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The devil is in the dispersers: predictions of landscape connectivity change with demography

Nicholas B. Elliot[1], Samuel A. Cushman[2], David W. Macdonald[1]* and Andrew J. Loveridge[1]

[1]*Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Oxfordshire OX13 5QL, UK; and* [2]*USDA Forest Service, Rocky Mountain Research Station, 2500 S Pine Knoll Dr., Flagstaff, AZ 86001, USA*

Summary

1. Concern about the effects of habitat fragmentation has led to increasing interest in dispersal and connectivity modelling. Most modern techniques for connectivity modelling have resistance surfaces as their foundation. However, resistance surfaces for animal movement are frequently estimated without considering dispersal, despite being the principal natural mechanism by which organisms move between populations.

2. We collected Global Positioning System data over 10 years from 50 African lions *Panthera leo* (11 male natal dispersers, 20 adult males and 19 adult females) and used a path level analysis to parameterize demographic-specific resistance surfaces for the Kavango Zambezi Transfrontier Conservation Area (KAZA) in Southern Africa.

3. Lion path selection varied according to demographic grouping: adult females were most averse to risky landscapes such as agro-pastoral lands, towns, areas of high human density and highways. Male natal dispersers were the least-risk averse suggesting they are potentially the most prone demographic to human–lion conflict. Adults of both sexes selected bushed grassland and shrubland habitats and avoided woodland. Male natal dispersers displayed the opposite trend suggesting con-specific avoidance and/or suboptimal habitat use.

4. We used the resistance surfaces to calculate factorial least-cost path networks for each demographic-specific resistance surface and present results that show substantial differences between predicted patterns of connectivity for male natal dispersers, adult females and adult males.

5. *Synthesis and applications*. Resistance surfaces are widely used to create connectivity models, which are promoted for use by conservation managers. Our results suggest that the demographic category used to parameterize resistance surfaces may lead to radically different conclusions about connectivity. Failure to include dispersing individuals when parameterizing resistance surfaces intended for connectivity modelling may lead to erroneous conclusions about connectivity and potentially unsound management strategies.

Key-words: conditional logistic regression, connectivity, landscape resistance, least-cost path, natal dispersal, *Panthera leo*, path level analysis, resistance surfaces

Introduction

As ecosystems become more fragmented, the importance of dispersal is increasingly apparent since it is the principal mechanism by which organisms move between metapopulations and thereby maintain population viability and genetic diversity (Clobert *et al*. 2012). Thus, there has been increasing interest in identifying corridors and maintaining connectivity (for reviews see Sawyer, Epps & Brashares 2011; Zeller, McGarigal & Whiteley 2012). Resistance surfaces that indicate the cost of movement as a function of landscape features are the foundation of most contemporary methods for mapping potential corridors and predicting connectivity (Zeller, McGarigal & Whiteley 2012). In order to evaluate landscape connectivity, numerous techniques can be applied to the resistance surface, with least-cost modelling being the dominant tool

*Correspondence author. E-mail: david.macdonald@zoo.ox.ac.uk

(reviewed in Rudnick *et al.* 2012; Cushman *et al.* 2013). However, regardless of which connectivity metric is calculated, false assumptions pertaining to the underlying resistance surface may result in erroneous conclusions regarding connectivity (Janin *et al.* 2009). Since connectivity models are widely promoted as a conservation tool to address the effects of fragmentation, it is critical that the underlying resistance surfaces are reliable. To this end, recent research has investigated how the accuracy of resistance surfaces may be affected by the grain of environmental variables (Galpern & Manseau 2013), cost surface parameterization (Koen, Bowman & Walpole 2012) and the functions used to transform habitat suitability into resistance values (Trainor *et al.* 2013). However, as Zeller, McGarigal & Whiteley (2012) noted in a review of papers relating to resistance surfaces, it is also crucial to compare the data types used and how these may alter the resultant resistance surface.

Expert opinion is the most common basis for parameterizing resistance surfaces, followed by the use of genetic and detection data (Zeller, McGarigal & Whiteley 2012). Recently, the use of telemetry data has increased (e.g. Trainor *et al.* 2013) and arguably provides the most direct and informative means for identifying landscape features that affect connectivity under current landscape conditions (Cushman, Chase & Griffin 2010). Studies that incorporate telemetry data typically use data obtained from settled adult individuals (e.g. Cushman & Lewis 2010; Squires *et al.* 2013). For example, Cushman & Lewis (2010) created resistance surfaces based on telemetry data of adult American black bears *Ursus americanus* (Pallas, 1780) of both sexes. This gives rise to two limitations: first, grouping males and females may mask important differences between sexes (e.g. Koehler & Pierce 2003); second, data collected on settled adults may give a biologically misleading impression of the factors that are important to dispersing individuals and therefore connectivity. This is because data gleaned from settled adults reflect choices to optimize fitness within home ranges, while dispersers may 'make the best of a bad situation' and utilize suboptimal habitats (e.g. Palomares *et al.* 2000). It is therefore striking that although dispersal is widely recognized as the primary means of population connectivity, few studies have used dispersal data to parameterize resistance surfaces (but see Richard & Armstrong 2010), and none has compared resistance surfaces derived from resident adults as opposed to dispersers.

In this paper, we develop resistance surfaces and connectivity metrics for African lions *Panthera leo* (Linnaeus, 1758). Lion populations have become increasingly fragmented, with an estimated 75% range loss in the last 500 years (Riggio *et al.* 2013). A population genetics model predicted a minimum of 50–100 prides, with no limits to dispersal, are required to maintain long-term genetic diversity (Bjorklund 2003). Few remnant populations meet this criteria, raising the threat of diminished genetic diversity, shown to increase sperm abnormality and decrease reproductive performance (Packer *et al.* 1991). However, the degree to which remnant lion populations are isolated and the factors that may facilitate gene flow through dispersal are largely unknown.

To examine differences depending on whether models are parameterized from dispersing or adult individuals, we use telemetry data, spanning 10 years from 50 lions in three demographic categories based on 11 environmental variables. By parameterizing resistance surfaces based on data from male natal dispersers, adult males and adult females, we highlight the different results derived from each data set and lay the foundation for future connectivity modelling for this species.

Materials and methods

STUDY EXTENT

The study extent (≈1·4 million km^2) encompasses the entire Kavango Zambezi Transfrontier Conservation Area (KAZA-TFCA) and traverses sections of Angola, Botswana, Namibia, Zambia and Zimbabwe (Fig. 1). Approximately 31% (≈446 000 km^2) of the study extent is managed for wildlife, including 26 National Parks, 297 Forest Reserves and 117 Wildlife Management Areas. This extensive area is of great conservation importance for lions as it contains 13 'Lion Conservation Units' (IUCN 2006), and the Okavango-Hwange ecosystem is one of Africa's 10 remaining lion 'strongholds' (Riggio *et al.* 2013).

ENVIRONMENTAL DATA

We proposed, *a priori*, three groups of variables (land use, habitat and anthropogenic) known to influence lion movement (e.g. Hopcraft, Sinclair & Packer 2005; Valeix *et al.* 2012; Loarie, Tambling & Asner 2013; Schuette, Creel & Christianson 2013). We used open-source geographic information system (GIS) layers or created our own. Layers that had a resolution <500 m were retained in their original form. In order to maintain a consistent grain size for modelling purposes and inferential statistics, coarse-grained layers (>500 m) were resampled to 500 m using nearest neighbour (for categorical variables) or bilinear interpolation (for continuous variables) in ArcInfo Workstation (ESRI 2010).

Land use

We obtained GIS layers depicting wildlife areas from the World Database on Protected Areas (IUCN & UNEP 2010) and reclassified them as:

1. *National Parks*: Gazetted by government (IUCN Category II). 'Game Reserves' in Botswana (IUCN Category IV) were also included as they have the same function.
2. *Forest Reserves*: Government-owned land set aside for forest products, with a mandate for conservation.
3. *Wildlife Management Areas (WMAs)*: State, private or community-owned land managed for wildlife. The focus is on trophy hunting with a few areas devoted to photographic tourism.
4. *Agro-pastoral lands*: All land not included in the three categories above was converted into a layer where agriculture and pastoralism dominate.

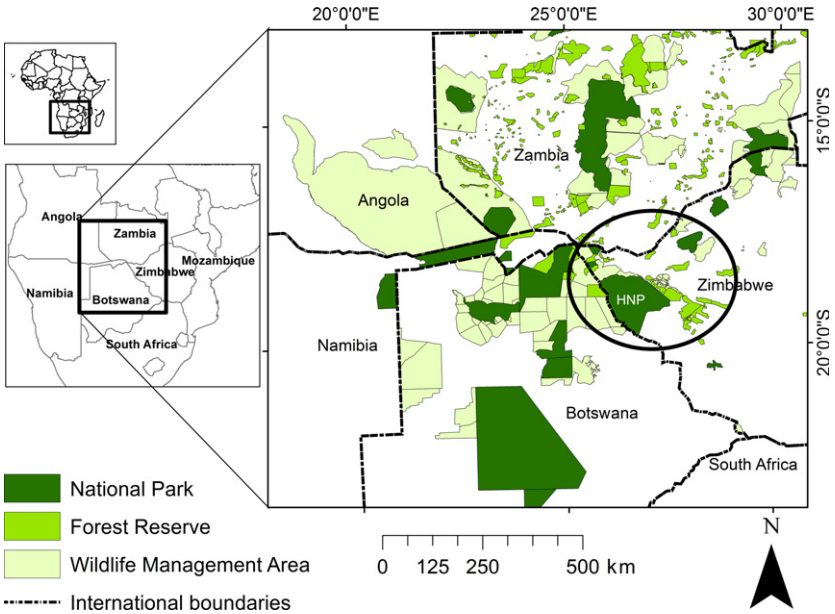

Fig. 1. Study extent for evaluation of movement paths of African lions in Southern Africa. The black ellipse details the approximate extent of the Global Positioning System telemetry data obtained from collared lions in the study.

Habitat

We used the European Space Agency (ESA) global land cover map, version 2.3 (ESA & UCLouvain 2010) consisting of 22 habitat classifications. Only nine categories occurred in our study extent and were reclassified according to habitat structure and placed into three broad groups: woodland, shrubland and bushed grassland (see Table S1, Supporting information). In addition, we used the Moderate Resolution Imaging Spectroradiometer (MODIS) Vegetation Continuous Fields data set (Hansen *et al.* 2005), which quantifies percentage tree cover.

Anthropogenic

1. *Human density*: We used the Gridded Population of the World (GPWv3) data set based on population data estimates from 2000 and projected (in 2004) to the year 2010 (CIESIN & CIAT 2005). Projections were based on growth rates from census data and United Nations statistics.

2. *Towns*: We digitized the extent of all towns in the study extent using DigiPoint3 (Zonum Solutions 2010) in Google Earth (Google Inc. 2011). To reflect the size and density of towns and how these physical structures may impact lion movement, this was converted to a point density layer by converting the raster to a point coverage and calculating the focal point density on that surface within a 5000-m-radius focal window (ESRI 2010).

3. *Highways*: All major roads were recorded using a handheld Global Positioning System (GPS) device (Garmin, Olathe, KS, USA) programmed to collect fixes at 100-m intervals (accuracy ± 4 m).

LION TELEMETRY DATA

Lion telemetry data were obtained from a source population in and around Hwange National Park (HNP), in north-west Zimbabwe (19°00′S, 26°30′E). The population has been intensively monitored without interruption since 1999 (for a description of the study area and lion population see Loveridge *et al.* 2010). Between 2003 and 2012, location data were obtained from 50 lions in different social groups (11 male natal dispersers, 20 adult males and 19 adult females). Each lion was fitted with a GPS radio-collar (see Loveridge *et al.* 2007 for details), programmed to take hourly fixes when lions are active (1800–0700). All lions were collared within HNP and surrounding areas but were not confined to this area. See Figs S1–S4 (Supporting information) for representative data for each demographic category.

DATA PREPARATION

To ensure accuracy, we only retained fixes with a Dilution of Precision <10 (Frair *et al.* 2010). To reduce the effects of non-stationarity (Cushman, Chase & Griffin 2005), the study period was split into sequential temporal windows of 30-day intervals. We created 229 temporal window periods, starting on 11 March 2003 and ending on 20 August 2012. The data for each individual lion were split according to these windows.

LION DEMOGRAPHIC CATEGORIES

Lions were classified as male natal dispersers (hereafter 'dispersers'), adult males or adult females, based on field observations:

Dispersing males: The transience phase was deemed to have commenced once the subadult left its natal pride and did not return thereafter. A dispersing individual was deemed to have established a territory when it had been in a consistent home-range for a minimum period of 2 months and occupied a fixed home-range thereafter. The onset of establishment was back-dated to the time the lion entered the new home-range. Only data gathered during dispersal were retained (70 windows).

Adults: All adults used in this study were at least 4 years old, either in established territories or, in a few cases, temporarily nomadic for short periods after being displaced from their territory (adult males = 371 windows; adult females = 486 windows).

PATH SELECTION AND SCALING

To predict lion movement as a function of landscape features, we converted the series of sequential locations for each utilized

window into a path in ArcInfo Workstation (ESRI 2010). Path selection functions are a robust method for comparing the attributes of landscape features along an animal's utilized path with those that would be encountered in available paths and is arguably the most powerful selection function for creating resistance surfaces (Cushman & Lewis 2010; Zeller, McGarigal & Whiteley 2012).

Ecological processes, such as dispersal, may be driven by environmental factors across a range of spatial scales (Wiens 1989), making it important to measure a response variable at the correct scale (Sawyer, Epps & Brashares 2011). Failure to do so may result in erroneous evaluation of a relationship or detection of a relationship altogether (Cushman & Landguth 2010). It is therefore recommended that one quantifies variables at multiple scales to determine scale dependency in the underlying process (Galpern & Manseau 2013). We used four scales to investigate relationships between lion movement paths and GIS variables detailed above. For each utilized path, we created nine matched available paths of identical topology to the utilized path at each scale. The available paths were then shifted a random distance in x and y and randomly rotated between 0 and 360°. The four spatial scales correspond to random shifts of: (1) no shift and distances between (2) 0–12·5 km, (3) 0–25 km, (4) 0–50 km. Thus, for each used path, we had nine random paths at each scale resulting in a total of 36 available paths per used path. Issues of autocorrelation are avoided by converting the points to paths, retaining the topology of the used paths and randomly rotating and shifting those paths (Cushman 2010). In total, our dataset comprised 927 utilized and 8343 available paths, each of 30-day duration.

CONDITIONAL LOGISTIC REGRESSION

Predictor variables were derived in ArcInfo Workstation (ESRI 2010) by calculating the mean value for each GIS variable of all pixels that fell along the utilized and available path trajectories. We used conditional logistic regression to compare each utilized path with the nine available paths at each scale, and thus, no intercept is estimated. With the present study design, conditional logistic regression is an appropriate modelling approach (Hegel *et al.* 2010). In addition, this approach is particularly powerful for studying fine-scale habitat selection (Compton, Rhymer & McCollough 2002) and provides a robust way to rank alternative hypotheses with Akaike's Information Criterion (AIC; Burnham & Anderson 2002; Cushman & Lewis 2010). Consistent with Coulon *et al.* (2008), we used Cox models and performed all statistical analysis in R 2.15.1 (R Core Team 2012) using package coxme v.2.2-3 (Therneau 2012). Lion ID was used as a random effect in all models.

We conducted the conditional logistic regression in two steps. First, for each demographic category, we performed a univariate scaling analysis (e.g. Thompson & McGarigal 2002) for each variable to determine which scale had the strongest relationship with lion path selection. We used model selection to identify the most supported scale for each variable based on Akaike Information Criterion corrected for small sample size (AICc). The scale with the lowest AICc ranking was inferred to be the one at which lions selected their paths and thus was retained for the next step (Table S2, Supporting information).

Second, for each demographic category, we created candidate models for each group of variables (land use, habitat and anthropogenic). Our candidate models were progressively more complex, starting with univariate models and finishing with the maximal model including all variables in the group (Table S3, Supporting information). Models were ranked using AICc, and relative support was assessed using Akaike weights (w_i). When one model was superior ($w_i > 0{\cdot}9$), this was used; otherwise, we averaged parameter estimates across models with AICc differences ($\Delta i < 4$) correcting for model weights (Burnham & Anderson 2002).

RESISTANCE SURFACES

Using the results from the second step of analysis, we produced resistance surfaces for each demographic category. For each group of models, we took the coefficients from the dominant model or those produced by model averaging and used them to produce resistance surfaces. Resistance surfaces were created in ArcInfo Workstation (ESRI 2010) by calculating $z = \beta_1 v_1 + \beta_2 v_2 + \ldots + \beta_n v_n$, where β_i is the coefficient for variable v_i and rescaling such that resistance = $(z * -1)/\min(z * -1)$. To explore similarity between the resistance surfaces for adult male, adult female and dispersing lions, we created relative difference grids (RDGs) by calculating the difference between two surfaces as a proportion of the dispersal resistance surface. RDGs were created for males and females by calculating (dispersal resistance − adult male or female resistance)/dispersal resistance.

FACTORIAL LEAST-COST PATHS

We calculated factorial least-cost path (LCP) networks (e.g. Cushman, McKelvey & Schwartz 2009) to illustrate the changes in connectivity and their implications for management. Factorial LCPs have an advantage over tradition LCP analyses since they calculate LCPs among many pairs of source and destination cells (Cushman & Landguth 2012). We created a uniform grid of 223 source points, spaced at 25 km and located within National Parks (Fig. 4a) and used UNICOR (Landguth *et al.* 2012) to calculate factorial LCPs with a 250 000 cost–distance threshold. This threshold roughly translates to 80 km through the most costly land use, agro-pastoral land, and is well within the dispersal ability of lions (Figs S2–S4, Supporting information).

We used FRAGSTATS (McGarigal, Cushman & Ene 2012) to quantify the differences in demographic-specific corridor networks in two different ways. First, we calculated four landscape metrics to quantify the extent and fragmentation of each predicted corridor network (PLAND – percentage of study extent covered by the predicted corridor network; NIP – number of isolated patches in the corridor network; Correlation Length – measure of total predicted corridor network; and Mean Shape Index – area-weighted shape index calculating the shape complexity of each patch in the corridor network). Second, we calculated the intersection of predicted corridors outside National Parks between each demographic category with intensity greater than mean plus one standard deviation (SD) and mean plus two SD. These signify weak and intense corridors, respectively, and quantify the degree to which predicted corridor networks for each demographic group are accurate surrogates for the others. UNICOR computes a factorial of least-cost paths across the resistance surface among all pairs of source points. Intense corridors therefore have many least-cost paths travelling through the same locations in the landscape.

Results

UNIVARIATE SCALING

AICc rankings showed that land use and anthropogenic variables were most frequently selected or avoided at broad scales (0–25 km), while habitat variables were either selected at small scales (0 km) or large scales (0–50 km; Table S2, Supporting information). There was strong and consistent selection of protected areas and avoidance of humans and agro-pastoral land by lions. National Parks were selected by all demographic categories across all scales; in each instance, the most supported scale was 0–25 km. Agro-pastoral land and areas of high human density were avoided at all scales by all demographic categories, again 0–25 km being the most supported scale. Towns and highways were generally only avoided at larger scales, while avoidance was not detected at small scales.

MULTIVARIATE ANALYSIS

Models and model comparison statistics for each demographic-specific group of analyses can be found in Table S3 (Supporting information).

Land use

All three demographic categories avoided agro-pastoral lands, but the extent to which they did so varied, as evidenced by the coefficients (Table S4, Supporting information). Dispersing males showed the weakest avoidance of agro-pastoral lands, followed by adult males (twice that of dispersers). Adult females showed the strongest avoidance of agro-pastoral lands (seven times that of dispersers) and the strongest selection for National Parks. Dispersing males had the weakest selection for National Parks, followed by adult males. Forest reserves were selected by dispersers, with weak selection or avoidance by adult males and females of forest reserves and WMAs.

Habitat

Bushed grassland and shrubland areas were selected by adult males and females (Table S5, Supporting information). Conversely, dispersing males avoided these habitat types and selected woodlands which were avoided by adults of both sex. All three demographic categories avoided areas with higher percentages of tree cover.

Anthropogenic

Each of the anthropogenic parameters was avoided by all demographic categories, but to varying degrees (Table S6, Supporting information). Both highways and humans were least avoided by dispersing males, with adult males displaying intermediate avoidance and adult females the strongest. Adult females avoided highways to an 11-fold greater extent than did dispersers and adult males five times more than dispersers. Adult females most strongly avoided areas of human density (four times that of dispersers) with adult males having intermediate avoidance (twice that of dispersers). Towns were most strongly avoided by adult females, then dispersers, followed by adult males.

RESISTANCE SURFACES

Resistance surfaces produced from all 11 variables for each demographic category are displayed in Fig. 2. The study extent was less fragmented and more permeable for dispersing males than for the other two demographic categories: mean resistance for adult males was twice as high (mean $\pm$ SD = 61·096 $\pm$ 191·2) as that of dispersing males (mean $\pm$ SD = 29·8 $\pm$ 101·9), while adult females had the highest resistance (mean $\pm$ SD = 82·7 $\pm$ 448). The RDGs illustrate these differences (Fig. 3), with larger negative values indicating areas where the paired demographic category (either males or females) had higher resistance than dispersers and positive values indicating areas where the paired demographic category had lower resistance than dispersers.

FACTORIAL LEAST-COST PATHS

The model indicated substantial differences between patterns of connectivity predicted for dispersers (Fig. 4b), adult females (Fig. 4c) and adult males (Fig. 4d). For example, the extent of the landscape occupied by the corridor network for dispersers was 22·6% higher than for adult females and 37·7% higher than for adult males. Similarly, the total fragmentation of the network, as judged by number of isolated patches, was 233% higher for adult males and adult females than for dispersers (see Table S7, Supporting information for full set of differences and explanations).

The intersection analysis (Table 1) revealed that for both weak and intense corridors, there is low intersection among demographic groups: for all combinations, there is no case where the intersection amounts to 50% of the corridor network (Table 1 all values <0·5). In addition, the degree of intersection for all combinations of demographic group is smaller in the upper triangle (Table 1) than in the lower triangle, indicating that there is proportionally more overlap for weak corridors than for intense corridors. Finally, the intersection between the predicted corridor network for adult male lions and dispersers was higher than between females and males, or females and dispersers (especially for the most intense corridors – upper triangle) suggesting that resident males and dispersers have the most similar optimal corridor networks.

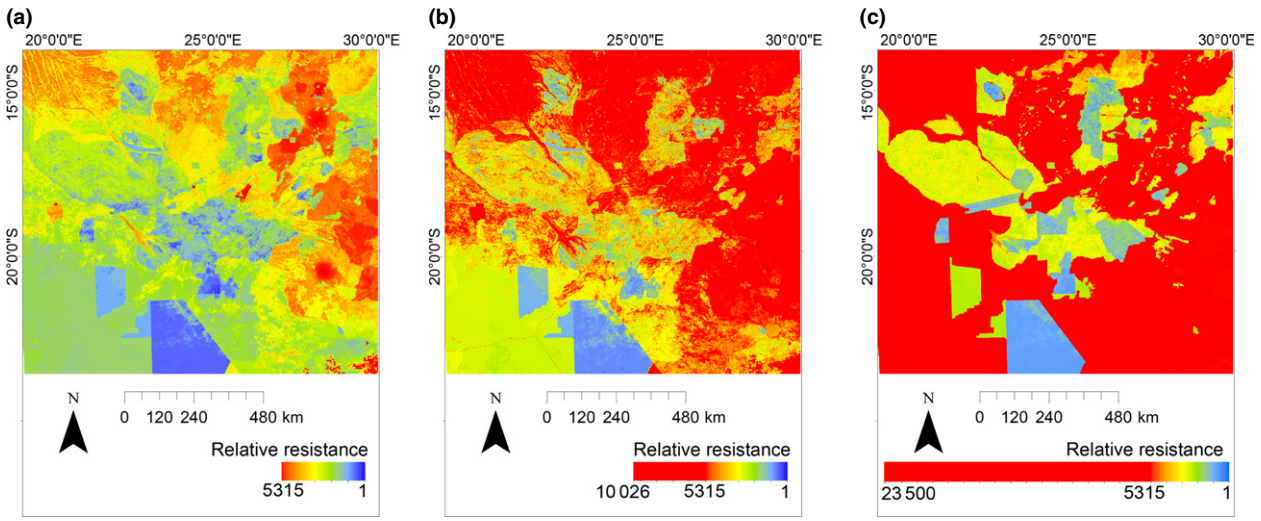

Fig. 2. Resistance surfaces for Southern Africa parameterized from Global Positioning System telemetry data obtained from (a) dispersing male lions, (b) adult male lions and (c) adult female lions. Resistance surfaces were created by calculating $z = \beta_1 v_1 + \beta_2 v_2 + \ldots + \beta_n v_n$, where β_i is the coefficient for variable v_i and rescaling such that resistance = $(z * -1)/\min(z * -1)$. For display, we stretched the adult male and adult female surfaces to match the scale of the disperser resistance surface.

Discussion

Our results show that strikingly different resistance surfaces and connectivity metrics can be predicted depending on whether data on the movements of dispersing, adult male or adult female lions are used to parameterize models. The differences arise primarily because dispersing male lions avoided what might be interpreted as risky conditions (agro-pastoral lands, highways and humans) to a lesser extent than did adults. The movements of adult females were only weakly affected by habitat type, but, like adult males, they selected for bushed grasslands and shrubland habitats while avoiding woodland. Dispersers showed the opposite trend: selecting for woodland and avoiding bushed grassland and shrubland. We propose that such differences are likely to occur in other species since dispersal through a habitat patch may be driven by different factors to those affecting movements of adults (Wasserman *et al.* 2010).

In dimorphic and polygynous species, males are more likely to take risks than females (Trivers 1985). Conversely, females, especially those with dependent young, may be more averse to raiding compared to males (e.g. Bunnefeld *et al.* 2006). Dispersal, on the other hand, is inherently risky, particularly when travelling through novel environments, and frequently results in mortality (Bonte *et al.* 2012). Dispersing subadult males are smaller than adult males and during transience pass through occupied territories, where they are not tolerated (Packer 2001). It is therefore unsurprizing that dispersers, while searching vast areas for patches in which to settle, encounter anthropogenically risky environments more frequently than do territorial adults. Indeed, stock-raiding lions are frequently dispersing subadults (Stander 1990; Patterson *et al.* 2004), and our results highlight dispersers as the demographic group most prone to coming into contact with people and hence involved in human–lion conflict. This has important management implications since complete protection of land may aid, but not be essential to effectively link lion populations, provided lions are tolerated (e.g. Schuette, Creel & Christianson 2013). As such, conflict mitigation should be part of connectivity planning for this species.

The univariate scaling analysis identified the functional scale at which lion path selection was most related to each environmental variable. Avoidance of towns and highways was only detected at larger scales, highlighting the importance of assessing variables at multiple scales, without which an erroneous conclusion that lions do not avoid towns and highways may have been made. Our multivariate analysis revealed the magnitude of the effect for each variable at the most appropriate scale. The overall approach and resultant resistance surfaces integrate landscape patterns and behavioural processes to lay the foundation for realistic and accurate connectivity modelling. Future work should build on the resistance layers of dispersers to investigate changes in landscape connectivity under a range of management scenarios. These could include the addition or removal of protected areas, an increase in human density or the use of fencing. This would be timely since a recent, widely publicized study suggested that fencing lions populations would benefit their conservation (Packer *et al.* 2013), while others argue that promoting connectivity would be more effective (Creel *et al.* 2013).

Once a paradigm largely restricted to the Western world (Beier & Noss 1998), connectivity conservation is now widely promoted and has engendered considerable political and popular support globally (Doerr, Barrett &

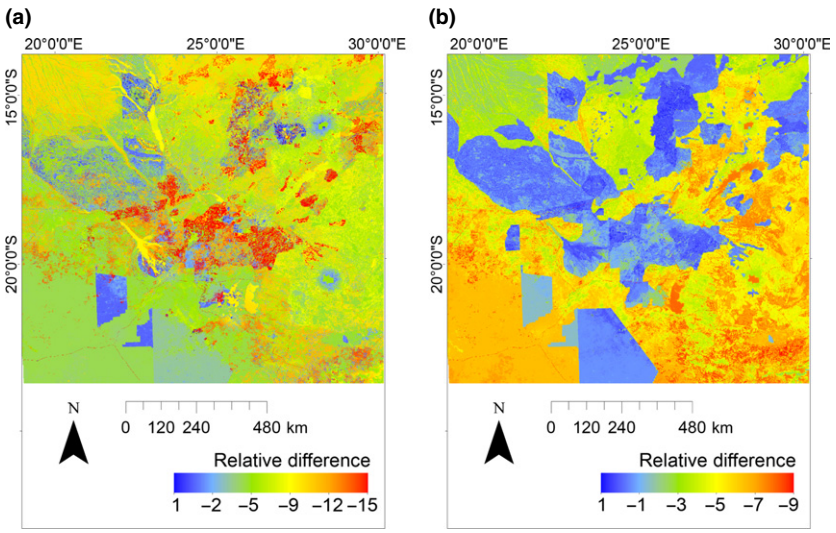

Fig. 3. Relative Difference Grids for paired demographics of lions in Southern Africa and highlight differences between resistance surfaces derived from (a) dispersal data compared to adult male data and (b) dispersal data compared to adult female data. Negative values indicate areas where the paired demographic category (either adult males or females) had higher resistance than did dispersers and positive values indicating areas where the paired demographic category had lower resistance than did dispersers.

Doerr 2011). In Africa, an initiative by Peace Parks Foundation (PPF) has elevated the study of connectivity from an academic pursuit to a necessity. Throughout Africa, PPF has developed Transfrontier Conservation Areas (TFCAs) with government-signed agreements for 10 TFCAs and plans for eight more (PPF 2013). Tens of millions of dollars have been raised, in part to achieve one of their core objectives: connectivity. KAZA-TFCA, which our study extent encompasses, is one such example and it is therefore critical that connectivity plans are created from realistic data.

Currently, most TFCA connectivity strategies are based on expert opinion, which has demonstrated limitations and weaknesses (Sawyer, Epps & Brashares 2011). While use of empirical data is an improvement, our results indicate that connectivity models which are not based on the most relevant demographic to connectivity, i.e. dispersers, may also lead to potentially unsound management decisions. The intersection analysis revealed that there was low overlap of predicted corridors among demographic groups. Similarly, we found that there was more overlap among weak predicted corridor networks than

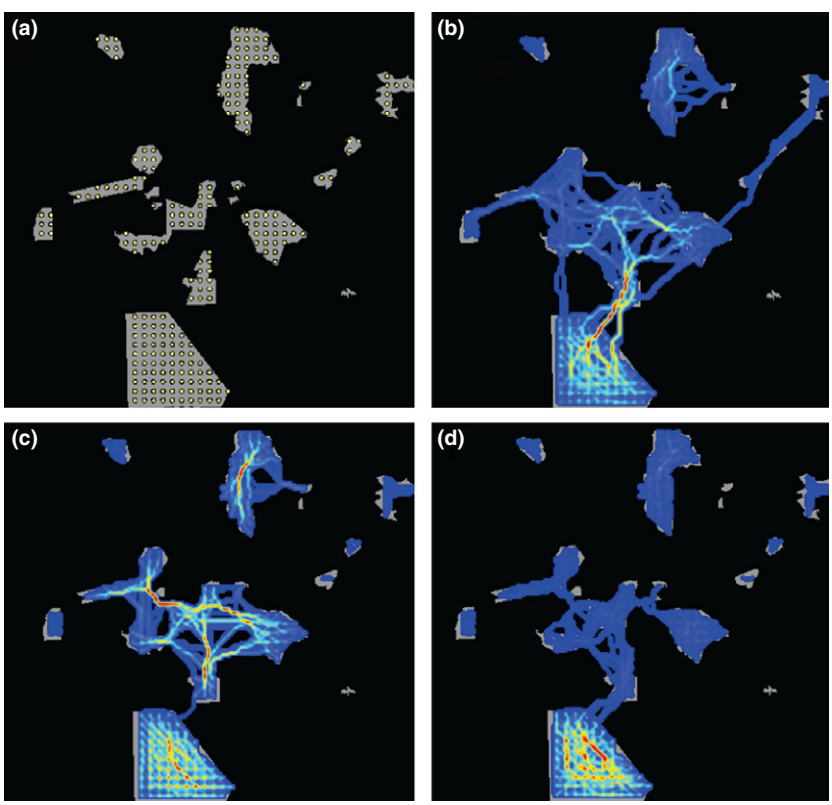

Fig. 4. Illustration of the differences in predicted connectivity for resistance maps derived from different demographic categories of lions. Panel (a) shows National Parks in grey and 223 source points in yellow. Panel (b) shows the predicted corridor network connecting source points within the cost distance threshold (250 000 cost units) for dispersing lions, (c) adult female lions and (d) adult male lions. The colour ramp indicates corridor intensity, as measured by the number of least-cost paths among combinations of source points passing through a given pixel, and ranges from 0 (black) to 197 (dark red).

Table 1. Intersection of predicted corridors outside National Parks between adult male, adult female and dispersing African lions

	Males	Females	Dispersers
Males	x	0·07	0·41
		0·03	0·24
Females	0·19	x	0·04
	0·14		0·03
Dispersers	0·27	0·27	x
	0·49	0·35	

Values in the upper triangle are for intersections of all corridors with intensity greater than $\bar{x}$ + 2SD ('intense corridors'). Values in the lower triangle are for intersections of corridors of intensity value greater than $\bar{x}$ + 1SD ('weak corridors'). The top value in each cell is the size of the intersection as a proportion of the demographic category listed in the row title; the bottom value is the size of the intersection as a proportion of the corridor network extent of the demographic group listed in the column titles. For example, column 1 row 2, the top value is 0·19, corresponding to the extent of intersection between male and female corridors more than one standard deviation greater than their mean as a proportion of the extent of the female $\bar{x}$ + 1SD network extent. This is interpreted as 19% of the extent of the female corridor network intersects with the male corridor network.

intense networks for the different demographic groups. This indicates that connectivity models developed from one demographic category are likely to be poor surrogates for other demographics, particularly for the most intense corridors, which are most likely to be prioritized by targeted conservation actions. In addition, the models of predicted connectivity for adult lions neglect that there may already be viable corridors between for instance HNP and Chizarira National Park and an intense corridor between Makgadikgadi and the Central Kalahari Game Reserve (Fig. 4). Thus, management decisions based on adult resistance surfaces might focus on areas that are not in line with existing dispersal routes.

Protecting dispersal corridors has become a cornerstone of modern conservation (Chetkiewicz, St. Clair & Boyce 2006; Rudnick *et al*. 2012). Their effectiveness for facilitating movement has been demonstrated in a variety of taxa (Haddad *et al*. 2003), but can be counterproductive, especially when based on scant biological data (Chetkiewicz, St. Clair & Boyce 2006). As a result, some authors argue that the importance of connectivity is overstated, primarily due to uncertainty in models, regarding for instance how dispersers search for habitat (Hodgson *et al*. 2009). Meanwhile, others suggest that advances in knowledge and theory on dispersal behaviour limit such uncertainty (Doerr, Barrett & Doerr 2011). We contend that both arguments are partly correct: there is uncertainty in many connectivity models, and there is a rapidly increasing understanding of dispersal. The uncertainties arise, however, largely because studies frequently do not incorporate empirical dispersal data and behaviour into connectivity models. Our results indicate that it is critical to do so.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Map of the core study area.

Fig. S2. Representative dispersal movement paths.

Fig. S3. Representative adult male movement paths.

Fig. S4. Representative adult female movement paths.

Table S1. Habitat reclassification table.

Table S2. Summary of the univariate scaling analysis.

Table S3. Summary of multivariate model selection statistics.

Table S4. Parameter estimates of conditional logistic regressions for land use type.

Table S5. Parameter estimates of conditional logistic regressions for habitat type.

Table S6. Parameter estimates of conditional logistic regressions for anthropogenic variables.

Table S7. FRAGSTATS metrics of extent and fragmentation of predicted corridor networks.