 random permutations suggests that for all elephants the tested models form a highly unimodal pattern of support (Table 19.7). For each of elephants 1–3, the actual sum of differences of adjacent cells in the hypothesis cube is lower

Table 19.6 Comparison of actual sum of differences between adjacent cells in the towns–villages–huts hypothesis cube with the distribution of summed differences from 99,999 random permutations. For each elephant, the actual sum of differences of adjacent cells in the hypothesis cube is lower than any of those obtained in permuting the adjacencies randomly. For all elephants there is a very strong and highly significant unimodal peak of support, indicating that the most supported cell in the hypothesis cube is a peak of support

Elephant	Minimum sum of differences of adjacencies across 99,999 permutations	Actual sum of differences of adjacencies	Probability of no difference
1	74.7	68.01	<0.00001
2	165.5	154.9	<0.00001
3	88.1	85.8	<0.00001
4	138.2	117.8	<0.00001

Table 19.7 Comparison of actual sum of differences between adjacent cells in the Settlements–Water–Fences hypothesis with the distribution of summed differences from 99,999 random permutations of the hypothesis cubes. For elephants 1–3, the actual sum of differences of adjacent cells in the hypothesis cube is lower than any of those obtained in permuting the adjacencies randomly. In the case of elephant 4, the actual sum of differences of adjacencies was ranked 29th from the least of 99,999. For all elephants there is a very strong and highly significant unimodal peak of support. The most supported cell in the hypothesis cube is a peak of support

Elephant	Minimum sum of differences of adjacencies across 99,999 permutations	Actual sum of differences of adjacencies	Probability of no difference
1	73.3	60.6	<0.00001
2	264.4	213.8	<0.00001
3	117.1	93.8	<0.00001
4	228.4	245.8	0.00029

than any of those obtained in permuting the adjacencies randomly. In the case of elephant 4, the actual sum of differences of adjacencies was ranked 29th from the bottom of 100,000. For all elephants there is a strong and highly significant unimodal peak of support.

19.3.4 Mapping the Average Model

The scaling and weighting analysis identified a best model for each elephant. In all cases, this best model was the top of a unimodal peak of support in the parameter space. We combined these four best models into a global model by averaging the resistance surfaces predicted by these models across the four elephants (Fig. 19.3). The value of each pixel in this map is the expected resistance of that location to elephant movement, as predicted by the combined model. Resistance in the map ranges from a minimum of 1, for example along rivers far from human settlements, to a maximum resistance of 10.

19.3.5 Cost Distance Mapping

Cost distance increases away from the destination pixel in Sioma National Park as a function of the least cumulative cost across the resistance map (Fig. 19.4). Figure 19.4 illustrates that fences seem to exert a dominant effect on isolation of parts of northern Botswana from Sioma, with human settlements also contributing substantially to isolation in the north eastern part of the study area. Figure 19.5 shows the relative change in least cost distance from each pixel in the study area to the Sioma destination cell between the current landscape, including fences, settlements and roads, and a hypothetical historic resistance landscape without human development.

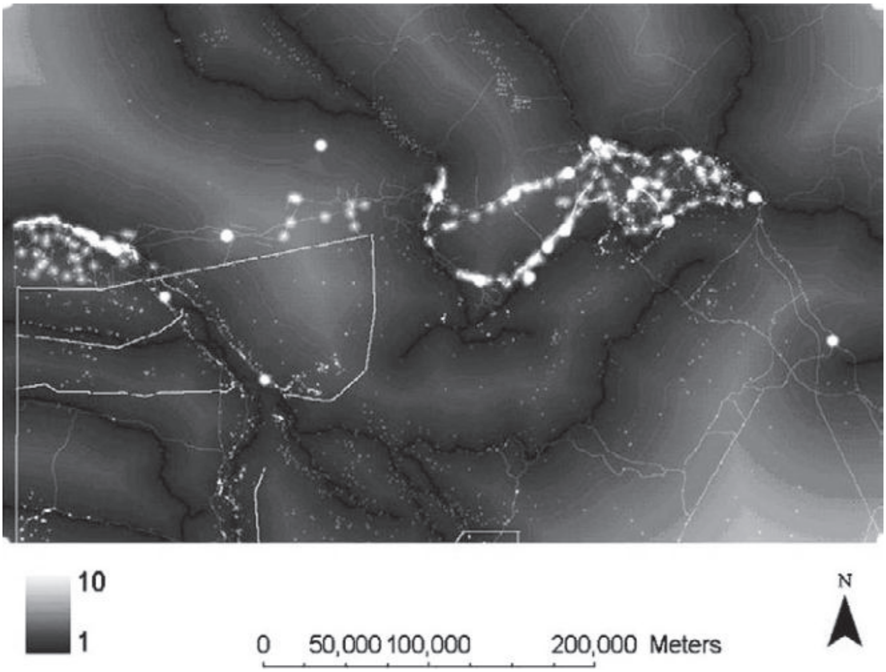

Fig. 19.3 Best resistance model, created by averaging the maps produced by the scaled and weighted resistance models for each of the four elephants. Lighter shades indicate higher resistence

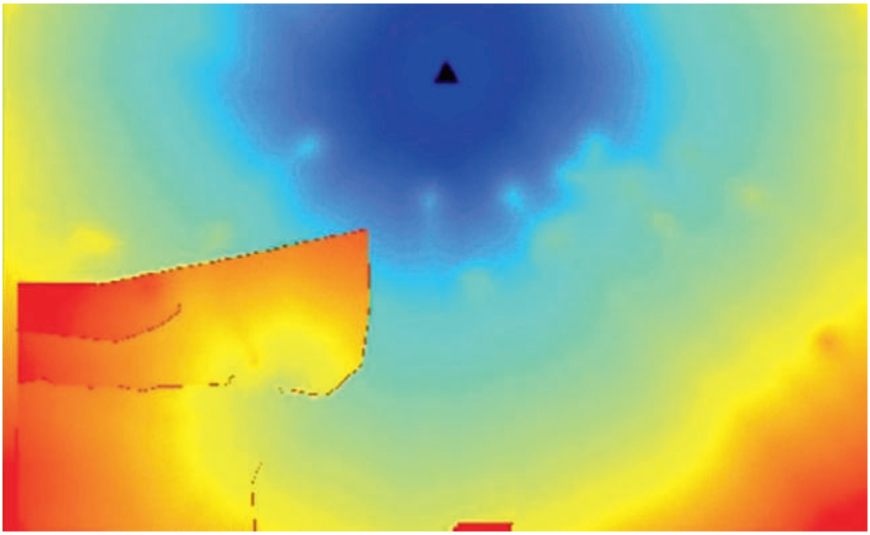

Fig. 19.4 Map of cost distance from every cell in the study area to the destination cell in Sioma National Park. Veterinary fences in the southwest corner of the study area have a dominant effect on cost distance, with settlements in the northwest part of the study area also having a substantial influence on cost distance to Sioma National Park

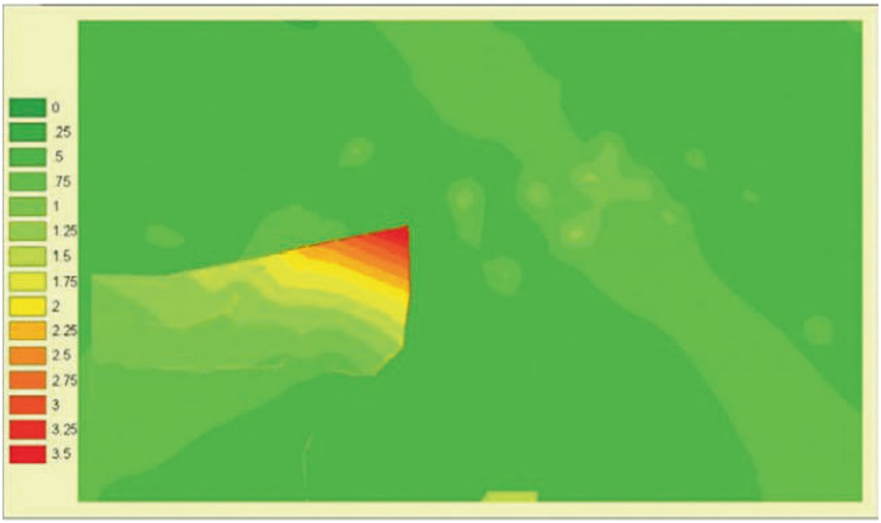

Fig. 19.5 Relative change in cost distance between the current landscape and a hypothetical landscape without human settlements, fences or roads. Areas within the perimeter of the Border Cordon and Northern Buffalo fence are predicted to have an increase of between 100 and 400% in cost distance to Sioma National Park. The dense human settlements in the Caprivi Strip result in much less increase in cost distance in the northeast portion of the study area

Areas in dark green are those for which there is little or no change in cost distance to Sioma National Park. Areas in light green are predicted to have between 100 and 175% increase in cost distance in the current landscape compared to historic. Areas in yellow and orange are predicted to have an increase of between 175 and 300%, and red over 300% in cost distance to Sioma National Park.

19.3.6 Cost Path Corridor Mapping

Figure 19.6 shows the density of least cost paths to Sioma National Park in a historic landscape without human development (Fig. 19.6a), and the current landscape (Fig. 19.6b). The corridor analysis for the historic landscape indicates that the least cost route of elephants to Sioma will be approximately straight lines, except when the path moves into proximity to rivers, in which cases the paths are altered to preferentially follow the river courses.

Figure 19.6 shows several major corridors, most notably a large central corridor flowing along the Kwando and Botetti Rivers, which collects the paths from most of the central portion of the study area. Three other notable corridors exist also. First, a corridor is predicted from the upper Okavango panhandle across the dry uplands of Caprivi and south east Angola. Second, a substantial corridor is predicted from the Chobe/Linyanti region in the east-central portion of the study area and

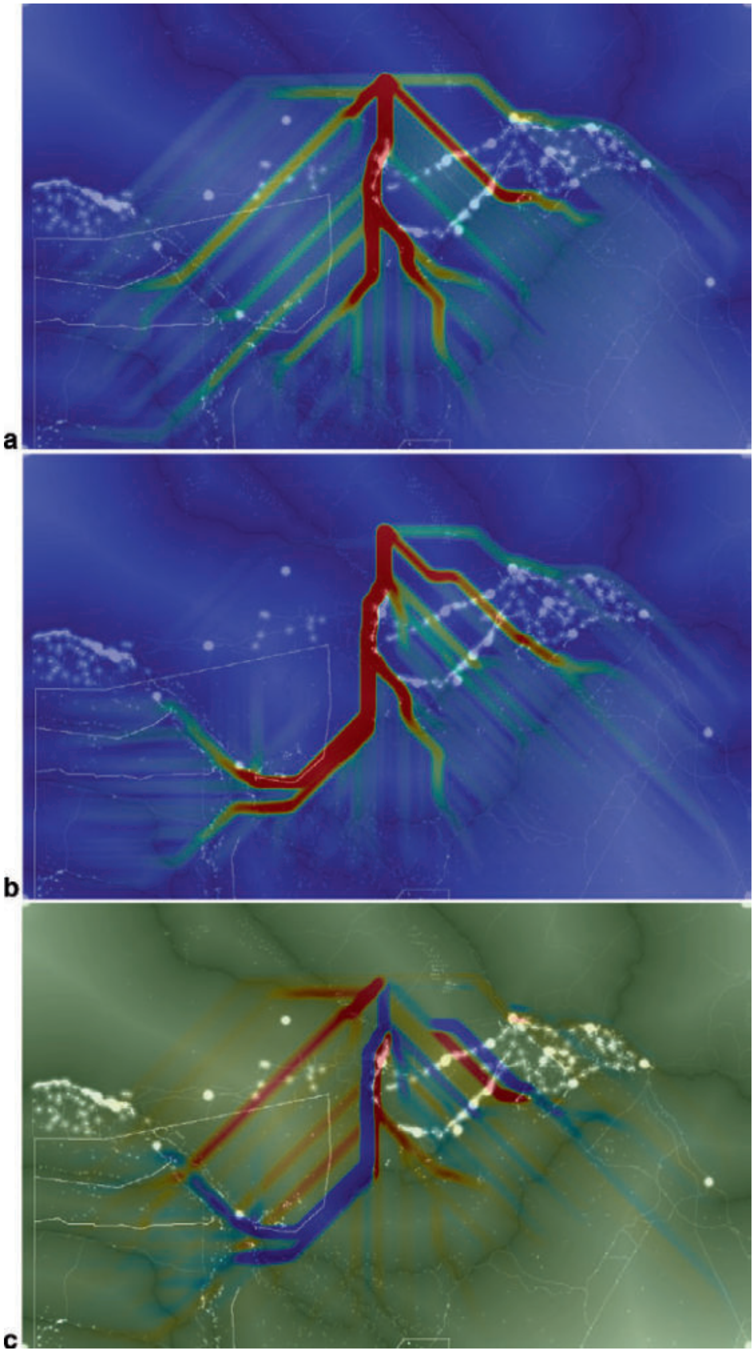

Fig. 19.6 Map of least cost path corridors from 1183 points uniformly distributed across the study area to Sioma National Park for (**a**) the landscape in the absence of human settlements, roads or fences, (**b**) the current landscape including human settlements, roads and fences, and (**c**) the proportional difference between current and historic corridors. Maps 5a and 5b are scaled from blue, reflecting very low density of least cost paths, to red, reflecting very high density of least

across Caprivi and south west Zambia to Sioma. Finally, a relatively minor corridor is predicted to Sioma along the Zambeizi River corridor.

Figure 19.6b shows the expected corridor density in the current landscape and 6c shows the difference between the two corridor maps, scaled as a proportion change of the maximum of Fig. 19.6a. The most notable difference is the elimination of the movement corridors from the Okavango Delta in the west central part of the study area to Sioma, and their rerouting south and around to the east to connect with the central Kwando–Botetti corridor due to the barrier effects of the Border Cordon and Northern Buffalo veterinary fences. Another notable change is the rerouting of much of the south east branch of the Kwando–Botetti corridor in the current landscape north between gaps between towns and villages in the Caprivi strip due to human settlement along the Kwando River along the Angola–Zambia border. A third notable change is the slight rerouting of the Chobe-Linyanti corridor to the northeast to pass through gaps between towns in the Caprivi strip.

19.4 Discussion

19.4.1 Resistance of Utilized Pathway Compared to Available Paths

We used a multi-factorial approach to assess the influences of multiple landscape factors on the selection of elephant movement paths. Focusing on the entire movement path as an observational unit, rather than individual relocation points, resolves several challenges, including spatial autocorrelation among locations, pseudoreplication of observations and most importantly allowed us to powerfully assess the cumulative cost of elephant movement paths. The path randomization procedure produces a large number of available paths of identical spatial topology with which to compare to the utilized path for each individual elephant. This provides a strong means to evaluate use versus availability based on cumulative resistance of movement paths, while holding the length and shape of the paths constant, which is necessary for meaningful comparison among paths.

Formal scaling analyses are critical to identify the spatial scale at which each landscape feature had the strongest relationship with the selection of elephant movement paths. Given the strong differences observed in the apparent relationships

Fig. 19.6 (continued) cost paths. Areas in yellow to red indicate major predicted movement corridors from the study area to Sioma National Park. Map 5c shows the difference between current and historically available corridors, scaled as proportion of maximum of 5a. In 5c areas in grey are predicted to have very little change from historic to current in the density of least cost paths. Areas in blue are areas that were predicted to be corridors in the historic landscape that are not longer available due to human settlements. Areas in yellow to red in 5c are areas in the current landscape that are predicted to be corridors that were not corridors, or were weaker corridors, in the historic landscape between different kinds of human settlements and elephant movement paths, it is clear that careful consideration of scaling relationships between landscape features and animal movement path selection is critical to avoid spurious results.

Factorial weighting analysis is useful to assess the relative influence of each factor and identify a combined model that was maximally supported. The large differences in the degree of support across the range of weighting combinations for each elephant illustrate the importance of proper weighting of resistance factors. Failure to conduct this weighting analysis would at best leave the analysis as a single weighting without evaluation of the relative predictive power of alternative variable weights. At worst, it could result in dramatically incorrect conclusions.

19.4.2 Evaluating Unimodality of Support

The factorial weighting analysis also enabled us to evaluate the unimodality of support across a multidimensional cube of alternative hypotheses. In this paper we presented a new approach to assess unimodal peaks of support among multiple hypotheses using a permutation procedure. We can use the level of homogeneity or unimodality across a quantitative hypothesis cube to assess global significance. If there is a single optimum in the parameter space at which the significance of the chosen statistical test is highest, and significance decreases monotonically away from that peak in all dimensions of the space, then any permutation of this space would result in lower values of the test statistic. The factorial permutation procedure provides a statistical test of the significance of a unimodal peak of support for a globally best model in cases where the tested hypotheses comprise a quantitative cube of parameter combinations.

19.4.3 Consistency Among Elephants in Scaling and Weighting

The analysis indicated that all four elephants strongly avoided towns, villages and huts, and that towns had a larger distance effect (5 km in ¾ of tested elephants) than either villages or huts (1 km in ¾ of tested elephants). Similarly, the analysis showed that the movement paths of all tested elephants were significantly related to distance to water, and that in ¾ of the tested elephants the square root of distance to water was statistically the best or tied for the best scaling of effects of water on movement. These scaling results show both strong effects of these landscape features and high consistency among individual elephants in the scales at which they are most important. This ability to identify the correct scale in pattern–process relationships is a central challenge in ecology (Wiens 1989; Levin 1992) that has been largely neglected in studies of animal movement.

Similarly, the factorial weighting analyses showed high levels of consistency among elephants. Three of the four elephants showed identical patterns of support across the hypothesis cube for Settlements–Water–Fences. This analysis suggests that the maximum resistance due to settlements is equal to that of fences, and 10 times that of distance to water, at the pixel level. This does not imply that water effects are globally subordinate because water effects extend synoptically across the landscape. In contrast, fence effects only accrue when an elephant encounters a fence pixel and settlement effects only accrue within the specified kernel distance of a town, village or hut. Thus, water effects actually dominate path selection at the broadest spatial scales, but are highly subordinate to settlement and fence effects at fine spatial scales. The three elephants that uniformly avoided human settlements at fine scales, did not cross wildlife fences, and selected movement paths preferentially based on the square root of distance to water. In contrast, fence effects were greatest for elephant 4, with five times the effects of either settlements or water. The reason for this difference is evident from this elephant's elongated east–west movement path bounded on the south by the Caprivi Border Fence along the Botswana border (Fig. 19.1). This fence is a double, electrified, high tensile fence that creates is an effective barrier to elephants and other wildlife.

19.4.4 Landscape Resistance, Barriers and Corridors: Implications for Conservation

Combining multiscale analysis of landscape resistance (Fig. 19.3) with cost distance (Fig. 19.4) and least cost path mapping (Fig. 19.6) provides a comprehensive picture of both the factors driving connectivity and the functional effects of landscape structure in creating movement corridors and barriers. This analysis identified several major historical movement corridors between northern Botswana and Sioma National Park. The location and strength of these historic corridors may be useful to guide managers in identifying priority areas for conservation or mitigation to maximally facilitate elephant movement. In addition, comparing the historical to current corridors provides managers with explicit information about the effects of fences and human settlement on historical elephant movement corridors (e.g. Osborn and Parker 2003).

Our analysis also indicated that veterinary fences in north eastern Botswana have a dominant effect of landscape connectivity for elephants. The Border Cordon and Northern Buffalo Fence are predicted to cut off several major movement corridors, most notably between the Okavango panhandle and Sioma. The fence also largely separates the panhandle from the rest of the Okavango Delta. The Okavango is an area of extremely high ecological importance, which supports a very dense elephant population. The veterinary fences result in an increase in cost distance of between 200 and 400% between the northern parts of the Okavango Delta and Sioma, which probably effectively isolates the northern Okavango Delta from much of the rest of the study area. Given the apparent dominant effects of the fence system on elephant population connectivity, it is important for managers to be aware of their influences and consider ways to reduce their negative effects on migration and dispersal, while also preserving the substantial protections the fences provide in places to wildlife from encroaching livestock and human populations

The analysis indicates that the relatively high density of human development in the Caprivi strip and along the Kwando River may act as a partial barrier to elephant movement. However, our analysis suggests that this barrier is highly porous and that it acts to reroute and filter elephant movements, but does not, at existing development levels, block potential dispersal routes to Sioma. The analysis identified three key corridors through this area of relatively high human development (Fig. 19.6b, c). These should be the focus of conservation and mitigation efforts designed to maintain the integrity of the corridor. Similar to Sitati et al. (2003), our results suggest that human settlement density is a major factor affecting elephant movement. The most effective way, therefore, to maintain the integrity of these corridors will likely be to limit future human development within them. Assuming governmental will and ability to direct patterns of future development, an effective strategy may involve limiting development in the corridors we identified and directing it to areas predicted to be less important for habitat connectivity (Osborn and Parker 2003). Of course, habitat connectivity for elephants is only one of many environmental and economic concerns, and decisions about future development must consider other factors, such as protecting critical habitat for other species and economic costs and benefits (Sitati et al. 2003; Lee and Graham 2006; Chamaille-Jammes et al. 2007).

19.5 Conclusion

In the trans-frontier region of northern Botswana, Namibia, Angola and Zambia, effective management of a growing elephant population will depend in part on managers' ability to facilitate dispersal from Botswana to neighboring countries. Understanding the factors that affect elephant movements between and within these nations is essential, as is the application of this knowledge to identify critical movement corridors and barriers. The combination of empirically-derived landscape resistance mapping and least cost path analysis provides a powerful analytical framework for assessing habitat isolation and identifying corridors and barriers to organism movement. In this study we evaluated the degree of isolation of Sioma National Park in Zambia from a large area of northern Botswana and mapped corridors connecting northern Botswana to Sioma National Park. We identified several major movement routes and found that human development has likely substantially altered regional population connectivity for elephants, with veterinary fences and human settlements both increasing isolation of portions of the study area and changing the routes of least cost movement corridors. This information on how human development has affected regional population connectivity and detailed predictions of the location of specific corridors and barriers will be valuable in ongoing efforts to conserve the spectacular elephant population in northern Botswana.

Acknowledgments This project was made possible with funding from the African Elephant Conservation Fund of the U.S. Fish and Wildlife Service, Conservation International, Elephants Without Borders, Player Crosby, Gale Family Foundation, Swiss Agency for Development and Cooperation, Shikar Safari Club, the United States Forest Service and the University of Massachusetts. T. Nkala, K. Landen, L. Patterson, and P. Pearlstein provided critical logistical support for collaring elephants. We wish to thank the Botswana Department of Wildlife and National Parks and the Namibia Ministry of Environment and Tourism for allowing us to undertake this study. We are grateful for the support and encouragement of J. Hanks, O. Langrand, L. Braack, P. Lindeque, H. Kolberg, R. Mojaphoko, D. Mughogho, C. Taolo, T. Mangwe, S. Sekute, G. Gwapela, M. Vandewalle and K. Alexander.

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