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RESEARCH ARTICLE

A multi-scale assessment of population connectivity in African lions (*Panthera leo*) in response to landscape change

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Abstract
Context Habitat loss and fragmentation are among the major drivers of population declines and extinction, particularly in large carnivores. Connectivity models provide practical tools for assessing fragmentation effects and developing mitigation or conservation responses. To be useful to conservation practitioners, connectivity models need to incorporate multiple scales and include realistic scenarios based on potential changes to habitat and anthropogenic pressures. This will help to prioritize conservation efforts in a changing landscape.
Objectives The goal of our paper was to evaluate differences in population connectivity for lions (*Panthera* leo) across the Kavango-Zambezi Transfrontier Conservation Area (KAZA) under different landscape change scenarios and a range of dispersal distances.
Methods We used an empirically optimized resistance surface, based on analysis of movement pathways of dispersing lions in southern Africa to calculate resistant kernel connectivity. We assessed changes in connectivity across nine landscape change scenarios, under each of which we explored the behavior of lions with eight different dispersal abilities.
Results Our results demonstrate that reductions in the extent of the protected area network and/or fencing protected areas will result in large declines in the extent of population connectivity, across all modeled dispersal abilities. Creation of corridors or erection of fences strategically placed to funnel dispersers between protected areas increased overall connectivity of the population.
Conclusions Our results strongly suggest that the most effective means of maintaining long-term population connectivity of lions in the KAZA region involves retaining the current protected area network, augmented with protected corridors or strategic fencing to direct dispersing individuals towards suitable habitat and away from potential conflict areas.

Keywords Connectivity · Fragmentation · FRAGSTATS · Resistant kernel · Scale · UNICOR

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Introduction

Habitat loss frequently results in small, isolated populations, which have increased vulnerability to local extinctions due to environmental and demographic stochasticity (Winterbach et al. 2013). In addition, subsequent loss of genetic diversity may increase disease susceptibility (e.g., Trinkel et al. 2011) and decrease reproductive success (e.g., Packer et al. 1991). Management actions that facilitate the movement of individuals between isolated populations have the potential to increase effective population size, thereby reducing the risks associated with inbreeding depression (Schwartz and Mills 2005). In order to aid this decision-making process, there has been a proliferation in connectivity models (for reviews see Sawyer et al. 2011; Zeller et al. 2012; Cushman et al. 2013) published which assess functional connectivity given a particular population size, dispersal ability and landscape resistance pattern.

Given that connectivity is scale, species and system dependent (Cushman 2006), it is difficult to reliably predict population connectivity (Rudnick et al. 2012; Cushman et al. 2013). For a particular species in a particular system, population connectivity is the result of the combined effects of the distribution and density of the population, composition and configuration of the landscape, and species specific dispersal characteristics including sex and age differences, effects of different landscape features on movement, and how these combine to shape the dispersal kernel. In most populations, however, there is substantial uncertainty about species distributions and densities (Cushman 2006), how different landscape features affect movement (Zeller et al. 2012), and limited understanding of species dispersal abilities (Elliot et al. 2014a). These uncertainties combine to limit the reliability of connectivity modeling results. In a few cases (e.g., Elliot et al. 2014b) these parameters have been included in the development of resistance surfaces, which are the foundation of most contemporary methods for predicting connectivity (Zeller et al. 2012).

In order to develop effective conservation strategies to reduce habitat loss and fragmentation it is essential to assess how population connectivity varies according to landscape change and the dispersal ability of the focal species. Throughout Africa, landscape change is occurring at a rapid and accelerating rate and is impacting the amount of land set aside for wildlife. Human and livestock populations are growing, coinciding with an increased demand for land. In addition, African economies are expanding and land that is currently set aside for wildlife may be perceived as being more profitable if converted to agriculture or mining. These factors, combined with recent nationwide and partial bans on trophy hunting in Botswana and Zambia respectively, have led to concerns that land which is not officially protected by governments may be converted into land uses that exclude wildlife.

Growing human and livestock populations, together with an increased demand for land, has resulted in increased human-wildlife conflict (Woodroffe and Frank 2005). In the case of the African Lion (*Panthera leo*), human-wildlife conflict and habitat loss are thought among the primary drivers of their recent declines (Bauer et al. 2012). In addition, edge effects have significant negative impacts on protected lion populations (Loveridge et al. 2010). Packer et al. (2013a) conducted a meta-analysis across 42 lion populations and related lion density to management practices. They demonstrated that in fenced reserves lions are closer to their carrying capacities and cost less to manage and protect compared to unfenced reserves in which lion populations occur at lower densities relative to their potential densities and are more likely to decline to extinction. This led the authors to conclude that fencing and other measures to mitigate edge effects are highly effective management strategies for conserving lions. Nevertheless extensive fencing of lion populations would drastically increase population fragmentation and eliminate existing connectivity and dispersal between subpopulations, leaving lions, and other species, in genetic isolation. It is therefore imperative that the effects of landscape change and potential management solutions are empirically tested with data from dispersing individuals so that sound decisions can be made.

African lion populations have suffered an estimated 75 % range reduction in the last 100 years (Riggio et al. 2013) and are increasingly divided into small and isolated remnant populations within protected areas. Bjorklund (2003) used a population genetics model to show that a minimum of 50–100 prides, with no limits to dispersal, is required to maintain long-term genetic diversity. Very few remnant populations provide near this number of prides and some populations have suffered declines in genetic diversity, which has been shown to decrease reproductive performance (Packer et al. 1991) and increase susceptibility to disease (Trinkel et al. 2011). Thus, given the insufficient size of many extant protected areas to provide sufficient population size for long term viability, dispersal among remnant populations may be critical to maintain long-term genetic health and provide demographic rescue of regional lion populations. However, the degree to which remnant lion populations are functionally isolated and the factors that may facilitate gene flow between them through dispersal are largely unknown.

In this paper we used a resistance surface that was empirically optimized based on analysis of the movement pathways of dispersing lions in southern Africa (Elliot et al. 2014b) to calculate resistant kernel connectivity (Compton et al. 2007) across the Kavango-Zambezi Trans-frontier Conservation Area (KAZA) for each of nine landscape change scenarios and eight lion dispersal abilities. Our work was designed to evaluate five hypotheses relating to the effects of landscape change on population connectivity for lions in southern Africa.

Hypothesis 1 Loss of protected area status for WMAs would result in very large decreases in population connectivity across all dispersal abilities.

Hypothesis 2 Extensive fencing of protected areas would likewise lead to very large increases in population subdivision and isolation.

Hypothesis 3 Designation and protection of corridors or fences strategically placed to funnel dispersing individuals between protected habitats would increase population connectivity.

Hypothesis 4 An increased human population would result in large decreases in population connectivity across all dispersal abilities.

Hypothesis 5 The effects of all landscape change scenarios would be scale-dependent, with larger effects on connectivity when lions disperse over shorter distances and smaller relative effects when dispersal is less geographically limited.

Materials and methods

Study extent

The study extent ($\approx$1.5 million km^2) encompasses the entire Kavango Zambezi Transfrontier Conservation Area (KAZA-TFCA) and traverses sections of Angola, Botswana, Namibia, Zambia and Zimbabwe (Fig. 1). Approximately 31 % ($\approx$458,520 km^2) of the study extent is managed for wildlife, including 26 national parks (145,570 km^2), 297 Forest Reserves (52,776 km^2) and 117 wildlife management areas (WMAs) (260,273 km^2). National parks, forest reserves and WMAs are all gazetted wildlife 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).

Resistance surface

We used a resistance surface that was empirically optimized by Elliot et al. (2014b) who 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. Elliot et al. (2014b) used path-level (e.g., Cushman et al. 2010a, b; Cushman and Lewis 2010) randomization and multi-scale mixed-effects conditional logistic regression to predict landscape resistance to dispersal as functions of land use, land cover, human population density and roads. As such the analysis was multi-scale, single level. The analysis was multi-scale in space but not time, since the shift was a spatial shift of paths that were constant in time (30 day long movement segments). The scales that were evaluated included shifts of 0, 12.5, 25, and 50 km (5 scales), and each variable was evaluated across the five scales in a univariate conditional logistic regression, with the scale with the lowest AIC value chosen for inclusion in multivariate models.

The disperser data used in Elliot et al. (2014b) was parsed into 997 segments corresponding to 30 day

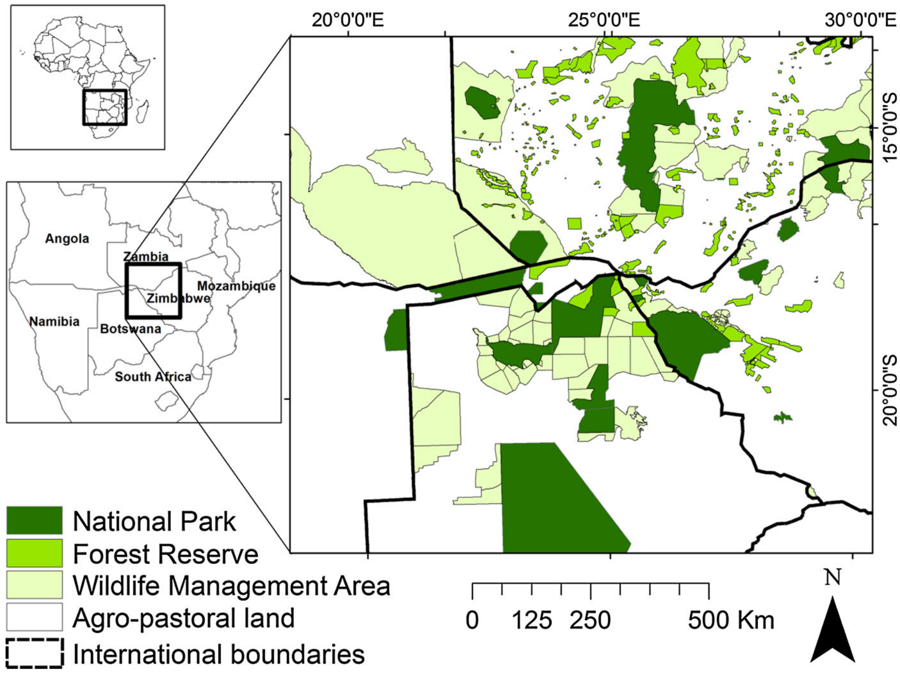

Fig. 1 Study area orientation map

movement periods. The average displacement across those 30 day segments was 11.7 km with standard deviation of 13.6 km. Based on a normal distribution we would expect 99.7 % of path segments have less than 50 km displacement, 97.8 % to have less than 25 km displacement, and 52 % to have less than 12.5 km displacement. Thus the range of scales considered spans the range of available habitat that could be reached by a lion in a 30 day movement bout and spans from relatively small extent of available habitat to relatively large, given the movement ability of the species.

Elliot et al. (2014b) found that 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. We used the resistance map for dispersing sub-adult male lions in this paper, since genetic exchange among populations of lions is primarily mediated by dispersal. The resistance surface was created with a 500 m cell size, with 2384 rows and 2618 columns, corresponding to an extent of 1,192 km by 1,309 km, or 1.56 million square kilometers.

Landscape change scenarios

Our analysis evaluated nine different scenarios of changing landscape resistance, which we divided into five groups (Table 1; Fig. 2).

The first group of landscape change scenarios involved conversion and reduction of the extent of protected lands. An increasing human population density and potential economic growth in the region is certain to put increasing pressure on protected areas such that it is conceivable that in the future some areas currently protected for wildlife could be developed. Scenario 1 evaluated the current situation (as predicted by Elliot et al. 2014b). In scenario 2 we held landscape resistance the same as under the current situation, but reassigned all WMAs in Botswana and Zimbabwe (142,912 km^2) to unprotected agro-pastoral lands and recalculated their landscape resistance using the equation in Elliot et al. (2014b). This scenario was evaluated as an extreme outcome of proposed mining activity in the WMAs of Zimbabwe and a trophy

Table 1 Five hypotheses relating to change in landscape connectivity for African lions (*Panthera* leo) were evaluated for each of nine landscape change scenarios at eight dispersal abilities

Group	Scenario	Rationale	References	Hypothesis
1	1. Current situation	If the status quo can be maintained		
	2. No wildlife management areas in Botswana and Zimbabwe	Concerns that a ban of trophy hunting and mining activity could reduce land available for wildlife	1, 2	H1
	3. National parks only	Extreme scenario of human pressure for land resulting in the conversion of all non-National Parks to agro-pastoral land	3	H1
2	4. Designation of protected corridors	Peace Parks Foundation facilitated the establishment of KAZA and have expressed interest in establishing corridors	4	H3
	5. Erection of funneling fences[a]	Fences could be used to ensure lions do not disperse into areas where there is no ecological value of doing so	5, 6, 7, 8, 9	H3
3	6. Fenced National Parks[a]	Fences could be used to protect National Parks from human encroachment and prevent animals from leaving	5, 6, 7, 8, 9	H2
	7. Botswana veterinary fences and fenced boundary of HNP[a]	Existing veterinary fences in Botswana could be enhanced and a new fence erected in HNP	5, 6, 7, 8, 9	H2
4	8. Doubling of human population	Human populations are growing rapidly in Sub-Saharan Africa—Africa's population is expected to double by 2050	3	H4
5	9. Only fenced national parks remain[a]	Extreme scenario where all wildlife areas have been lost except National Parks, which are then fenced	5, 6, 7, 8, 9	H1, H2

Predictions were formulated based on hypotheses and findings from the following sources: (1) Lindsey et al. (2006); (2) Lindsey et al. (2012); (3) Population Reference Bureau (2013); (4) PPF (2013); (5) Packer et al. (2013a); (6) Creel et al. (2013); (7) Packer et al. (2013b); (8) Woodroffe et al. (2014); (9) Pfeifer et al. (2014)

[a] All fences were made impermeable to lion movement

hunting ban in Botswana, both of which could potentially result in a landscape dominated by anthropogenic activity, such as in agro-pastoral lands. In scenario 3 we reassigned all areas not designated as National Parks (313,050 km^2) to unprotected agro-pastoral lands and recalculated their landscape resistance.

In the second group of landscape change scenarios we evaluated the effect of fencing and corridors on landscape permeability. Designation of corridors and building of fences to direct dispersing individuals toward suitable habitat and away from areas of high mortality risk are approaches proposed to improve population connectivity and mitigate for habitat loss (Beier et al. 2008). Scenario 4 investigated the effect of designating and protecting four wide dispersal corridors across breaks between protected areas and assigning them resistance equivalent to national parks, while scenario 5 evaluated the effect of building impermeable fences to funnel dispersing individuals toward protected areas and away from areas of high human population density (Fig. 2).

In the third group of scenarios, we evaluated two scenarios related to fencing. Recently, Packer et al. (2013a) suggested that one option to mitigate against the edge effects associated with rapid human population and economic growth, is to fence lion populations. In scenario 6, we evaluated the effects of fencing existing National Parks, while keeping all protection outside the parks as existing currently. Scenario 7 evaluated the potential impact that existing veterinary and forestry fencing coupled with potential new fencing along the eastern boundary of Hwange National Park might have if made impenetrable to lion dispersal.

There was a single scenario in each of the fourth and fifth groups. Scenario 8 evaluated a doubling of the human population, while keeping all current protected lands in their present status. Scenario 9 combined aspects of both reduction of the extent of protected land and use of fences. Specifically, this scenario involved the transfer of all non-national park lands to agro-pastoral use and fencing of National Parks.

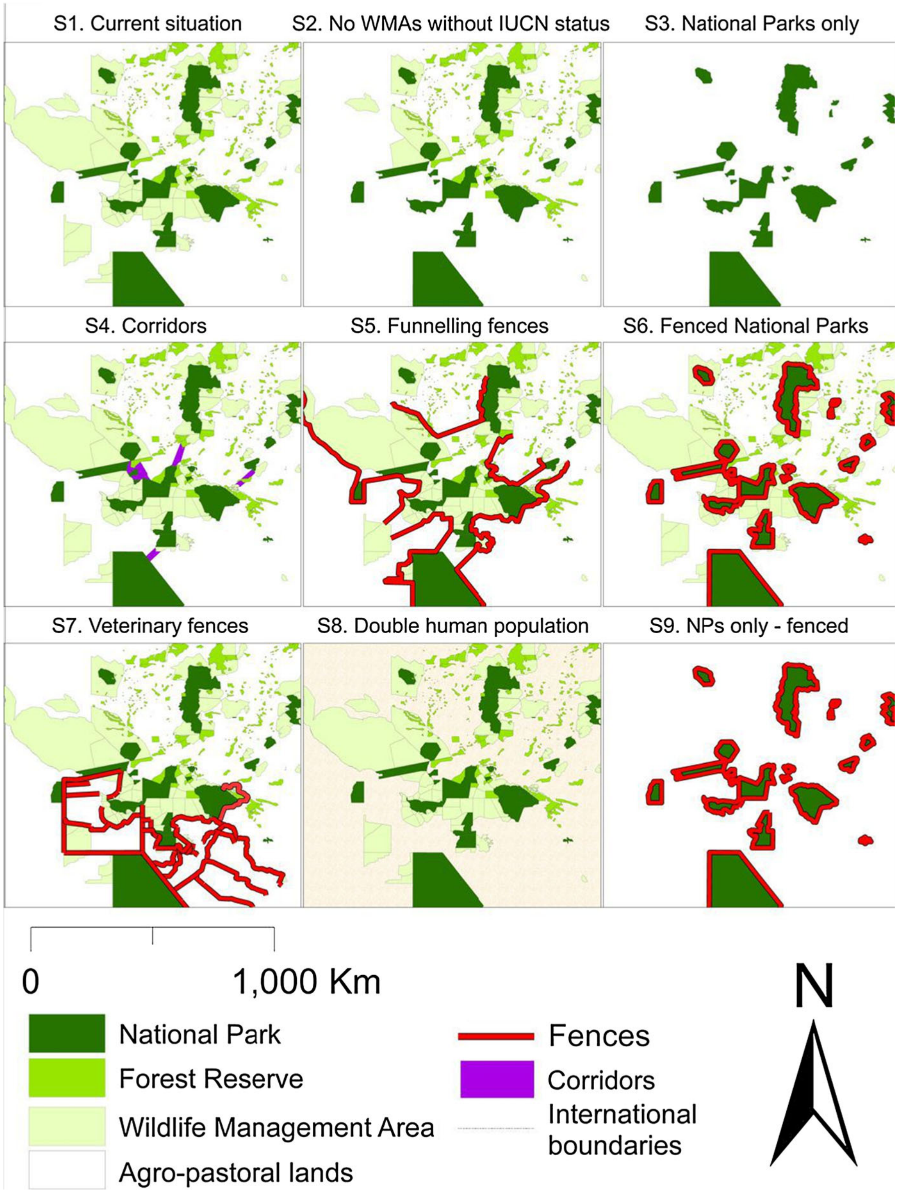

Fig. 2 Visual depiction of the nine landuse change scenarios

Evaluation of influences of a range of dispersal abilities

Empirical optimization such as presented by Elliot et al. (2014b) can provide robust estimates of the relative resistance costs of different landscape conditions. However, information on relative cost of movement across a landscape does not enable reliable prediction of population connectivity without knowledge of the dispersal ability of the species, in terms of how much cumulative cost a disperser is able to traverse. For most organisms information on dispersal ability is absent or anecdotal. However, recent studies of lion dispersal have vastly improved our knowledge on movement (Elliot et al. 2014a), connectivity (Elliot et al. 2014b) and survivorship of dispersing individuals (Elliot et al. 2014c). This uncertainty in dispersal ability is particularly important given recent work which showed that dispersal ability may often have a larger effect on population connectivity than differences in the resistance map itself (e.g., Cushman et al. 2012, 2013). We evaluated the sensitivity of connectivity predictions to

Table 2 Description of eight dispersal abilities evaluated

Dispersal ability scenario number	Dispersal ability in cost units of Elliot et al. (2014b) resistance map	Expected maximum dispersal distance through protected national park land (km)
1	500,000	41.7
2	1,000,000	83.3
3	1,500,00	125.0
4	2,000,000	166.7
5	2,500,000	208.3
6	3,000,000	250.0
7	3,500,000	291.7
8	4,000,000	333.3

dispersal ability by evaluating eight different dispersal abilities, designated in cost units (Table 2). We sought to bracket the plausible range of lion dispersal from a value lower than the probable true dispersal ability of the species (e.g., 500,000 cost units), to a value higher than the probable true dispersal ability of the species (e.g., 4,000,000 cost units). These dispersal abilities correspond to geographical distances of potential movement ranging from 41.7 km (at 500,000 dispersal ability) through 333.3 km (at 4,000,000 dispersal ability) through suitable protected habitat (in this case the average resistance within Hwange National Park). The data for the Elliot et al. (2014b) resistance surfaces paper included GPS data from eleven dispersing individuals. Five of those individuals were collared prior to dispersal and remained collared until they had established a territory. The number of days dispersing ranged from 90–539 and total distance walked during dispersal ranged from 728–4765 km. Net displacement (distance from natal area to area of establishment averaged 55 km with 120 km being the maximum dispersal distance (most of which being outside national parks). The maximum distance between the two furthest points on a dispersal trajectory was 251 km. Given this, our range of dispersal abilities used in the present paper is accurately reflected by our telemetry data (Table 3).

Source points for connectivity modeling

The resistant kernel (Compton et al. 2007) approach to connectivity modeling that we utilized is based on least-cost dispersal from a defined set of sources. Thus, a realistic definition of source point location and density is fundamental to producing informative results (e.g., Cushman et al. 2013). For each scenario, source points were established by intersecting the protected area extent in that scenario with a map of estimated site carrying capacity for lions based on climatic correlates of prey biomass (Loveridge and Canney 2009). This intersection produced a spatial layer indicating the expected number of lions per 100 km^2 within protected areas in each scenario, and took the conservative approach of assuming no lions outside of protected areas. We converted these densities into source points for connectivity modeling by taking the product of the density layer and a raster layer of uniform random values between 0 and 1 and 500 m pixel size, and stochastically drawing from this product to produce a random distribution of individuals with density matching Loveridge et al. (2007) within the protected areas in each scenario.

Resistant kernel modeling

Unlike most methods to predict and map dispersal corridors, the resistant kernel approach is spatially synoptic and provides prediction and mapping of expected dispersal rates for every pixel in the study area extent, rather than only for a few selected "linkage zones" (e.g., Compton et al. 2007; Cushman et al. 2014). Also, in resistant kernel modeling, scale dependency of dispersal ability can be directly included to assess how species of different vagilities may be affected by landscape fragmentation (e.g., Cushman et al. 2010a). Resistant kernel modeling is also computationally efficient, enabling simulation and mapping beyond the entire KAZA study area across multiple dispersal abilities and resistance scenarios.

The resistance map produced by Elliot et al. (2014b) provides resistances for all locations in the study area, in the form of the cost of crossing each pixel relative to the least-cost condition. These costs are used as weights in the dispersal function, such that the expected density of dispersing individuals in a pixel is down-weighted by the cumulative cost from the source, following the least-cost route (Compton et al. 2007). The initial expected density was set to 1 in each cell containing a source point. The model calculates the expected relative density of dispersers in each pixel around each source point, given the dispersal ability of the species and the resistance of the landscape (Compton et al. 2007; Cushman et al.

Table 3 Listing of number of days, total distance traveled, net displacement and maximum displacement for 11 dispersing lions used in the Elliot et al. (2014b) analysis of landscape resistance for lion dispersal in southern Africa

	Number of days	Number of fixes	Total distance travelled (km)	Net displacement (distance in km between first and last fix)	Max displacement (distance in km between two furthest points)
NYMfM2[a]	539	8990	4765	56	112
MAKbM1[a]	180	2193	1835	24	114
BALfM1[a]	150	1598	1168	49	154
CATaM1[a]	118	939	728	120	181
SOAcM2[a]	90	1406	748	26	59
SPIbM5	450	5527	4035	10	251
NEHcM4	164	903	732	20	59
UMTaM1	149	2366	1511	24	49
GEMM1	90	459	622	39	77
SPIcM6	39	266	237	33	49
SPIcM5	15	76	82	43	45

[a] Individuals for which the entire dispersal event was recorded via GPS collars

2010a). These individual dispersal kernels for each source point are summed to create a cumulative reistant kernel surface whose values indicate the relative density of dispersers in every location of the landscape. We used UNICOR (Landguth et al. 2012) to calculate the cumulative resistant kernel density for each of the eight dispersal distances (Table 2) in each of the nine resistance scenarios (Table 1). The cumulative resistant kernel density can be interpreted as the probability of a dispersing lion traversing that pixel, given the location of the source points and the resistance of the landscape.

Analysis of resistant kernel maps

In their raw form the resistant kernel density depicts the expected density of dispersing individuals in each resistance and dispersal scenario combination. These densities indicate the distribution of connected populations. It is necessary to define a threshold kernel density for delineating connected populations. Given lack of an objective means to define the kernel density threshold, we chose a cutoff where all values above 0 were considered to be “connected”. Note that this is a highly liberal definition of connectivity, as values close to zero have very low probability of having dispersing individuals cross them. Thus our results should be interpreted as a best case for connectivity in each scenario. Thus, we reclassified the kernel density maps into binary form of value 1 where the kernel density probability of dispersal is greater than 0 (e.g., Cushman et al. 2012; Cushman and Landguth 2012).

We used FRAGSTATS (McGarigal et al. 2012) to calculate the percentage of the landscape, largest patch index, and number of patches that are predicted to be connected habitat for each combination of scenario and dispersal ability. The percentage of the landscape is the simplest metric of landscape composition, and quantifies how much of the study area is predicted to be connected habitat for each kernel map. The largest patch index (McGarigal et al. 2012) reports the extent, as a proportion of the size of the study area, of the largest patch of connected habitat, which is a measure of connectedness of the population. Lastly, we calculated the number of patches of internally connected habitat for each map which is a measure of fragmentation.

Results

Group 1 scenarios: potential effects of habitat loss and fragmentation (comparison of scenarios 1–2, 1–3)

Scenario 2. No WMAs in Botswana and Zimbabwe

The conversion of WMAs to agro-pastoral lands in Botswana and Zimbabwe reduced the extent of the

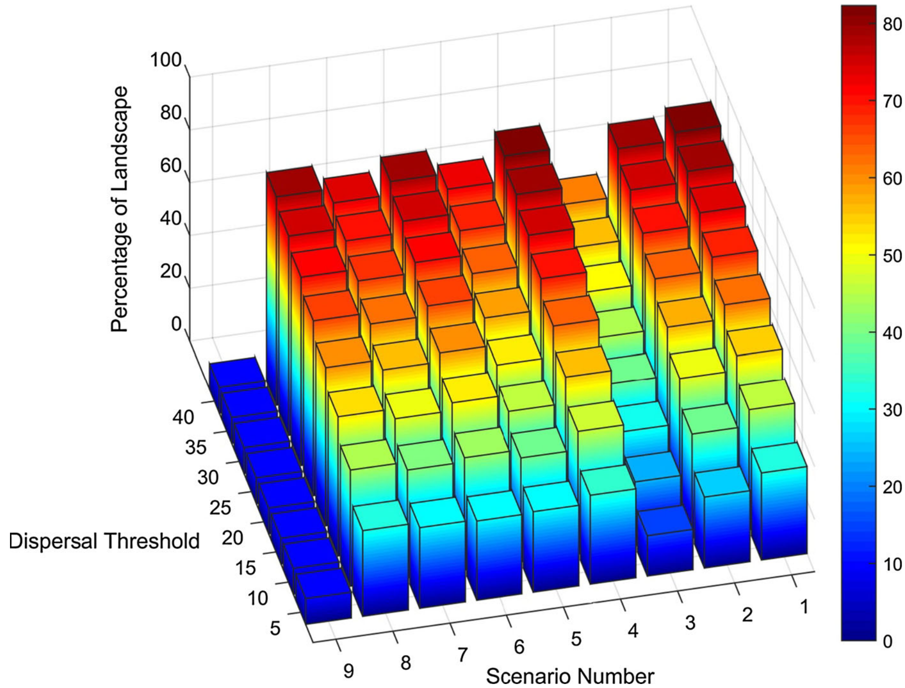

Fig. 3 Change in percentage of the KAZA landscape connected by dispersal across scenarios and dispersal abilities. Dispersal abilities are 5, 500 k; 10, 1000 k; 15, 1500 k; 20, 2000 k; 25, 2500 k; 30, 3000 k; 35, 3500 k; 40, 4000 k cost units

study area connected by dispersal across all dispersal abilities (Fig. 3; Figs. S1, S2). For example, at the 500,000 cost unit dispersal threshold removal of these WMAs was predicted to reduce the extent of the landscape connected by dispersal by 18.5 % from the current situation. This effect decreased with increasing dispersal ability, as lions with larger dispersal ability were able to partially bypass these potential barriers. Similarly, loss of protection for the WMAs resulted in large reductions in the extent of the largest patch of connected habitat (Fig. 4). At the 500,000 cost unit dispersal threshold we predicted loss of protection for the WMAs would result in a 43.7 % reduction in the extent of the single largest patch of connected habitat, with the effect again declining as dispersal ability increased. Loss of protection of the WMAs was also predicted to increase the number of isolated patches of internally connected habitat for the 500,000 and 1,000,000 cost unit dispersal thresholds (Figs. 5, 6).

Scenario 3. National parks only

Removal of all lands not protected as national parks and ascribing them the resistance of equivalent agro-pastoral lands had large effects on predicted connectivity across all dispersal abilities modeled (Fig. 3; Figs. S1, S3). For example, the percentage of the landscape connected by dispersal was predicted to be reduced by 53.6 % from the current condition if all protected lands outside national parks were converted to agro-pastoral lands at a 500,000 cost unit dispersal threshold, with a still very large reduction of 26 % at the largest dispersal threshold of 4,000,000 cost units. This scenario had an even bigger effect on the extent of the largest patch of internally connected habitat (Fig. 4). At the 500,000 cost unit dispersal threshold we predicted a 73.7 % decrease in the extent of the largest single patch of connected habitat, with a 26 % reduction predicted at the largest dispersal threshold. At the 500,000 cost unit dispersal threshold we predicted a 31 % reduction in the number of isolated patches, as a result of attrition and elimination of populations outside the parks (Fig. 5).

Group 2 scenarios: Potential effects of corridors and funneling fences (comparison of scenarios 1–4 and 1–5)

Scenario 4. Corridors

The percentage of the landscape connected by dispersal increased slightly for all dispersal abilities when

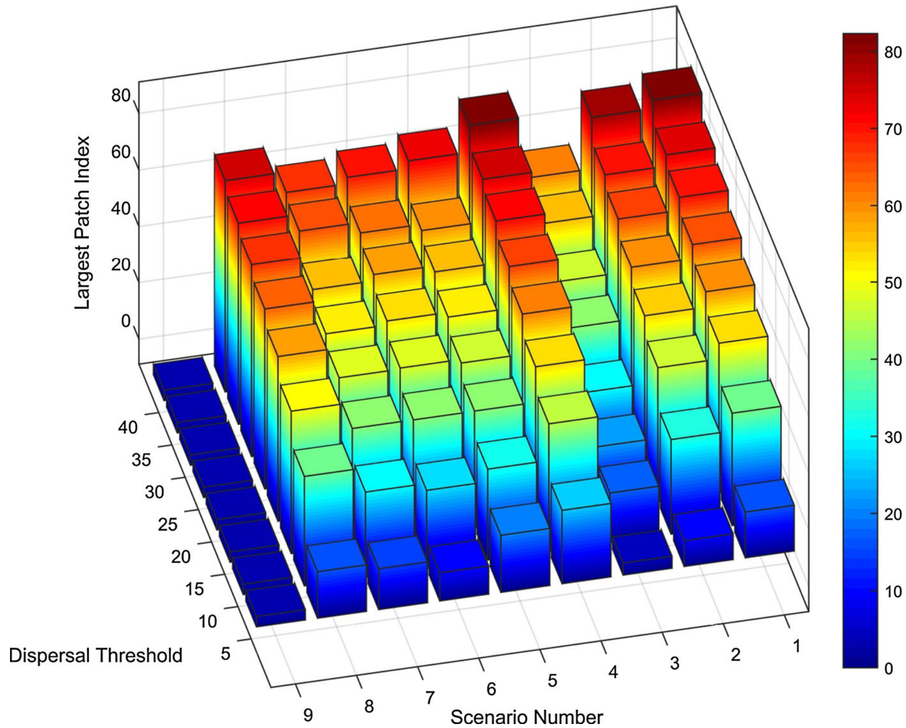

Fig. 4 Change in extent of the largest patch of connected habitat as a percentage of the total KAZA landscape across scenarios and dispersal abilities. Dispersal abilities are 5, 500 k; 10, 1000 k; 15, 1500 k; 20, 2000 k; 25, 2500 k; 30, 3000 k; 35, 3500 k; 40, 4000 k cost units

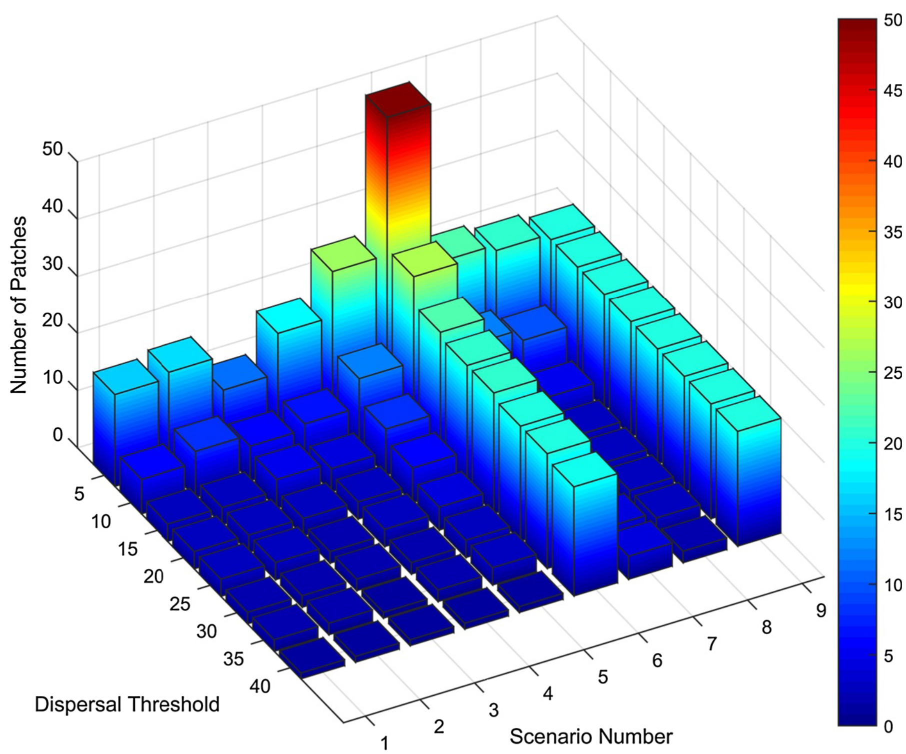

Fig. 5 Change in number of isolated patches of occupied habitat in the KAZA landscape across scenarios and dispersal abilities. Dispersal abilities are 5, 500 k; 10, 1000 k; 15, 1500 k; 20, 2000 k; 25, 2500 k; 30, 3000 k; 35, 3500 k; 40, 4000 k cost units

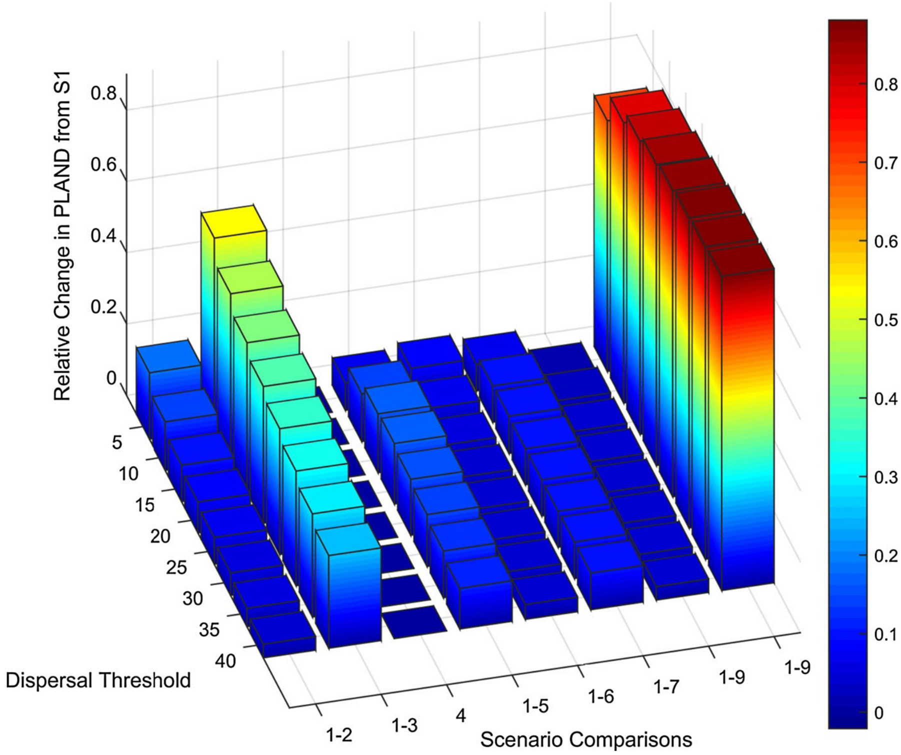

Fig. 6 Proportional change in the percentage of the landscape connected by dispersal between current and each alternative scenario of resistance and dispersal ability. Dispersal abilities are 5, 500 k; 10, 1000 k; 15, 1500 k; 20, 2000 k; 25, 2500 k; 30, 3000 k; 35, 3500 k; 40, 4000 k cost units

corridors between protected areas were established (Fig. 3; Figs. S1, S4). Specifically, the area connected by dispersal in the corridor scenario was predicted to be about 2 % larger than current at the 500,000 cost unit dispersal threshold, decreasing to a 0.02 % increase at the 4,000,000 cost unit dispersal threshold. The corridor scenario had a very large effect on the extent of the largest patch of connected habitat at the shorter dispersal thresholds (Fig. 4). For example, at the 500,000 cost unit dispersal threshold the corridor scenario had a 60 % higher extent of the single largest patch of connected habitat than the current condition. This effect dropped rapidly with increasing dispersal distance and was essentially zero effect at the 4,000,000 cost unit dispersal threshold (Fig. 5).

Scenario 5. Funneling fences

In contrast, the funneling fences were predicted to reduce the area connected by dispersal in all scenarios, with the impact increasing with dispersal ability (Fig. 3; Figs. S1, S5). For example, at the 500,000 cost unit dispersal threshold we predicted a 7.6 % percent decrease in the percentage of the study area connected by dispersal, compared to 11.4 % decrease at the 4,000,000 cost unit dispersal threshold. The funneling fences scenario also led to a large increase (25 %) in the size of the single largest patch of connected habitat at the 500,000 cost unit dispersal threshold (Fig. 4). In contrast, at larger dispersal thresholds, the funneling fences scenario reduced the extent of the largest patch of connected habitat, as compared with the current landscape (Fig. 5).

Across all dispersal thresholds the corridor and funneling fences scenarios resulted in an increased number of isolated patches not interconnected by dispersal. For example, at the 500,000 cost unit dispersal threshold the corridor scenario increased the number of isolated patches by 12.5 % and the funneling fences scenario increased the number of isolated patches by 62.5 %. Both of these effects decreased as dispersal ability increased, such that at the 4,000,000 cost unit dispersal threshold there was no difference between the number of internally connected patches relative to the current landscape resistance condition.

Group 3 scenarios: Potential effects of enclosing protected areas within impermeable fences (1–6 and 1–7)

Scenario 6. Fenced national parks

Fencing of the existing National Parks, while keeping all protection outside the parks as existing currently, resulted in consistent reductions in the extent of connected habitat across all scenarios, ranging from 9 % at the 500,000 cost unit scenario to 4.1 % at the 4,000,000 cost unit dispersal scenario (Fig. 3; Figs. S1, S6). This scenario produced large and consistent reductions in the extent of the largest patch of connected habitat, as the fencing broke formerly contiguous patches into isolated subpopulations. This resulted in a 38 % reduction in the size of the single largest connected patch at the 500,000 cost unit scenario and a 16 % reduction at the 4,000,000 cost unit scenario (Fig. 4). This was accompanied by very large increases in the number of isolated patches. Across all scenarios the number of isolated patches increased by between 215 % (for the 500,000 cost distance scenario) to 1800 % for the 4,000,000 cost unit scenario, reflecting fragmentation of formerly connected populations into isolated fragments by fencing of the parks (Fig. 5).

Scenario 7. Veterinary and forestry fencing coupled with new fencing along the eastern boundary of Hwange National Park

The extensive network of impermeable veterinary and forestry fencing was predicted to result in moderate reductions in the extent of connected habitat across dispersal distance scenarios (7.4 % at 500,000 cost units and 10.3 % at 4,000,000 cost units; Fig. 3; Figs. S1, S7). Similarly, the largest patch of internally connected habitat was predicted to decrease 10 % in the 500,000 cost unit threshold and 17.5 % in the 4,000,000 cost unit dispersal threshold scenario (Fig. 4). Simultaneously, this fencing scenario was expected consistently to increase the number of isolated subpopulations across dispersal distances, with a 37.5 % increase in the number of isolated patches predicted at the 500,000 cost unit threshold, and 300 % increase at the 4,000,000 cost unit dispersal ability (Fig. 5).

Group 4, scenario 8. Projecting population increase

Doubling the human population across the landscape, while keeping all land use types in their present status, produced modest but consistent reductions in the extent of the KAZA landscape connected by lion dispersal (reductions ranging from 1.6 % for the 500,000 cost unit dispersal threshold to 4.1 % for the 3,500,000 cost unit threshold; Fig. 3; Figs. S1, S8). This scenario also resulted in modest reductions in the extent of the largest patch connected by internal dispersal but substantial increases in the number of isolated patches (Fig. 4). Specifically, the number of isolated patches was predicted to increase 31 % at the 500,000 cost unit dispersal threshold, and 100 % at the 4,000,000 cost unit dispersal threshold (Fig. 5).

Group 5, scenario 9. Transfer of all non-national park lands to agro-pastoral use and fencing the parks

This scenario, in which national parks would be fenced and lions outside of the parks would be eliminated, was predicted to result in very large reductions in the extent of the KAZA landscape connected by lion dispersal (70 % reduction in the 500,000 cost unit scenario increasing to 88 % reduction in the 4,000,000 scenario; Fig. 3; Figs. S1, S9). The extent of the largest connected patch was predicted to be reduced even more, with a 77 % reduction in the 500,000 cost unit scenario and 95 % reduction in the 4,000,000 cost unit scenario (Fig. 4). This was accompanied by a very large increase in the number of isolated patches, as formerly connected populations spanning several national parks and protected areas were broken and reduced to isolated sub populations within fenced parks (Fig. 5).

Discussion

Our analysis was designed to evaluate five hypotheses relating to variation in population connectivity for African lions due to landscape change (Table 1). The results are generally consistent with our hypotheses, with some striking differences among scenarios.

Our first hypothesis proposed that loss of protected area status for lands outside of National Parks would result in very large decreases in population connectivity across all dispersal abilities. Removal of WMAs (scenario 2), which are one of several categories of protected areas outside National Parks, predictably had a smaller effect than removal of all non-National Park protected areas, but still was substantial, particularly at the smaller dispersal abilities. For example, at the smallest dispersal ability tested, loss of WMAs resulted in a large reduction in the total extent of population connectivity. The southern part of the KAZA landscape is composed of largely intact wildlife habitat extending west from Hwange National Park in Zimbabwe to the Okavango Delta in Botswana and encompassing the Okavango-Hwange Lion Conservation Unit (IUCN 2006), one of only six lion populations in Africa exceeding 2000 individuals (Riggio et al. 2013). Much of this area is composed of WMAs, which until a ban on trophy hunting was imposed in Botswana in 2014, were primarily protected for consumptive use of wildlife. Our results suggest that should the trophy hunting ban result in conversion of wildlife areas to activities that are less beneficial to wildlife (e.g., cattle ranching) there is a danger that the currently secure Okavango-Hwange population could be severely fragmented.

As expected, removal of all lands not protected as National Parks and ascribing them the resistance equivalent to agro-pastoral lands (scenario 3) greatly reduced population connectivity across all dispersal abilities. As predicted, this scenario had large effects even at the largest dispersal abilities. While the scenario is extreme, it illustrates the effects of what could happen in a future where human pressure on wildlife areas that are not formally protected as National Parks were to result in their conversion to agricultural/pastoral use.

Our second hypothesis, that fencing of protected areas would likewise lead to very large increases in population subdivision and isolation, was also very highly supported. Fencing National Parks while maintaining protected status and current lion populations outside parks (scenario 6) had relatively little effect on the total extent of connected habitat, but very large impacts on the fragmentation of the population. For example, the number of isolated patches of habitat, which are vulnerable to inbreeding depression and demographic stochasticity, increased tremendously in this scenario, with the increases much greater for larger dispersal abilities. Even the relatively modest scenario 7, which involved improving existing veterinary fencing and building new fencing along the eastern boundary of Hwange National Park, was predicted to have very large impacts on population connectivity. The combination of fencing National Parks and transfer of non-national park lands to agro-pastoral land use (scenario 9) was predicted to result in immense reductions to the extent of connected habitat (between 70 and 88 % reduction, depending on dispersal ability) and the extent of the largest patch of connected habitat (between 77 and 95 % reduction), while vastly increasing the number of isolated patches not connected by dispersal. Creel et al. (2013) noted that fencing protected areas as a lion conservation strategy has a number of negative effects including ecosystem fragmentation, loss of dispersal and migration routes, genetic isolation, reduced conservation value of buffer zones (and consequent loss of wildlife-based economic benefits in buffer zones), and utilization of fencing materials for wire snare poaching. They argued that the best conservation strategy for lions would combine improved funding for conservation and focus on preserving large connected landscapes. The large reductions in population connectivity we predicted in the scenarios where protected areas were enclosed inside fences confirms that such management strategies will likely result in large reductions in the extent of connected populations and increasing isolation of remnant populations.

The two fencing and the one fencing and land conversion scenarios are varying severities of a strategy of land management that has been implemented broadly across southern Africa. For example, many private reserves are entirely fenced and rely on very expensive population management, including culling, translocation and intensive veterinary care to maintain populations (Miller and Funston 2014). Some of the major regional national parks, notably Kruger, are also largely fenced to contain wild animals. Fencing can be an effective means of reducing edge effects and limiting conflict with human populations and is widely and successfully used in many reserves in southern Africa that are isolated habitat fragments within human settled landscapes (Packer et al. 2013a). Fencing may become appropriate in areas where it becomes infeasible to protect the land and wildlife within protected areas from poaching and incursion as the human population in the surrounding land increases and it becomes likewise increasingly difficult to manage and mitigate human-wildlife conflict when animals such as lions and elephants roam out of protected areas and damage crops or kill livestock. Nevertheless, in landscapes where existing connectivity is high and ecosystems are largely intact, fencing can result in massive (in some cases more than nearly 20 fold) reductions in population connectivity, as illustrated in our fencing scenarios. While fences are likely the most appropriate intervention for small habitat fragments subject to high anthropogenic edge effects, our results suggest that it is risky to intentionally fragment functioning ecosystems with fences.

As an alternative to widespread fencing of large intact ecosystems, such as the KAZA landscape, we advocate the use of comprehensive land-use planning across national boundaries to establish trans-boundary protected area networks that include designation of strategically placed, protected movement corridors facilitating movement between core populations and perhaps judicious and strategic use of fences to funnel or direct dispersing wildlife toward suitable dispersal destinations within the protected area network and away from areas of high mortality risk and high potential for conflict with humans. We expected that designation of corridors among parks and funneling fences would increase connectivity overall. Our results suggest that designating corridors (scenario 4) and establishing strategic funneling fences (scenario 5) would both have modest effects on population connectivity, with the corridor scenario slightly increasing connectivity, while the funneling fence scenario slightly decreasing it. This, however, might be a misleading result, as the funneling fence scenario would likely both reduce mortality during dispersal by keeping dispersing individuals away from high risk areas and improve dispersal success by directing them toward suitable destinations. The modeling approach used here is unable to fully represent such behavioral effects, and this question therefore warrants further exploration with such methods as agent based movement models and spatially explicit genetic simulation of potential effects.

Our fourth hypothesis (scenario 8) evaluated the potential lion population connectivity effects that would result from a doubling of the human population. Throughout Africa, the human population is expected to double by the year 2050, with Sub-Saharan Africa experiencing the majority of that growth (Population Reference Bureau 2013). Our results showed modest reductions in the extent of the landscape connected by dispersal and the extent of the largest patch. However, there was a substantial increase in the number of isolated patches (up to 100 %). While this result is suggestive of the impacts of a growing human population (for example, an increased number of isolated patches could lead to inbreeding depression among those isolated patches), our approach does not fully encapsulate the impacts of a growing human population, since our models do not incorporate mortality risk that would undoubtedly increase with a larger human population.

Our last hypothesis was that the effects of these scenarios on population connectivity would decrease with increased dispersal ability as more mobile animals are better able to overcome areas of high movement cost and circumvent partial barriers. This is an oft stated assumption in movement ecology (Carr and Fahrig 2001), and some of our results support this. For example, in scenarios that did not involve barriers to dispersal, but only involved changes to the extent of protected areas, increasing dispersal ability was universally predicted to reduce the relative effects of the scenario on population connectivity. However, this does not take into consideration the potential effects of direct mortality in any scenario. Our simulation only evaluates the ability of organisms to traverse the landscape, and does not consider the risk they may encounter and elevated mortality rates. Therefore, while our results are correct within the scope of our analysis, the implications for population size may be different. For example, lions may be able to disperse quite far into agro-pastoral lands (Elliot et al. 2014b, c) and so the net reduction in total “connectivity” as defined here decreases with dispersal ability. However, at the same time, high dispersal abilities are likely to expose the individuals to much higher mortality risk in human-dominated landscapes outside of protected areas. While relatively little research has been done to show this effect in carnivores, a substantial literature has explored this phenomenon in amphibians (e.g., Cushman 2006). For example, in a study of five amphibian species across a gradient of habitat loss, Gibbs (1998) found that organisms with low dispersal rates had better persistence in landscapes with low habitat area. This effect has also been seen in comparison of wood frog and spotted salamander habitat occupancy (Newcomb Homan et al. 2004). Carr and Fahrig (2001) suggest that highly vagile organisms may be at a disadvantage in landscapes with high mortality risk because of increased likelihood of mortality during dispersal. Cushman et al. (2010a, b), for example, found that the proportional effects of changing landuse on dispersing organisms greatly increased with dispersal ability. To fully explore the implications of this issue it will be necessary to utilize additional modeling methods, such as individual based, spatially explicit genetic models and agent based movement models to explore the interactions of individual behavior and risk of mortality across scenarios.

In contrast to the scenarios involving only loss of habitat, scenarios involving fragmentation of habitat by barriers (fences) universally increased in impact as dispersal ability increased, often dramatically. This is because a highly mobile animal can traverse a broad extent of the landscape, and when a barrier is placed across that landscape, such an individual is likely to have the extent it can reach proportionally reduced. This is in contrast to an animal with lower dispersal ability because the barrier is likely to cut off much less of the potentially available landscape.

As a result of the two factors mentioned above, the magnitude of impacts on survivorship in moving through high risk landscapes and the magnitude of impact of fragmenting features such as fences are likely to increase with increasing dispersal ability. Therefore, contrary to our expectation in Hypothesis 5, it is likely that once landscape risk is incorporated into the analysis, the true negative effects of the scenarios evaluated will increase further with increasing dispersal ability. This is disconcerting given that the focal species in this study, the lion, has dispersal ability at the high end of that evaluated in this simulation study (Elliot et al. 2014c).

These simulations provide a means to potentially evaluate and quantify the effects of alternative future scenarios. Using landscape pattern analysis such as FRAGSTATS enabled us to measure the effect of each scenario on the extent and pattern of connected habitat, and quantify loss of population extent and changes in isolation and fragmentation. Habitat loss and fragmentation are the driving mechanisms of the extinction crisis (Cushman 2006) and such a structural assessment of population connectivity is a valuable place to begin. However, as noted above, the population implications of these scenarios depend on other factors besides the extent across which dispersing organisms are able to travel. Among other things, it depends on how frequently such dispersal events occur, on the behavioral response of individuals to landscape change, and changes in mortality risk which could lead to population declines. For example, there may be an asymmetry between the risk dispersing lions perceive and the risk they actually experience during dispersal, leading to behavioral choices that are disadvantageous from a fitness standpoint. For example, dispersing juvenile lions may strongly avoid territorial males because of the obvious fitness costs of conflict with them. However, if in avoiding the intraspecific risk they choose to move into apparently ‘enemy free space’ outside protected areas, where there may appear to be abundant food (livestock) and low risk (no territorial males) they may actually face much higher mortality risk due to human conflict. A similar result was found by Kramer-Schadt et al. (2004) who simulated lynx dispersal in Germany with an individual based model that combined cost-weighted dispersal with context specific mortality risk. Their results indicated that most suitable patches could be interconnected by movements of dispersing lynx but when realistic mortality risks were applied, most patches become isolated. Thus their results suggested that patch connectivity is limited not so much by the distribution of dispersal habitat but by the high mortality of dispersing lynx and they argued that effective conservation must focus more on reducing road mortality rather than solely investing in habitat restoration.

Further modeling should explore these possibilities and elaborate on the implications of the connectivity changes predicted in this study. In particular, individual based, spatially explicit population and genetics models, such as CDPOP (Landguth and Cushman 2010) provide a powerful means to evaluate the population level implications of changing connectivity across these scenarios. For example, while the simulations presented here show changes in predicted connectivity, simulation modeling of dispersal, mating, and death as functions of these landscape scenarios will further aid decision making.

This study reveals several critical aspects relating to the scale dependency of population connectivity. In our study, scale was varied as a function of dispersal ability, across eight levels. By factorially combining these eight dispersal abilities across nine landscape resistance scenarios we were able to assess how scale of dispersal ability and landscape structure interact to affect population connectivity. Our results demonstrate that reductions in the extent of the protected area network and/or fencing protected areas will result in large declines in the extent of population connectivity, across all modeled dispersal abilities. Creation of corridors or erection of fences strategically placed to funnel dispersers between protected areas increased overall connectivity of the population. The most effective means of maintaining long-term population connectivity of lions in the KAZA region involves retaining the current protected area network, augmented with protected corridors or strategic fencing in order to direct dispersing individuals towards suitable habitat and away from potential conflict areas.

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