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RESEARCH ARTICLE

Evaluating habitat connectivity methodologies: a case study with endangered African wild dogs in South Africa

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Abstract

Context In fragmented landscapes, connectivity between subpopulations is vital for species' persistence. Various techniques are used to assess the degree of connectivity between habitat patches, yet their performance is seldom evaluated. Models are regularly based on habitat selection by individuals in resident populations, yet dispersers may not require habitat which supports permanent residence.

Objectives and methods Using a database of African wild dog (*Lycaon pictus*) occurrence records in north-eastern South Africa (n = 576), we developed and compared ecological niche models (ENM) for wild dogs packs and dispersers. Additionally, we used least cost path (LCP) and current flow models to assess connectivity. Results were further validated using occurrence records (n = 339) for cheetah (*Acinonyx jubatus*).

Results and conclusions The ENM for wild dog packs identified large but isolated patches of suitable habitat, while the disperser ENM had greater suitability values for areas in between highly suitable patches. Without disperser-specific data, models omitted large areas which were confirmed to have provided connectivity. Although models derived from a potentially subjective cost layer have been criticised,

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the current flow model outperformed the other connectivity techniques and provided the most meaningful predictions for conservation planning. We identified five priority conservation areas for wild dogs, two of which had a greater feasibility for recolonisation. The scarcity of disperser-specific data promotes models using habitat data for resident individuals but here we illustrate the pitfalls thereof. Our study provides insights into the performance of these frequently employed techniques and how they may affect conservation management decisions.

Keywords Carnivores · Circuitscape · Current-flow · Ecological niche model · Fragmentation · Least cost path (LCP) · Maxent · Metapopulation

Introduction

Identifying and maintaining connectivity between key habitats has become increasingly important in conservation planning (e.g. Wilcove et al. 1998; Fahrig 2003; Cushman 2006). However, the validity and biological relevance of the various methods used to derive linkages are debated (Beier et al. 2008; Cushman et al. 2009; Richard and Armstrong 2010; Carroll et al. 2012). Factors that influence species distributions differ in their relative importance during different life stages. More specifically, habitat that facilitates dispersal may not meet the ecological requirements necessary to support permanent residence (Carroll et al. 2012) and dispersing animals will keep moving in search of mates. Assessing connectivity based on habitat selected by resident individuals, which is common and even advocated (Huck et al. 2011), may underestimate the extent and distribution of functional corridor habitat. Consequently, identifying and creating corridors based on empirical observations of dispersing individuals is one of the most reliable ways of designing connectivity networks (Hilty and Merenlender 2004; Graves et al. 2007). However, the required dispersal data are lacking for most species (Fagan and Calabrese 2006) and inferences of habitat suitability based on habitat selected by individuals within resident populations may not accurately represent habitat required for dispersal (Carroll et al. 2012).

In the absence of disperser-specific habitat selection data, the most common connectivity analysis method involves delineating corridors (Adriaensen et al. 2003; Sawyer et al. 2011). This is frequently performed using algorithms which determine the path between two predetermined points that have the lowest cumulative cost, a technique referred to as least-cost path (LCP) analysis (Adriaensen et al. 2003). This method implicitly assumes that a dispersing animal has a perfect knowledge of the landscape and bases movement decisions on this (Carroll et al. 2012). In contrast, the more recent current flow models assume that dispersers have no knowledge of the landscape more than one step ahead (Newman 2005) and have also been shown to be highly correlated with genetic distance in several plant and animal populations (McRae et al. 2008; Lee-Yaw et al. 2009). Unlike the linear paths calculated by LCP analyses (Sawyer et al. 2011), the zones identified by current flow modelling provide alternative linkages which may be important under changing climate, land-use change or environmental catastrophes (McRae et al. 2008; Carroll et al. 2012). Due to a lack of appropriate data, the effectiveness of corridors in providing connectivity is usually assessed subjectively (Beier et al. 2008).

Mammalian carnivores are particularly vulnerable to local extinction in fragmented landscapes because of their large ranges, low population densities, and persecution by humans (Noss et al. 1996; Woodroffe and Ginsberg 1998; Cardillo et al. 2005). Since carnivores play a pivotal ecological role and their status can be indicative of landscape connectivity, they can serve as a focal species to assess the degree of connectivity across large areas (Dobson et al. 2006). Connectivity would therefore support dispersal as well as facilitate movement stimulated by other social or ecological reasons, for e.g. changes in resource availability.

In South Africa, the endangered African wild dog (*Lycaon pictus*) is the rarest large carnivore with an estimated 554 free-ranging animals (391 adults and 163 pups) remaining (WAG-SA meeting minutes September 2014). The only unmanaged population inhabiting a protected area occurs in the 20,000 km^2 Kruger National Park, which supports a population of only 227 animals (154 adults and 69 pups). The remainder of the country's protected populations are scattered among several smaller reserves (Davies-Mostert et al. 2009) which are intensively managed as a meta-population through periodic translocation of individuals among the geographically isolated protected areas (Davies-Mostert et al. 2009). Two hundred wild dogs are distributed among the nine meta-population reserves (WAG-SA meeting minutes September 2014). Wild dogs occur at low densities even in protected populations (Creel and Creel 2002) and their highly dynamic populations are prone to large-scale fluctuations (Fuller et al. 1992), making connectivity between populations vital. The species remains threatened and since meta-population reserves have limited potential to support additional packs, conservation planning needs to assess the best possible long-term solution that would maximise the species' survival probability.

A large proportion of South Africa's wild dog population ranges outside the boundaries of formally protected areas (Lindsey et al. 2004). Despite high rates of mortality, wild dogs have the potential to disperse several hundreds of kilometres through human-dominated landscapes, find mates and form packs (Davies-Mostert et al. 2012; Masenga et al. In press). Sightings of wild dogs located outside of extant populations infer some level of connectivity to a source population. Maintaining connectivity is vital for immigration, emigration and gene flow, and may serve as an important conservation strategy for wild dogs in southern Africa (Davies-Mostert et al. 2009, 2012). Areas where wild dogs regularly occur are therefore of great conservation significance and could be regarded as priority conservation areas as they represent landscapes suitable for wild dog recolonisation (Davies-Mostert et al. 2009). While initial recolonisation could potentially be accelerated through reintroduction programs, connectivity to source populations is envisaged as the mechanism ensuring population viability (Lindsey et al. 2005a).

Given the global need to accurately identify habitats providing connectivity, we set out to evaluate the effectiveness of different methodologies. Using an extensive database of wild dog occurrence records, which importantly included records for both packs and dispersing groups, we aimed to: (1) evaluate the differences between ecological niche models (ENM) derived from occurrence data of packs and dispersing individuals; (2) test the functionality of corridors identified by the three different methods (maximum entropy, LCP, and current-flow) and evaluate the performance of these techniques; and (3) using an ecological niche model derived from records of wild dog packs, identify priority conservation areas with some degree of connectivity to source populations. Lastly, (4) we investigated the applicability of the priority conservation areas and corridors to another wide-ranging carnivore of conservation concern using distribution records for cheetahs (*Acinonyx jubatus*).

Methods

Study area

Within South Africa, the greatest numbers of wild dogs occurring outside of protected areas are located in the north-eastern part of the country (Lindsey et al. 2004) and was therefore used to define the extent of our study area (*c*. 192,000 km^2; Fig. 1). The region is dominated by the savannah biome, with the grassland biome present in the south and along the upper Drakensberg escarpment (Mucina and Rutherford 2006). The location of major towns and cities are shown in Fig. 1.

Occurrence records

Wild dog sightings outside protected areas (n = 576; 1996–2011) were sourced from Lindsey et al. (2004) and a database maintained by the Endangered Wildlife Trust, South Africa. Data were collected almost exclusively via reports to researchers or questionnaire surveys. Due to a lack of precise coordinates in most instances, locations of sightings were recorded at the central point of a property they were recorded on or the nearest 5 arc-min (0.083°) grid vertices. The precision of occurrence records was presumed to have little influence on the modelling work since wild dogs' cursorial habits would allow them to cover the distance introduced by any potential location error in less than an hour (Creel and Creel 2002). At the extent of the entire map area, the locations indicate the approximate location of wild dogs fairly accurately and are consequently valuable for conservation planning and model evaluation. To evaluate model outputs (below), we used a dataset of 339 occurrence records for cheetah. These records (2000–2010) were collected in the same manner as the wild dog records and obtained from the Endangered Wildlife Trust, South Africa.

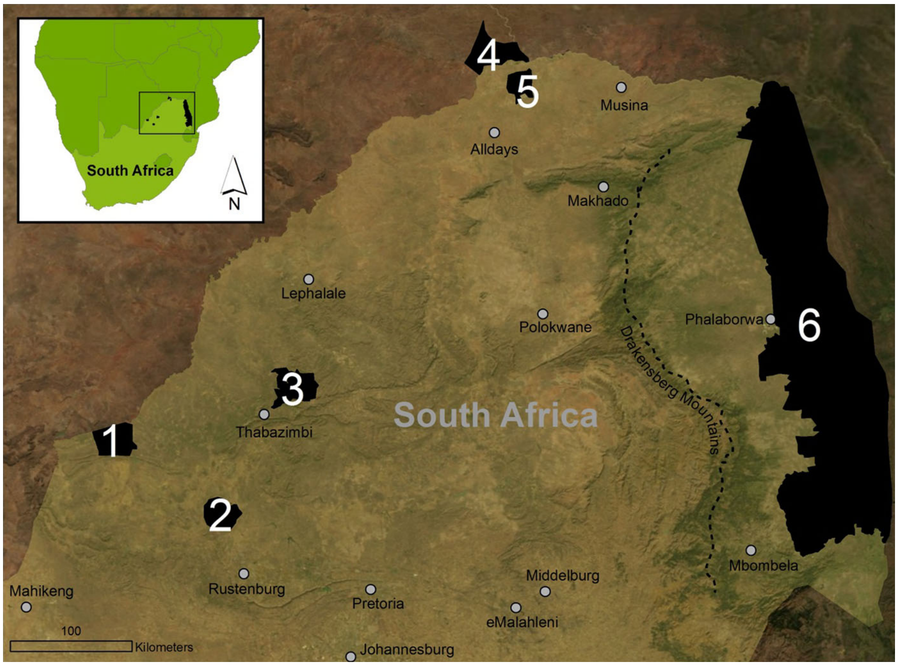


Fig. 1 Study Area located in north-eastern South Africa where potential wild dog source populations are illustrated in *black*: *1* Madikwe Game Reserve (750 km^2), *2* Pilanesberg National Park (572 km^2), *3* Marakele National Park (670 km^2), *4* Northern Tuli Game Reserve (Botswana; 720 km^2), *5* Venetia Limpopo Nature Reserve (330 km^2), *6* the greater Kruger National Park (21400 km^2; comprised of the Kruger National Park and the Balule, Klaserie, Umbabat, Sabie Sand, SabiSabi, Manyeleti and Timbavati Game Reserves). The Drakensberg escarpment, separating the higher inland plateau from the lower-lying eastern region, is indicated by the *dashed line*. (Color figure online)

Ecological niche model: habitat selection by wild dog packs and dispersers

Assessing connectivity based on habitat selection data obtained from resident animals is commonly employed, yet may result in an underestimation of functional corridor habitat. To gain an insight into this potential shortcoming, we used the two groups of occurrence records to assess whether habitat selection by wild dog packs and dispersers differed, mapping the distribution of each. Ecological niche models for (i) dispersing wild dogs and (ii) wild dog packs were developed using Maxent (Phillips et al. 2006). This correlative modelling approach is beneficial given its use of presence-only data and has performed favourably even with few occurrence records (Jackson and Robertson 2011) and when compared to other methods (Elith et al. 2006). Using occurrence records and a set of environmental predictor variables, Maxent estimates a species' ecological niche by determining the distribution of maximum entropy, subject to the constraint that the expected value of each environmental variable under this estimated distribution matches its empirical average (Phillips et al. 2006). Models were produced using default parameters in Maxent (version 3.3.3; feature selection automatic; regularisation multiplier at unity; maximum iterations 500; convergence threshold 10^{-5}; and random test percentage at zero) and five-fold cross validation. Factors affecting carnivore movement across landscapes are largely governed by land cover type, human population density and main road density (Merrill et al. 1999; Carroll et al. 2012). We used these predictor variables (Table 1) which were processed in ArcMap 10 (ESRI).

To investigate whether dispersing wild dogs and wild dog packs utilised different habitats, occurrence data were sorted into two groups. Although individuals may occasionally disperse in large groups, dispersing groups usually number 1–8 individuals (McNutt 1996). Records documenting 1–8 individuals within a group (n = 426) were used to represent dispersing animals. Groups of nine or more animals (n = 150, range 9–35) were consequently defined as

Table 1 Predictor variables used in the ecological niche model

Variable	Source	Comments
1. Land cover	National Landcover Classification for South Africa (2000)	All original classes used
2. Human population Density	Environmental Potential Atlas, department of environmental affairs and tourism, RSA	All original classes used
3. Main road density	Derived from main roads, Environmental Potential Atlas, department of environmental affairs and tourism, RSA	Calculated line density of main roads layer

"packs". Sample sizes for these records do not include more than one presence record at any specific location and are all located within the map area. Since dispersing groups often number fewer than eight individuals, we conducted a sensitivity analysis to ensure that our classification of dispersers and packs did not result in erroneous model predictions. Four scenarios were considered, namely where group size numbered (a) ≤ 2 (n = 119), (b) ≤ 4 (n = 290), (c) ≤ 6 (n = 195) and (d) ≤ 8 (n = 426). Models derived from occurrence records where group sizes numbered 4, 6 or 8 were very similar. The models using records where group size was 2 resulted in substantially less habitat predicted as suitable (Supplementary material Fig. 1). Furthermore, the model using occurrence records of 8 or fewer wild dogs had the greatest AUC value for test data. Assessing connectivity should not overlook potential corridors and we consequently consider our classification of dispersers and packs appropriate for the purposes of our study. An additional consideration would be that territorial behaviour may result in density dependent effects forcing newly formed packs, often numbering fewer than eight individuals, to occupy less favourable habitat.

Areas identified as having a high probability of occurrence by the models therefore indicate habitat that largely meets the ecological requirements of (a) dispersing individuals or (b) packs. Since dispersers are usually single-sex groups in search of mates (McNutt 1996) they cover great distances in search of members of the opposite sex (Davies-Mostert et al. 2012; Masenga et al. in press). Habitat identified as suitable for this group may therefore specifically have a low resistance to movement, facilitating connectivity. For example, varied land uses involving agriculture or livestock production would not be expected to pose a significant barrier to movement, while urbanised landscapes would. In contrast to dispersers, packs may be relatively more sedentary and suitable habitat would therefore infer that ecological requirements necessary to support permanent residence are met as well as some level of connectivity to a source population. Consequently, the output for the wild dog pack model may be useful for identifying priority conservation areas (below).

Assessing connectivity

The Maxent model for dispersers (described above) provides an indication of habitat functioning as corridors between the various source populations. In addition to this ecological niche model, we assessed habitat connectivity across the study area using current-flow analysis and by least-cost paths (LCP). These two methods were performed using Circuitscape (McRae et al. 2008) and Linkage Mapper (McRae and Kavanagh 2011), respectively. Both current flow and LCP techniques require a resistance layer and a set of focal nodes between which connectivity is calculated.

The resistance layer was created from the three predictor variables listed in Table 1. In addition to these, a fourth layer representing steep, mountainous slopes was included (see supplementary material). In particular, certain sections of the Drakensberg escarpment in north-eastern South Africa (see Fig. 1) present a barrier to movement. This natural barrier was incorporated into the weighted layer using a 90 m digital elevation model (DEM; srtm90). The standard deviation for each cell was calculated in ArcMap (ESRI). This was done using a square cell neighbourhood area comprising 3 cells in height and in width, thus indicating variations in altitude at a very fine scale

(2.49 km × 2.49 km). The highest values correspond to the steepest parts of the escarpment. The minimum value which represented a barrier to movement was determined by visual assessment using contour lines corresponding with the steepest parts of the escarpment. This also resulted in certain steep sections of other mountain ranges in the study area being exposed, such as the Waterberg. This process did not result in saddles between the steepest parts being incorporated into the steep slope category, so these natural corridors are adequately represented in the cost layer. The four layers were weighted and added (see supplementary material) using the "weighted sum" function in ArcMap 10 (ESRI). The classes within each predictor variable were assigned weights ranging from 1 to 10, with 1 having the least resistance to movement. Since human populations and their associated activities represent the greatest threats and barriers to wild dogs (Woodroffe and Ginsberg 1999), this layer received a weighting of 10, while land cover, main road density and steep mountain slopes received a weighting of 5 (see supplementary material).

Connectivity was assessed in a pairwise manner between protected areas that were home to resident packs of wild dogs during the time period when occurrence records were collected (Fig. 1). These are the only sources of wild dogs that are formally protected and thus have a reasonable chance of persisting into the future. While sources could exist outside protected areas, these animals are vulnerable to persecution and their long-term survival is not ensured. Reserves included were the greater Kruger National Park (including Balule, Klaserie, Umbabat, Sabie Sand, Sabi Sabi, Manyeleti and Timbavati Game Reserves), Venetia Limpopo Nature Reserve, Madikwe Game Reserve, Pilanesberg National Park, Marakele National Park and the Northern Tuli Game Reserve [located in Botswana, bordering South Africa and Zimbabwe, with recorded dispersal events into South Africa and Zimbabwe (Davies-Mostert et al. 2012)].

Evaluation of the current flow output

The current flow connectivity analysis uses the resistance layers to assess connectivity between the designated source populations and is thus derived independently from wild dog occurrence records. In the current flow output, areas predicted to provide greater ease of movement, and thus facilitate connectivity, have greater cell values. Consequently, if the model accurately reflects areas that would have facilitated wild dog movement from source populations, the occurrence records should be located within grid cells that, on average, have greater values than the values associated with a set of randomly generated points. We created a set of 300 random points in ArcMap which were distributed throughout the map area, but not located inside any of the source populations. Furthermore, to determine whether the current flow connectivity network may be of importance to other threatened carnivores, we overlaid the 339 cheetah occurrence records onto the current flow connectivity map. The current flow grid cell values were extracted to each random point and to the wild dog and cheetah occurrence records. Analysis of variance (ANOVA) was conducted to compare current flow values associated with the random points, cheetah and wild dog packs and wild dog dispersers. We also calculated AUC values for the current flow model using wild dog disperser occurrence records and cheetah occurrence records as presence records and 300 randomly selected records as absences.

Identifying priority conservation areas

Since a large proportion of South Africa's wild dog population occurs outside of protected areas, this portion of the population is of great significance in the conservation of the endangered species (Davies-Mostert et al. 2009). Priority conservation areas, which we define here as landscapes suitable for re-establishing wild dog populations or ensuring survival of existing populations, would need to be large, relatively ecologically intact, spatially contiguous and interspersed with minimal amounts of human activities which are incompatible with large carnivores (Woodroffe and Ginsberg 1999). Given the importance of immigration and emigration for population viability, habitats for permanent occupation would additionally need to have some degree of connectivity to a source population.

The Maxent model using occurrence records for wild dog packs identifies areas with the greatest potential to support a resident population. The small grid cell size used in the Maxent model (0.83 km × 0.83 km) results in habitat suitability maps being expressed at a fine scale. Grid cell values range from zero (highly unsuitable) to one (highly suitable). Contiguous suitable habitat is therefore characterised by several neighbouring grid cells with values that are close to one. At a landscape scale, as opposed to a local scale, mean habitat suitability at a coarser resolution (e.g. 5 km $\times$ 5 km) would be more informative of landscape level habitat quality. This will facilitate the identification of large contiguous areas which are required to support one or more packs and could be assessed further in an attempt to identify priority conservation areas.

To assess landscape level-habitat quality, we performed a spatial filter on the output from the Maxent wild dog pack model. A filter was applied to calculate the mean grid cell values around focal grid cells. The filter calculated the mean value of the grid cells surrounding each focal cell using a kernel of 10 $\times$ 10 grid cells in size (equivalent to 8.3 km $\times$ 8.3 km = 68.9 km^2). To identify the distribution of the highest quality landscapes, we used the grid cell values and selected only the highest 10 % of all the cells. The selection of the highest quality regions delineates high quality habitat patches which vary greatly in size. Priority conservation areas should be able to support at least a single resident wild dog pack. Although it has been proposed that protected areas as small as 200 km^2 may be suitable for wild dog reintroduction in South Africa (van Dyk and Slotow 2003), we used a more conservative minimum area requirement of 500 km^2 which is still relatively small. Consequently, all high quality habitat patches smaller than 500 km^2 were excluded from subsequent analysis.

The viability of potential priority conservation areas, although all larger than 500 km^2, could vary greatly and would be influenced by factors such as patch size, perimeter-area ratio (indication of risk of edge effects), degree of fragmentation by main roads, and extent of existing protected areas (percentage covered). These factors were calculated for each potential priority conservation area, in addition to the degree of connectivity, since they would assist in quantifying the potential and viability of priority conservation areas.

Results

Habitat selection by wild dog packs and dispersers

Evaluating the ecological niche model's performance using the area under the curve (AUC) statistic indicated that the wild dog pack model performed better than the disperser model, with variation in the permutation importance of the three predictor variables. Mean values following five-fold cross validation for wild dog packs: training AUC = 0.881; test AUC = 0.850; predictor variable permutation importance: main road density = 47.9 %, land cover = 36.9 %, human population density 15.2 %. Disperser model: training AUC = 0.776; test AUC = 0.750; predictor variable permutation importance: land cover = 36.9 %, main road density = 32.7 %, human population density 30.4 %.

The Maxent model for dispersing wild dogs (Fig. 2b) was noticeably more general than that for the wild dog packs (Fig. 2a), as larger areas of higher suitability were identified. Values associated with training records used in the wild dog pack model (mean = 0.56) were significantly greater than those in the dispersal model (mean = 0.52; P = 0.038; Mann–Whitney rank sum test; U-statistic = 21879.0).

A histogram (Fig. 3) with ten classes between zero and one indicated that values associated with dispersal records were more evenly distributed than the pack records, with a peak (19.6 %) between 0.4 and 0.5. The values for pack records were distributed more towards the higher suitability classes, peaking (28.5 %) between 0.6 and 0.7. Furthermore, a comparison of Shannon diversity values using a *t* test (Hutcheson 1970), which accounts for both abundance and evenness of the distribution of records across the ten classes, indicated a significant difference between the two groups (P = 0.033, t = 2.15, df = 200.35). The quality of habitats utilised by dispersing individuals thus varied more widely compared to resident packs.

Habitat connectivity

The current flow model (Fig. 4) had some similarities to the Maxent disperser model (Fig. 2b), but is far easier to interpret (for reclassified binary maps, see supplementary material). The linkages identified by the least cost path model were located within areas identified as providing connectivity by the current flow model, but the single paths result in the omission of extensive areas which provide connectivity (as confirmed by occurrence records and as predicted by the current flow model). Notably, the areas highlighted as providing connectivity by the current flow model

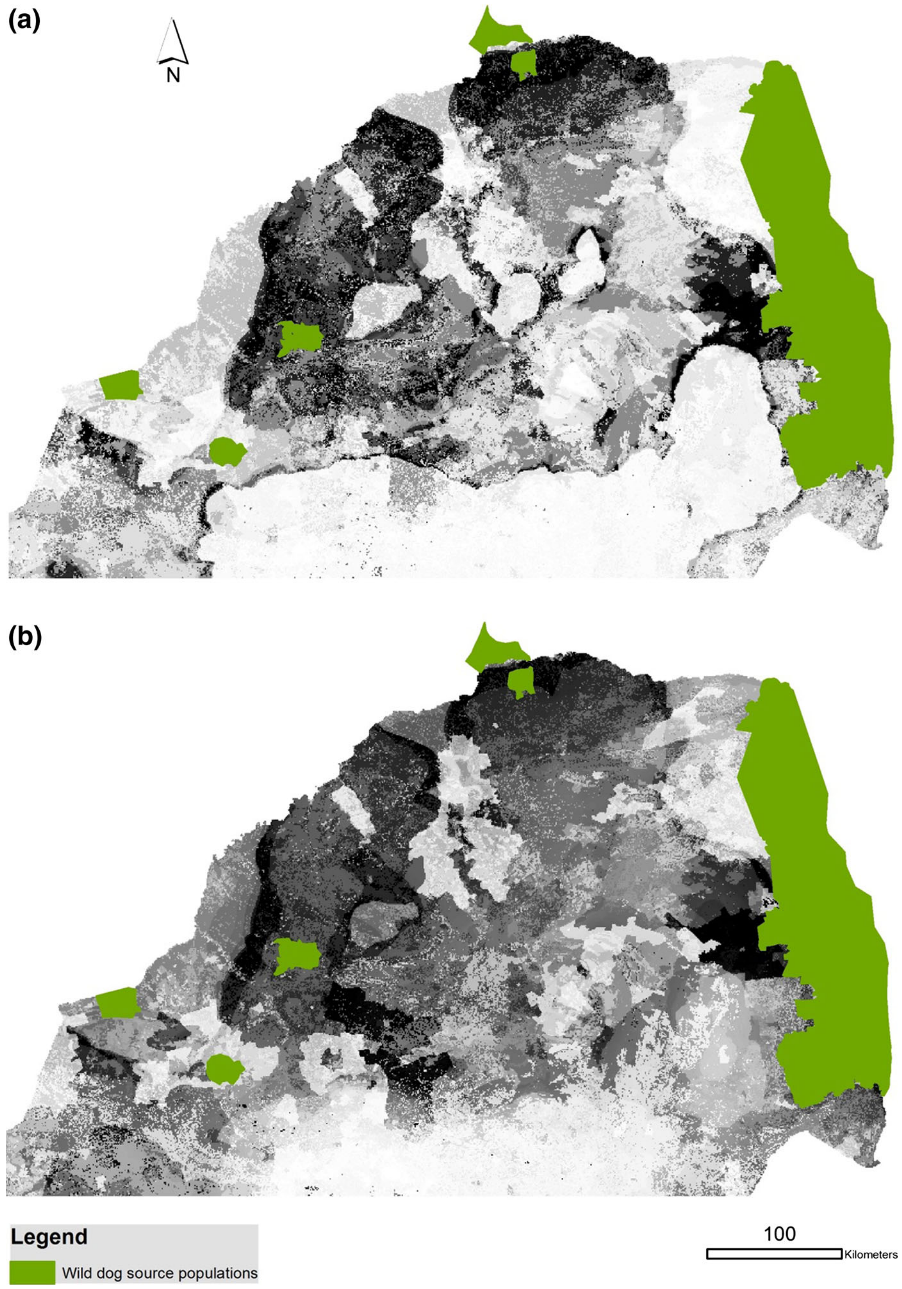


Fig. 2 Areas identified as potentially suitable to support **a** resident wild dog packs and **b** wild dog dispersal. *Black* = most suitable; *white* = totally unsuitable. Protected areas which served as potential source populations are shown in *green*. (Color figure online)

largely captured the wild dog and cheetah distribution records. Contrasting the proportion of map area identified as suitable by the dispenser, pack and current flow models at different threshold values revealed that the disperser model predicts larger areas of suitable habitat at most thresholds (Fig. 5). It is therefore a more general model compared to the pack and current flow models.

The current flow model had the greatest AUC values when contrasting these values for the three models (Table 2). Furthermore, the ANOVA indicated a significant difference between the current flow values associated with cheetah, wild dog packs, wild dog dispersers and the random points in the study area ($H = 244.9$, $df = 4$, $P = < 0.001$). The pairwise multiple comparison procedure using Dunn's method revealed that the current flow values associated with the cheetah and both wild dog groups were significantly greater than those for the random locations ($P = < 0.05$), but there was no difference among the cheetah and wild dog groups (Fig. 6).The wild dog and cheetah location data were therefore associated with significantly higher current flow values than the random samples, thus indicating the model's biological relevance and good performance.

We hypothesized that wild dog dispersers would utilise a broader variety of habitat qualities than packs. The data in Fig. 6 indicates that, in addition to a lower median value, the spread of current flow values (which translates to habitats) within the disperser group is far greater than that recorded within the pack group, supporting our hypothesis.

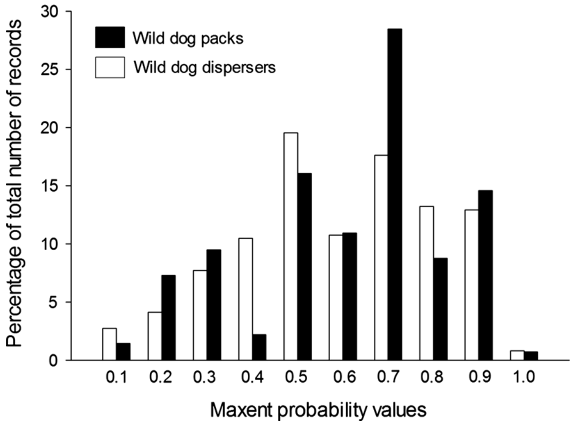


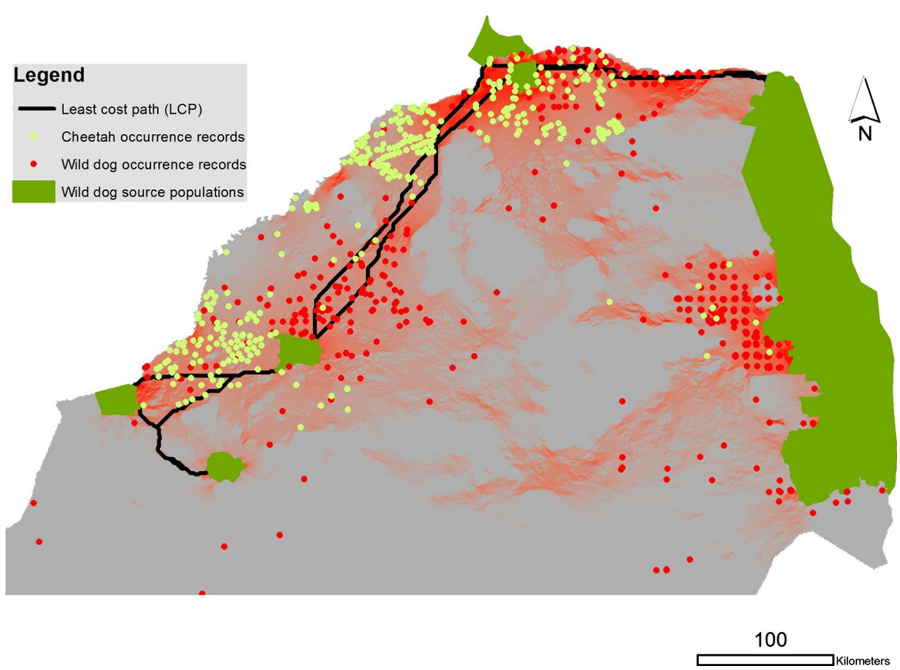
Fig. 3 Histogram indicating the distribution of probability values extracted from Maxent models associated with occurrence records for wild dog packs and dispersers in each of the two models. Highly suitable habitat has a higher value

Priority conservation areas

The criteria used to identify priority conservation areas yielded five areas greater than 500 km^2 in size (Fig. 7). These patches ranged from 537 to 5215 km^2 in size (Table 3). Of the 576 wild dog and 339 cheetah location records, 311 (54 %) and 139 (41 %) fall within these five regions, respectively. Of the 311 wild dogs records, 191 (61.4 %) were dispersers and 120 (38.6 %) were packs.

Evaluating the feasibility of the five focal conservation areas can be aided by a graphical display of their proximity to source populations, degree of connectivity, extent of existing unpopulated protected areas, fragmentation due to main roads and the distribution of occurrence records (Fig. 7).

Fig. 4 Connectivity between source populations based on current flow modelling with the *black lines* indicating least cost pathways. The records of wild dog occurrence are shown in *red* and cheetah in *green*. Although these records were not used in the model, they are largely contained within the areas predicted to facilitate connectivity (*darker red* = more suitable; source populations in *green*). (Color figure online)



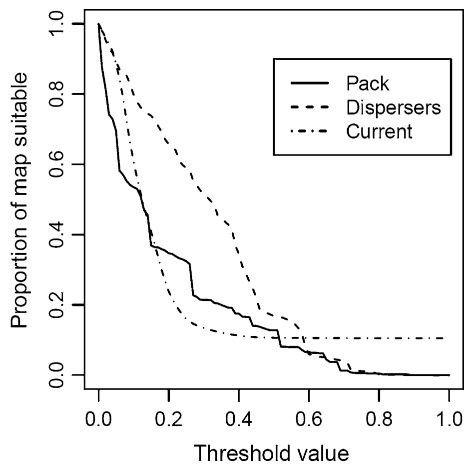


Fig. 5 The proportion of the map area predicted as suitable at different thresholds for the Maxent pack model, the Maxent disperser model and the current flow model

Table 2 Area under cure (AUC) values for the Pack, Disperser and Current flow models using the occurrence records for dispersing wild dogs (Dispersers) and cheetah (Cheetah)

Occurrence records	Model		
	Pack	Disperser	Current flow
Dispersers	0.729	0.766	0.774
Cheetah	0.742	0.765	0.804

As absence records were not available to calculate AUC values, 300 randomly selected records were used instead

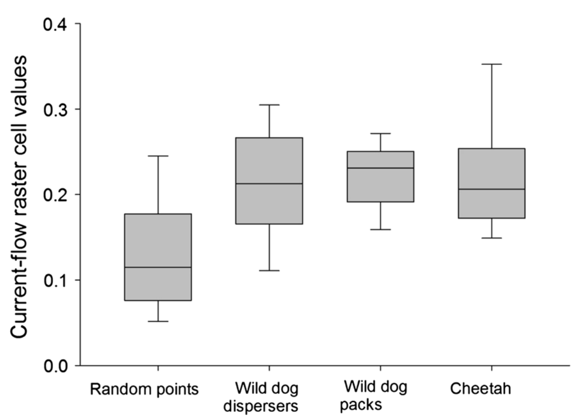


Fig. 6 The raster grid cell values from the current flow model linked to the locations of random points, wild dog dispersers, wild dog packs and cheetah across the study area. Median values indicated by the *line* in the *boxes*, the inter-quartile range by the *boxes*, and the range by the *error bars*

Discussion

Identifying suitable habitat for resident and dispersing wild dogs

While habitat selection data of resident animals may be available for many taxa, it is rarely available for dispersing individuals. This is an important consideration in modelling work since habitat which facilitates movement between patches or populations may lack key features and resources required for long-term occupancy (Carroll et al. 2012). As a consequence, connectivity models based on ecological information from resident animals may lead to inaccurate conclusions. Most notably, such models may not identify habitat that facilitates movement, thereby overestimating the degree of habitat fragmentation. Failure to detect corridor habitat precludes these key areas from receiving conservation attention, further exacerbating isolation. Although studies have documented how dispersing carnivores use lower quality habitat than resident conspecifics (e.g. Palomares et al. 2000), we could not find any literature specifically comparing models derived with separate empirical data for dispersers and residents and our results thus provide insights into this debated issue.

Modelling and contrasting wild dog habitat suitability based on occurrence records associated with wild dog packs and disperser groups indicated that dispersing individuals were less habitat-specific. These results also confirm that our differentiation of wild dog packs and dispersing groups based on documented patterns of group size sufficed for the purposes of our analyses. In the wild dog pack model, large patches of highly suitable habitat were isolated, separated by extremely unsuitable regions (Fig. 2a). In contrast, predictions for wild dog dispersers identified habitat linking the highly suitable patches, indicating some level of connectivity (Fig. 2b). This habitat facilitated wild dog movement (as confirmed by occurrence records) and was also identified to provide linkage by both the LCP and current flow models. Huck et al. (2011) argue that the shift in habitat selection for dispersing animals arises primarily as a result of necessity and not actual active selection and that data from resident individuals may be more appropriate for establishing dispersal corridors. Using empirical data, our study illustrates the short-comings of such an approach; using wild dog pack data for

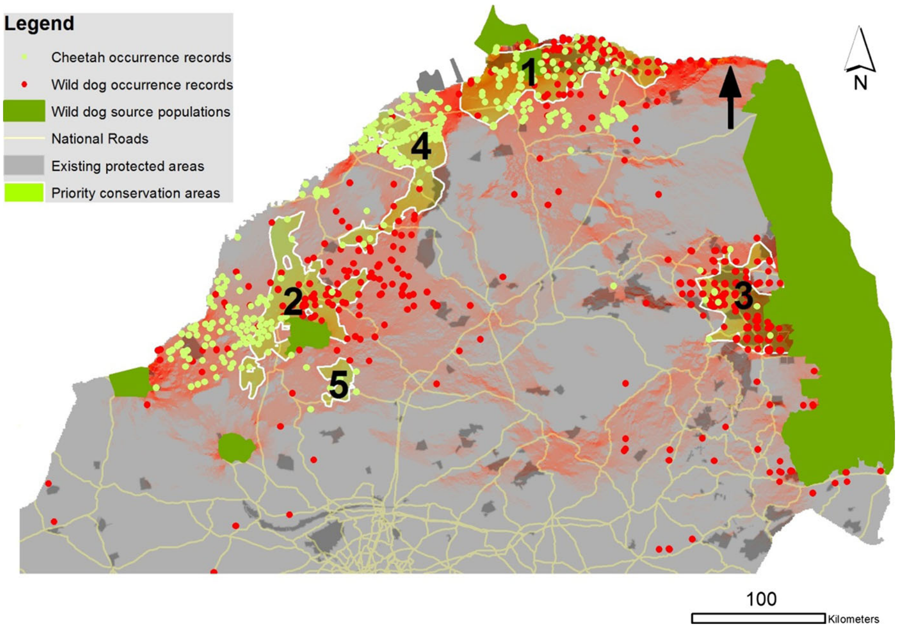


Fig. 7 The five priority conservation areas (numbered) are shown in *light green* and encapsulated by a *white line*. These are overlaid onto the current flow connectivity network (in *red*) indicating the potential connectivity between the priority conservation areas and source populations (*dark green*). Existing protected areas shown in *dark grey*. Wild dog occurrence records are shown as *red dots*, cheetah as *light green dots*, with major national roads in *yellow*. The black arrow indicates an important corridor providing connectivity between the Kruger National Park and the northern parts of the study area. (Color figure online)

Table 3 Characteristics of the five focal areas (Fig. 7) and the number of wild dog occurrence records occurring within each

Focal area	Size (km^2)	Perimeter-area ratio	% covered by PA	Main roads (km)	Km road/km^2	Number of wild dog records
1	5215	9.1	21	237	0.045	105
2	4316	5.1	9	116	0.027	39
3	3139	6.4	60	190	0.061	178
4	2969	4.8	12	97	0.033	7
5	537	3.2	0	24	0.045	1

corridor determination did not identify habitat which did in fact provide connectivity for dispersing wild dogs. Overlooking these corridors in an initial conservation planning phase would preclude them from receiving the adequate conservation attention, impeding effective conservation planning. Flexibility in selecting conservation areas is important in conservation planning (Margules and Pressey 2000) and using pack data alone would reduce the number of land parcels identified as suitable, thereby limiting the options for implementing corridors. Furthermore, we only used occurrence data from outside of protected areas where occupied habitat may have been of a lower quality than within protected areas. If pack data from within protected areas had been included, it is likely that the differences between disperser and pack models would have been greater, further weakening corridor identification based on such data.

Insights into the performance of alternative habitat connectivity models

It has been argued that using expert opinion to assign costs to predictor variables in order to create a cost layer is subjective and not based on sound biological grounds (Ray and Burgman 2006; Huck et al. 2011). We created and used a cost layer in both the LCP and current flow models. The current flow model resulted in a good spatial match between occurrence records and landscapes predicted to facilitate linkage, indicating that the model was indeed reliable. Furthermore, the values associated with the independent occurrence data were significantly greater than would be expected by chance, indicating that the model accurately predicted areas that would support both wild dog and cheetah movement. The records from the wild dog dispersers showed a lower mean value and far greater spread than values associated with records for resident packs, explicitly indicating how dispersing individuals use habitat of variable suitability that would not necessarily support permanent residence. Since the occurrence records confirmed the use of the identified habitat by both these species, the same corridors may be important in providing connectivity for other species in the region. The current flow model also had high AUC values when tested using independent records for wild dogs and for cheetah, providing further evidence that the current flow model was successful.

Testing the performance of the relatively new current flow methodology has to date not been possible due to a lack of disperser occurrence records (Carroll et al. 2012). Our evaluation and results therefore provide strong support for the performance of the current flow methodology. Since habitat selection data for dispersing individuals are often lacking for species of conservation concern, this technique may be particularly useful in conservation planning. Although assumptions regarding obstacles to a species' movement may be subjective, in our case it resulted in a useful model that is directly beneficial to conservation planning. The Maxent model for dispersing wild dogs has some similarities to the current flow model, but interpreting habitat providing linkage is more difficult. While the LCP did traverse habitat which was utilised by wild dogs, the current flow model considers all possible routes between predefined patches and is thus biologically more realistic and comprehensive. Although the LCP linkages were captured by the current flow model, the distribution of wild dog and cheetah records (Fig. 4) indicate that the LCP greatly underestimates habitat facilitating connectivity, unlike the current flow model.

Identifying priority conservation areas

Wild dogs occurring outside of protected areas in South Africa need to be prioritized in future conservation initiatives (Davies-Mostert et al. 2009). In particular, restoration should attempt to promote connectivity as the natural movement it facilitates increases population viability (Davies-Mostert et al. 2009). Dispersing wild dogs will travel through unfavourable habitat, but pack formation and persistence is restricted to areas of higher quality and is dependent on individuals finding mates. The regular occurrence of wild dogs will decrease the negative mate-finding Allee effects within a given area. In addition, increasing distance between areas is negatively correlated with connectivity for carnivores (Ferreras 2001). Consequently, selecting the most viable potential recolonisation site will depend largely on these factors.

The five priority conservation areas represent the most feasible areas to potentially re-establish populations of African wild dogs within their historical range, or ensure survival of existing animals. Apart from accommodating additional packs, these areas may serve as stepping stones between existing wild dog populations, reducing anthropogenic mortality risks and increasing the probability of dispersing animals successfully finding mates and forming packs (Davies-Mostert et al. 2012). Areas 1 and 3 (Fig. 7) have the greatest number of occurrence records (86 % of records occurring within the five areas), the most favourable perimeter-area ratio, and the largest extent of currently protected areas. Importantly, both areas are large and well connected to source populations; Area 1 is connected to the Tuli Block (Botswana) and parts of southern Zimbabwe which are home to resident and dispersing wild dogs, while Area 3 is directly alongside the greater Kruger National Park ecosystem and the wild dog population it supports. The wild dogs occurring here are consequently managed as part of the greater Kruger National Park population and including this area in conservation planning for wild dogs would increase the area available to the population's conservation. Although 60 % of Area 3 is protected, it also has the highest density of main roads which represents a serious mortality risk to wild dogs (Woodroffe and Ginsberg 1999). Furthermore, Area 1 is relatively close to the Kruger National Park with the shortest route between the two being identified as suitable dispersal habitat.

Consequently, maintaining this ecological corridor between the two (indicated by an arrow in Fig. 7) is of vital importance. For the purposes of connectivity between populations this corridor could be viewed as a priority conservation area.

In comparison to Areas 1 and 3, Areas 2, 4 and 5 are generally less suitable for attempting to re-establish a self-sustained wild dog population. This is due largely to a far lower incidence of wild dog presence which will limit gene flow and decrease the likelihood of pack formation. Fewer wild dogs are attributable to the increased distance from large source populations and, as indicated by the connectivity analysis, the greater degree of isolation given limited suitable dispersal habitat to these areas. Lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) are scarce outside protected areas in South Africa (Lindsey et al. 2005a), which increases the potential suitability of those areas, given that those species are major competitors with wild dogs (Creel and Creel 2002; Swanson et al. 2014).

Future conservation efforts in these areas would need to take specific factors into account to realise the area's true conservation potential. Prey availability is assumed to be sufficient given the semi-natural state of much of the suitable areas and given the high frequency of wildlife ranching in those areas. Despite the ecological suitability of the areas, high rates of anthropogenic mortality would negate the viability of otherwise suitable areas. Due to a lack of relevant data, land use could not be incorporated into our models. Even if a region is ecologically intact, land uses associated with low predator tolerance such as livestock farming or wildlife ranching based on consumptive wildlife use or breeding of rare wildlife species directly influence a region's suitably for re-establishing a wild dog population or transient dispersing animals (Lindsey et al. 2005a). Increased mortality due to deliberate killings of wild dogs (Thorn et al. 2013) will hamper population establishment and persistence and greatly reduce the probability of dispersing individuals successfully moving between populations. The knowledge of conservation officials familiar with these regions and land use practices will be helpful in refining conservation strategies. In particular, tolerance among land owners would need to be addressed. One approach for improving tolerance may be to establish research projects where conservationists actively engage with land owners on a regular basis to listen to complaints, and to improve understanding among ranchers of the vast areas used by wild dogs so that they understand that any negative impacts are likely to be spread across a corresponding area.

Encouraging the development of policies that encourage land uses conducive to tolerance towards predators would be another important step. Tolerance tends to be higher in areas where is used for ecotourism and where ranches have been combined into larger conservancies (Lindsey et al. 2009). By contrast, attitudes tend to be more negative where the primary land use is livestock production, consumptive wildlife use, and the breeding of rare and valuable wildlife (which is also associated with erection of predator proof fencing) (Lindsey et al. 2005a). Both Areas 1 and 3 are comprised of a large proportion of informally (private) protected areas where land use would be expected to be compatible with large carnivores. Since ecotourism is the main form of utilisation within these areas, the reintroduction of wild dogs may be received particularly favourably as they are attractive to tourists (Lindsey et al. 2005b).

Expanding conservation areas based on the requirements of single species is unlikely to be a realistic proposition. The most viable areas and the linkages between them would not only be of importance to wild dogs. Our use of cheetah occurrence data supported this assumption and indicates how other species of conservation concern may also benefit should these areas receive more conservation attention. Furthermore, wild dogs and cheetah are large carnivores near the top of the trophic level. Should these areas successfully support populations of these and other large carnivore species, it would indicate that the lower trophic levels were in place and that the greater ecosystem was functioning, and thereby acting as an umbrella species and aiding the conservation of biodiversity in general (Dalerum et al. 2008).

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