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Characterizing multispecies connectivity across a transfrontier conservation landscape

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Abstract

1. Connectivity conservation is aimed at sustaining animal movements and ecological processes important to ecosystem functioning and the maintenance of biodiversity. However, connectivity conservation plans are typically developed around a single species and rarely empirically evaluated for their relevance to others, thereby limiting our understanding of how connectivity requirements differ across species.
2. We used an omnidirectional application of circuit theory and GPS data from six species to evaluate connectivity at multiple scales for multiple species within the world's largest transfrontier conservation landscape in southern Africa. We evaluated the effects of linear barriers, natural habitat types and anthropogenic land use on movement. We identified multispecies connectivity hotspots as areas where current flow was concentrated or channelled through pinch points. To evaluate surrogate species for connectivity, we evaluated the correspondence among single-species connectivity across the entire landscape and also examined whether a more localized corridor for African savanna elephant *Loxodonta africana* captured high multispecies connectivity values.
3. Connectivity models revealed many intact areas across the landscape with diffuse current flow, but also evidence that fences, rivers, roads and areas of anthropogenic use acted as strong barriers to movement—particularly in the case of fences, which completely blocked female elephant movement. Tests of correspondence among single-species connectivity models revealed spotted hyaena and African wild dog as the strongest surrogate species of connectivity. Female elephants were found to be the weakest surrogate species of connectivity at the landscape scale. However, focusing within a localized elephant corridor revealed the areas of concentrated or channelled connectivity for most species in our study.

4. *Synthesis and applications*. Our results suggest that the single-species focus permeating connectivity literature may result in conservation plans that poorly conserve the connectivity needs of co-occurring species. Our study also highlights the importance of testing the efficacy of surrogate species for connectivity at multiple scales. We recommend evaluating multispecies connectivity to prioritize areas for conservation that safeguard the connectivity needs of multiple species of conservation concern.

KEYWORDS

circuit theory, connectivity, elephant conservation, multispecies connectivity, step selection functions, transfrontier conservation, umbrella species, wildlife corridors

1 | INTRODUCTION

Large conservation landscapes aim to conserve biodiversity by encompassing and securing the ecological patterns (e.g. habitat and species distributions) and processes (e.g. migration and gene flow) necessary for ecosystem function and climate resilience (Baldwin et al., 2018). Animal movement is a key driver of such pattern and process at multiple scales, but as habitats and protected areas today tend to be embedded within an anthropogenic matrix of degraded and developed land, important animal movements across large, mixed-use landscapes can become altered, constrained or extinguished (e.g. Harris, Thirgood, Hopcraft, Cromsigt, & Berger, 2009). For these landscapes, conservation efforts increasingly prioritize connectivity as a strategy to facilitate movement and maintain biodiversity (e.g. Baldwin et al., 2018; Dinerstein et al., 2019; Heller & Zavaleta, 2009). Most connectivity conservation plans, however, are developed around a single species and are rarely empirically evaluated as relevant movement pathways for others.

Because resource requirements, movement strategies and degrees of sensitivity to anthropogenic activities are likely to differ from one species to the next, connectivity conservation plans developed for a single species may not reflect the connectivity needs of other species (Brodie et al., 2015; Epps, Mutayoba, Gwin, & Brashares, 2011; Wang, McShea, Li, & Wang, 2018). Typically, large-bodied, wide-ranging mammals are selected as the focus of connectivity research because of their large area requirements, role in maintaining broad-scale ecosystem processes, conservation status and sensitivity to human disturbance (e.g. Beier, Majka, & Spencer, 2008; Epps et al., 2011). These species also tend to have flagship appeal (e.g. Roever, van Aarde, & Leggett, 2013; Wang et al., 2018) and/or potential value as umbrella species for conservation (Beier et al., 2008; Epps et al., 2011).

The umbrella species concept is appealing because species of this nature (i.e. charismatic species with large space needs) are thought to provide a connectivity umbrella to other species, which then broadens the relevance of single-species connectivity plans. Indeed, several studies have recorded overlapping space use in movement corridors among umbrella species and other co-occurring species, but the degree of overlap was not consistent across species, body sizes or life-history strategies (Beier, Majka, & Newell, 2009; Breckheimer et al., 2014; Brodie et al., 2015; Epps et al., 2011; Wang et al., 2018). Wide-ranging species, for example, may not provide a connectivity umbrella to other wide-ranging species, except perhaps to those within the same trophic guild (Brodie et al., 2015; Epps et al., 2011). In other cases, habitat generalists may not provide a connectivity umbrella to habitat specialists (Beier et al., 2009, but see Cushman & Landguth, 2012) and larger bodied animals may not always be the best umbrella species for connectivity (Cushman & Landguth, 2012). These differences suggest a need to evaluate connectivity across multiple species.

A more direct approach to identifying movement routes important to multiple species is to model connectivity separately for different species and then combine or overlay mapped results to identify hotspots where pathways (via least cost paths) or high current flow (via circuit theory) overlap (Brodie et al., 2015; Epps et al., 2011; Wang et al., 2018). Empirically estimating connectivity for multiple species, however, relies on a significant investment in species-specific data. While studies have used detection data (e.g. Brodie et al., 2015; Epps et al., 2011; Khosravi, Hemami, & Cushman, 2018; Pliscoff, Simonetti, Grez, Vergara, & Barahona-Segovia, 2020; Wang et al., 2018) or expert opinion (e.g. Cushman & Landguth, 2012) to inform connectivity models, the use of movement data (e.g. GPS or telemetry data) will arguably provide a more realistic understanding of how various landscape elements facilitate or impede movement (Zeller, McGarigal, & Whiteley, 2012). However, the connectivity literature to date contains few formal models of multispecies connectivity using fine-resolution movement data or assessments of surrogate species for connectivity (but see Meyer, Moreno, Reyna-Hurtado, Signer, & Balkenhol, 2020).

We evaluated connectivity using movement data for six mammal species in the Kavango–Zambezi (KAZA) transfrontier conservation landscape in southern Africa. We modelled movement using step selection functions (SSFs) and applied circuit theory using a wall-to-wall omnidirectional approach to model landscape current flow potential (i.e. connectivity), identifying areas where movement may be concentrated through pinch points, spread out through intact areas or impeded due to barriers. The primary goals of our study included:

(a) evaluate the effects of anthropogenic and natural barriers on multi-species movement and connectivity; (b) evaluate and compare single-species connectivity patterns across the study area; (c) combine single-species connectivity models to identify areas where multispecies connectivity is channelled and impeded and (d) evaluate surrogate species for connectivity with a focus on evaluating the efficacy of African savanna elephants *Loxodonta africana* as an umbrella species for connectivity. In KAZA, elephants are an iconic flagship species considered to be an umbrella species because they have large area requirements and co-occur with other species of conservation concern (Roever et al., 2013). Elephants are also of particular research and management concern in the region due to the effects of habitat loss, human-wildlife conflict and poaching pressure (e.g. Chase & Griffin, 2009; Roever et al., 2013; van Aarde & Jackson, 2007).

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted our study in the central portion of KAZA, the world's largest transfrontier conservation landscape spanning more than 500,000 km^2 over portions of Angola, Botswana, Namibia, Zambia and Zimbabwe (Figure 1). This region encompasses a vast network of wildlife areas (e.g. national parks and wildlife management areas), communal property and other land use types in which large mammals can occur near humans (Figure 1). Many species in the region move long distances and adjust their movements to access permanent water in the dry season and ephemeral water in the wet season (Loarie, van Aarde, & Pimm, 2009; Naidoo et al., 2016; Naidoo, Du Preez, Stuart-Hill, Jago, & Wegmann, 2012). Growing human settlements, roads and the presence of widespread veterinary fences meant to prevent the spread of disease from wildlife to cattle have disrupted movement and reduced the space available to wildlife at multiple scales (e.g. Bartlam-Brooks, Bonyongo, & Harris, 2011; Loarie et al., 2009). Thus, connectivity and corridor evaluation have been recognized as a conservation priority (KAZA TFCA Secretariat, 2014) and are a focus of recent research in the region, though this has largely centred on elephants or lions (e.g. Cushman, Elliot, Macdonald, & Loveridge, 2016; Naidoo et al., 2018; Roever et al., 2013).

2.2 | Movement data

We modelled connectivity for six large mammal species across the study area using more than 930,000 GPS locations collected at

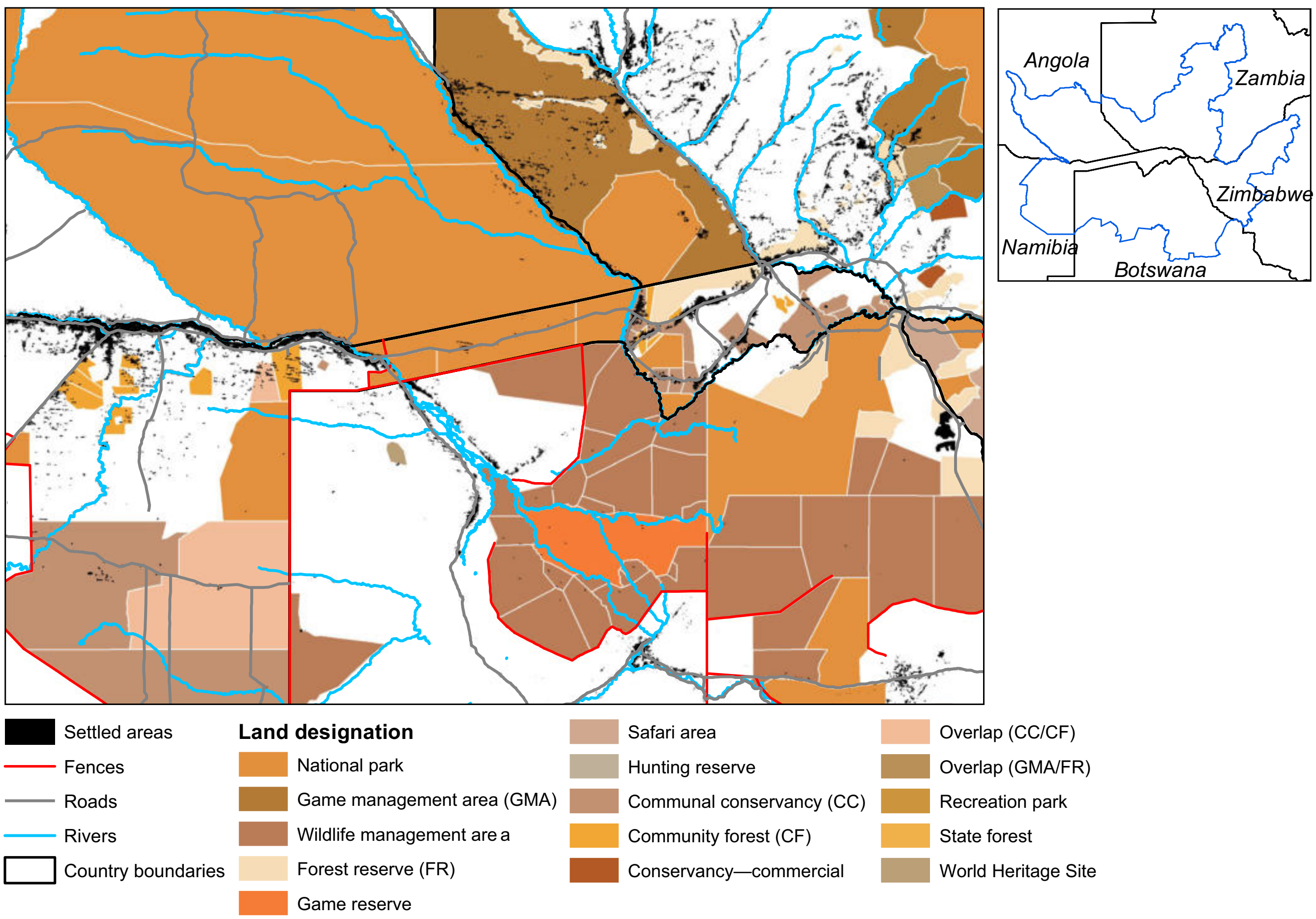

FIGURE 1 Map of the study area within the Kavango–Zambezi (KAZA) transfrontier conservation area (blue outline in the inset map) [Colour figure can be viewed at wileyonlinelibrary.com]

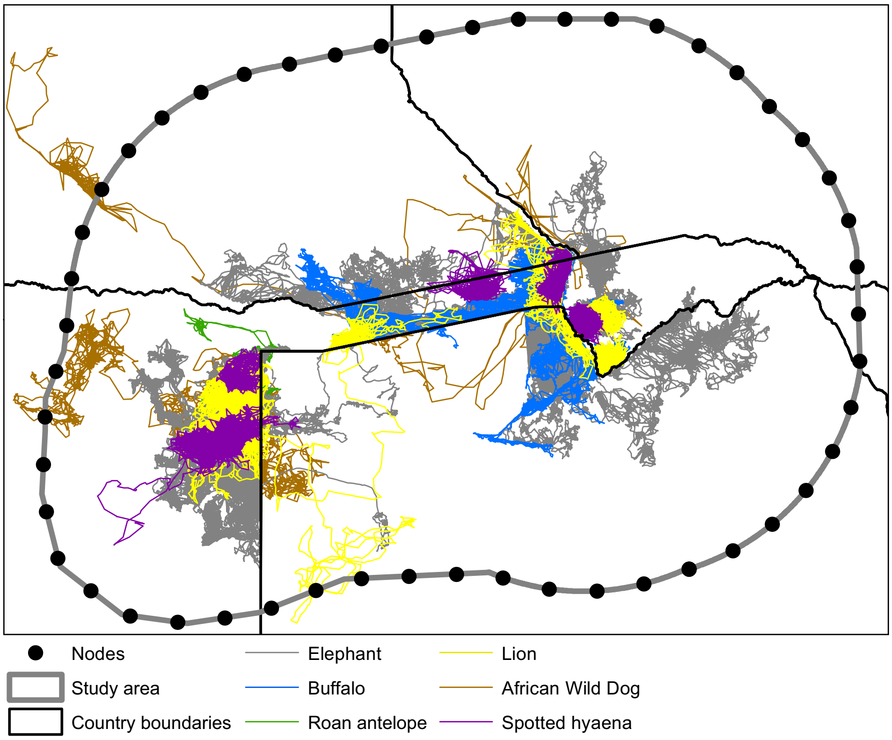

FIGURE 2 Map of species movements and node placement along study area boundary [Colour figure can be viewed at wileyonlinelibrary.com]

1-, 4- or 5-hr intervals from 163 individuals including 58 African savanna elephant (46 female and 12 male), 35 female African buffalo *Syncerus caffer*, 10 roan antelope *Hippotragus equinus* (7 female and 3 male), 34 African lion *Panthera leo* (18 female and 16 male), 10 male African wild dog *Lycaon pictus* and 16 spotted hyaena *Crocuta crocuta* (9 female and 7 male; Figure 2 and see Appendix S1 for data summaries). GPS collars were deployed in Khaudum, Bwabwata, Mudumu and Nkasa Rupara national parks within the Namibian portion of the study area (Figure 1) and were operational for various durations from 2007 through 2018. We did not target juvenile dispersal in our analysis, as the majority of our collared individuals were adults that exhibited nomadic, migratory or non-migratory movement behaviour.

2.3 | Landscape covariates

We examined 10 variables that characterize anthropogenic land use, important habitat types and quality, and potential physical barriers to movement (see Table S2-1 for spatial layer sources). We combined land cover classes describing human settlements and agricultural areas into a single anthropogenic use variable (referred to as settled areas) because they tended to co-occur and were dominated by open-land cultivation. We also examined several potentially important habitat classes: bushland thicket, woodlands, grasslands and floodplains/wetlands.

We used Enhanced Vegetation Indices (EVI) as an index of vegetation quality and quantity, obtained from 250-m resolution, 16-day surface reflectance data recorded by the Terra Moderate Resolution Imaging Spectroradiometer (MODIS). As a measure of woody vegetation, we used the yearly MODIS Vegetation Continuous Fields (VCF) product at 250-m resolution that describes the per cent of a grid cell covered by tree canopy. We included VCF in our analysis as a continuous-variable complement to categorical land cover variables such as woodland and grassland.

For potential barriers to movement, we examined large-scale veterinary fences, roads and rivers. We compiled data on large-scale veterinary fences (Bartlam-Brooks et al., 2011; Loarie et al., 2009) and adjusted these where necessary using aerial imagery. We examined national and main roads (using Tracks4Africa) given their relatively high human and vehicle densities and potentially strong effects on animal movement (e.g. Chase & Griffin, 2009; Naidoo et al., 2012; Roever et al., 2013). Similarly, we examined primary and secondary rivers to represent watercourses with higher flow volumes and the strongest potential to act as barriers, but that were also considered important water sources for wildlife (e.g. Chase & Griffin, 2009; Naidoo et al., 2012).

2.4 | Modelling landscape resistance

Circuit theory-based connectivity models require a landscape resistance grid describing the cost of moving through each grid cell (Zeller et al., 2012). We modelled landscape resistance using step SSFs. SSFs are used to compare habitat characteristics at 'used' and 'available' steps (steps refer to pairs of consecutive animal locations) to quantify an animal's selection and avoidance of landscape attributes during movement (Thurfjell, Ciuti, & Boyce, 2014). To conduct this analysis, we first rarefied the movement data to include steps with intervals equivalent to an individual's median GPS fix rate (see Appendix S1 for fix rates). We then drew a sample of 10 random 'available' steps for each observed step using the empirical distribution of step-distances and turning angles. We calculated step-distances to ensure that the median step-distance for each species was greater than the resolution of the landscape covariates (see Appendix S1; Thurfjell et al., 2014). For barrier variables, we identified whether used and available steps intersected each feature (steps intersecting feature = 1; steps not intersecting feature = 0). For all other variables, we extracted values at the end points of used and available steps (e.g. Meyer et al., 2020; Viejou et al., 2018). Another approach is to characterize environmental covariates along the entire step path rather than at end points (e.g. Panzacchi et al., 2016; Zeller et al., 2016). We compared these two approaches in a supplementary analysis, finding similarity in the numerical results, and thus similarity in the inferences and recommendations using either method (Appendix S3).

We subset the data to focus on wet season (November–April) movement, because previous work suggests that movement in seasonal savannas is greatest in the wet season when ephemeral surface water is abundant and forage quality is high in areas away from permanent rivers (e.g. Buchholtz et al., 2019; Fryxell & Sinclair, 1988). Since connectivity patterns can differ by sex (e.g. Elliot, Cushman, Macdonald, & Loveridge, 2014; Roever et al., 2013), we modelled sexes separately when there was a sufficient number of individuals represented in a sex category (10 or more individuals). Our final dataset included eight different species by sex categories (hereafter referred to simply as species) including (a) female elephant, (b) male elephant, (c) female buffalo, (d) combined male and female roan antelope, (e) female lion, (f) male lion, (g) male African wild dog and (h) combined male and female spotted hyaena. We used 90% of each dataset to train models and estimate landscape resistance. The remaining 10% of the data was used to validate the connectivity models (see Section 2.5).

We examined correlations between all covariate values, and none were found to be strongly correlated ($r < 0.50$ in all cases). We standardized all continuous covariates and estimated SSF parameters using conditional logistic regression models where strata is included as an indicator of matched used and available steps (Avgar, Lele, Keim, & Boyce, 2017; Thurfjell et al., 2014). We included step distance as a variable in all models to better account for heterogeneity in available resources and reduce the effects of sampling bias on parameter estimates (Forester, Im, & Rathouz, 2009). We fitted the SSFs using the CLOGIT function in the SURVIVAL package (Therneau, 2019) in the statistical computing software R (R Core Development Team, 2017).

We combined model coefficients (non-standardized) with 250-m resolution grids of the landscape variables using a logit transformation to obtain probability surfaces with grid cell values ranging from 0 to 1 (Naidoo et al., 2018; Osipova et al., 2019). We then used the inverse of these grid cell values to generate landscape resistance surfaces (Zeller et al., 2012). For species who never intersected a particular barrier variable, we directly imposed a barrier effect by coding those grid cells in the resistance surface as NODATA (McRae, Shah, & Mohapatra, 2013). In these cases, the barrier variable was also left out of the SSF as this would lead to a coefficient that was not estimable. If no used and no available steps occurred anywhere near the barrier variable, it was only excluded from the SSF and not imposed as a barrier on the resistance surface.

2.5 | Connectivity models

We used a wall-to-wall omnidirectional application of circuit theory to model connectivity across the study area. Circuit theory is a modelling framework used to relate animal movement across a landscape to the flow of electrical current across a circuit. With this approach every pixel in a landscape grid is a resistor and animals are expected to move more readily through grid cells with lower resistance and via multiple pathways when they exist (McRae, Dickson, Keitt, & Shah, 2008). Current flow is modelled across the gridded surface from a source to a ground, representing the source and destination of movement. While this approach is frequently used to evaluate connectivity between a single source-destination pair, the application of circuit theory has expanded to multiple source-destination pairs and to wall-to-wall omnidirectional approaches used to model current flow potential across continuous landscape gradients (e.g. Dickson et al., 2019; Gray, Dickson, Nussear, Esque, & Chang, 2019; Koen, Bowman, Sadowski, & Walpole, 2014; McRae et al., 2016; Pitman et al., 2017). The wall-to-wall omnidirectional approach provides a framework for evaluating current flow potential (i.e. connectivity) within and between any source and destination pair across a landscape (e.g. Gray et al., 2019; Pitman et al., 2017), which is particularly appealing in large landscapes such as KAZA where not all potential sources and destinations of animal movement are understood (e.g. where potential range shifts or recolonization may occur).

To model wall-to-wall, omnidirectional connectivity, we placed 50 equidistant nodes along the study area edge (Figure 2; similar to Koen et al., 2014, but using equidistant rather than random placement to avoid random clustering of nodes). We used Circuitscape to apply circuit theory to each species' resistance surface and estimate current flow between all 1,225 node pairs (McRae et al., 2013). We summed together the 1,225 current maps to obtain an omnidirectional current map for each species. We then eliminated the effect of nodes on current density (i.e. current density is always highest around nodes) to examine current flow potential across the landscape. To do this, we generated a null model, by first creating a null resistance surface where all grid cell values were set to 1 to represent a flat surface with no variation in resistance (Keeley, Beier, Keeley, & Fagan, 2017; McRae et al., 2016; Reding, Cushman, Gosselink, & Clark, 2013). We then applied circuit theory to the null resistance surface to generate an omnidirectional current map across the same 50 nodes described above. The resulting null model depicts current flow only affected by distance between nodes (Figure S2-1). Lastly, we divided each species' current density map by the null model to correct for the effect of nodes on current density (Figure S2-1). Others have eliminated this node effect by placing nodes in a buffer around the study area and then removing buffered sections (e.g. Koen et al., 2014; Pitman et al., 2017). Using our approach, the resulting current maps are also normalized to the null model, where grid cell values near 1 indicate areas where current flow is roughly equivalent to the null model, suggesting diffuse flow (i.e. flow that is unimpeded and unchannelled) (Jayadevan et al., 2020; McRae et al., 2016).

To validate connectivity models, we used conditional logistic regression models on data withheld from model training to analyse whether used steps had higher current densities than available steps. Good connectivity models should have coefficients that are significantly greater than zero.

2.6 | Evaluating multispecies hotspots

We examined multispecies connectivity hotspots by summing together normalized current maps for all species. We then binned normalized grid cell values into the following five categories that describe current flow potential relative to the null model (similar to McRae et al., 2016): (a) diffuse flow, where current is spread out because there are few barriers and many possible pathways for flow to occur; (b) intensified flow, where current is concentrated due to barriers or unfavourable conditions; (c) channelled flow, where current is concentrated further around or through pinch points; (d) impeded flow, where current has limited ability to flow due to barriers or unfavourable conditions; and (e) severely restricted flow, indicating areas where little to no current can flow due to multiple or extensive barriers. We constructed these bins using the number of standard deviations from the mean, where a mean value of zero is equivalent to the null model.

2.7 | Evaluating surrogate efficacy at multiple scales

We assessed surrogate species for connectivity in grid cell-by-grid cell comparisons of normalized current values across the entire landscape. For these analyses we used Spearman's rank tests, where correlations with $r_s \geq 0.5$ indicated a potential for connectivity surrogacy. We also evaluated scatterplots to assess the effects of outliers.

Finally, we compared species connectivity within a corridor identified for female elephants as a test of their umbrella species potential for connectivity. We identified this corridor by selecting an area of contiguous high current flow (top 10% of grid cell values) between Sioma Ngwezi National Park in Zambia and Mudumu National Park in Namibia (Figure 1) because multiple lines of evidence suggest this area is an important corridor for elephants (KAZA TFCA Secretariat, 2014; Naidoo et al., 2018). For all other species, we compared values within this corridor to those within in 5- and 10-km buffers surrounding the corridor using Wilcoxon rank sum tests. The goal was to assess whether the elephant corridor was also capturing the areas of high current flow for other species, relative to a less-targeted area surrounding the corridor.

3 | RESULTS

3.1 | Step selection functions

There was evidence that veterinary fences acted as a strong barrier to movement for all species (Figure 3) and a complete barrier to female elephant movement, as collared female elephants were observed near fences on many occasions but were never recorded crossing fences. Roads were a stronger barrier to movement than rivers for female elephants, but for male elephants the effects of roads and rivers were similar. For all other species, there was evidence that rivers were a stronger barrier than roads. There was also evidence that most species in our study avoided human-settled areas, though in some cases this effect was poorly estimated (Figure 3).

3.2 | Evaluating connectivity and multispecies hotspots

In the tests of model performance, all current density coefficients were positive and 95% confidence intervals overlapped zero for

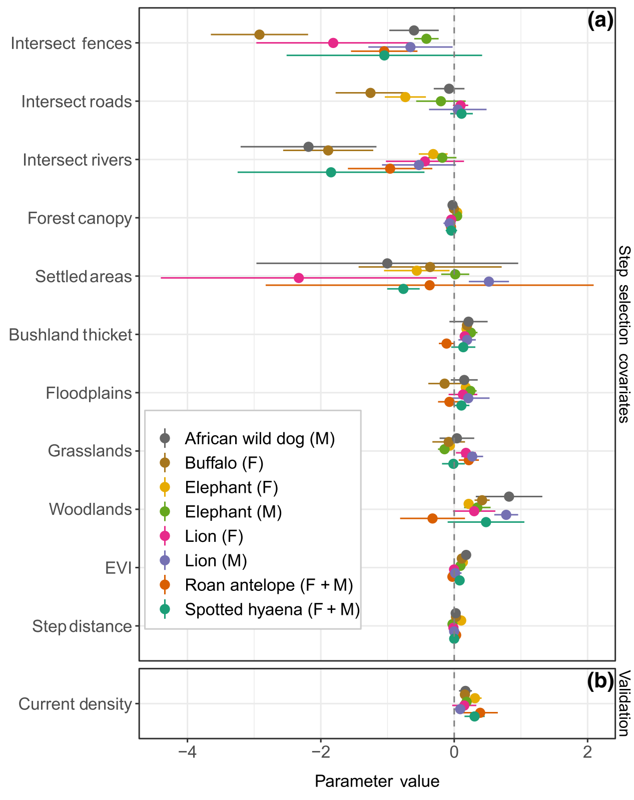

FIGURE 3 (a) Comparison of step selection parameter estimates and 95% confidence intervals among species. Fences acted as complete barriers to female elephants and thus were not estimated in step selection models. Roads were not evaluated in roan models, because in our study roan antelope were not observed moving in the vicinity of any major roads. (b) Comparison of model-validation parameter estimates and 95% confidence intervals among species. F, females; M, males [Colour figure can be viewed at wileyonlinelibrary.com]

only female and male lions (Figure 3), thus providing evidence that the areas of higher current flow generally reflected areas where animals were likely to move. The mean normalized current value for each species was near 1, suggesting that on average current values were equivalent to the null model. While this in turn suggests that on average the landscape is free of barriers to movement, allowing for diffuse current flow, there were in fact many areas of channelled and impeded current flow for all species (Figure 4). The female elephant current map, for example, depicts channelled current flow around the veterinary fences, suggesting that the fences create pinch points for elephant connectivity across the landscape (Figure 4). On the opposite side of the fences, the grey and dark grey areas illustrate how female elephant movement in Botswana may be impeded by the barrier effect of fences. The multispecies current map also depicts the current flow pattern from these fence effects, but additionally highlights multispecies hotspots of concentrated flow in Sioma Ngwezi and Chobe national parks, between Sioma Ngwezi and Mudumu national parks, along the Kwando River to the west of Mudumu National Park, and north and south of Chobe National Park (Figure 4; Figure S2-2).

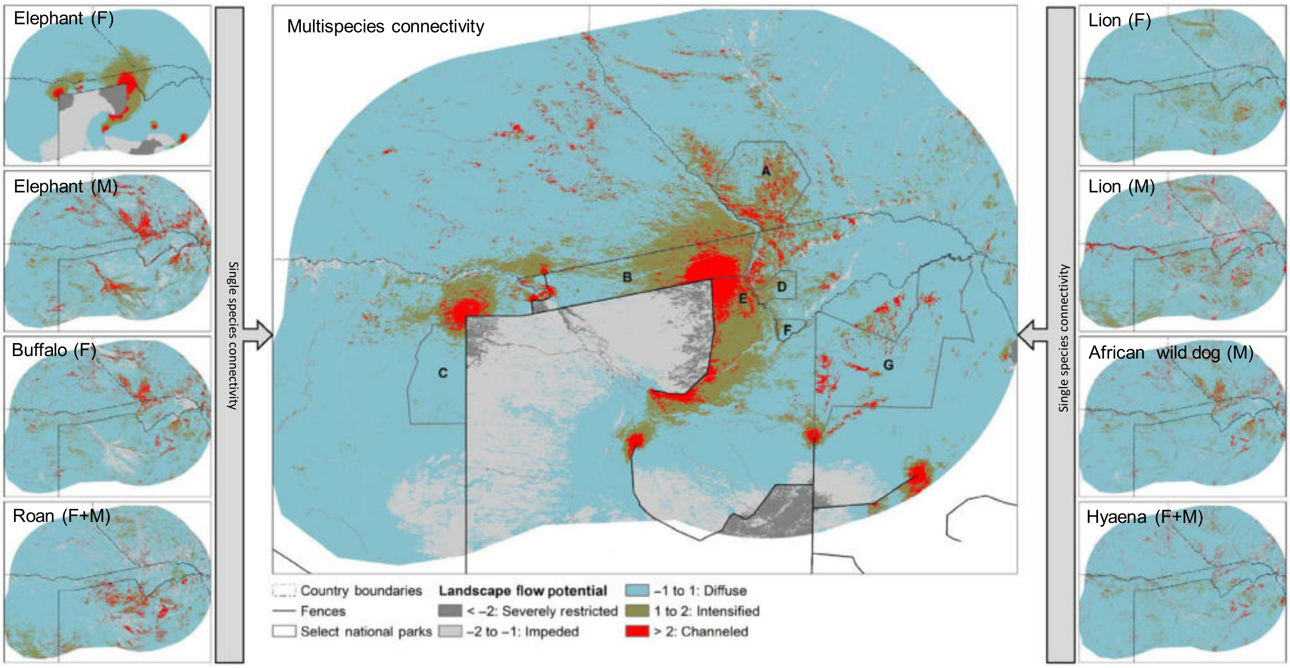

FIGURE 4 Normalized current values from single species models summed together to generate a multispecies connectivity model. Values were binned into 5 different categories of current flow that reflect the number of standard deviations from the mean. Six national parks (NP) and one river are highlighted for reference, including: (A) Sioma Ngwezi NP, (B) Bwabwata NP, (C) Khaudum NP, (D) Mudumu NP, (E) Kwando River, (F) Nkasa Rupara NP, and (G) Chobe NP. F, female; M, male [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Correlation matrix of single-species current density values

	African wild dog (M)	Buffalo (F)	Elephant (F)	Elephant (M)	Spotted hyaena (F + M)	Lion (F)	Lion (M)	Roan antelope (F + M)
African wild dog (M)	–	**0.69**	0.23	**0.52**	**<u>0.78</u>**	0.33	0.24	−0.23
Buffalo (F)	**0.69**	–	0.26	0.43	0.45	−0.09	−0.19	−0.34
Elephant (F)	0.23	0.26	–	0.23	0.08	−0.11	−0.15	−0.21
Elephant (M)	**0.52**	0.43	0.23	–	0.21	−0.14	−0.16	−0.85
Spotted hyaena (F + M)	**<u>0.78</u>**	0.45	0.08	0.21	–	**0.67**	**0.56**	0.15
Lion (F)	0.33	−0.09	−0.11	−0.14	**0.67**	–	**<u>0.82</u>**	0.49
Lion (M)	0.24	−0.19	−0.15	−0.16	**0.56**	**<u>0.82</u>**	–	0.4
Roan antelope (F + M)	−0.23	−0.34	−0.21	−0.85	0.15	0.49	0.4	–

Notes: Bold items indicate a Spearman's rank correlation coefficient $r_s > 0.5$. Underlined items indicate a Spearman's rank correlation coefficient $r_s > 0.7$.

Abbreviations: F, females; M, males.

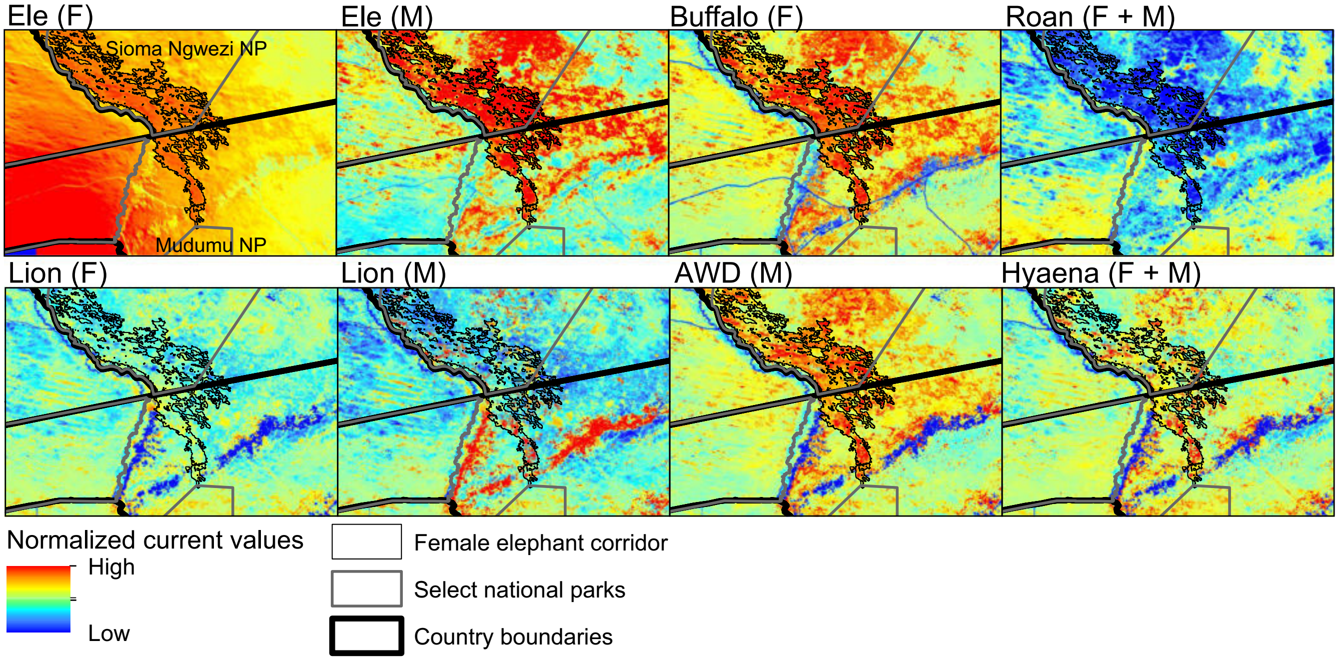

FIGURE 5 Comparison of normalized current density values among species within a corridor identified for female elephants between Sioma Ngwezi and Mudumu national parks (upper left panel). Colour map reflects a standard deviation stretch. AWD, African wild dog; Buff, buffalo; Ele, Elephant; F, female; M, male; NP, National Park [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Evaluating connectivity surrogacy

Spotted hyaena and African wild dog were correlated ($r_s \geq 0.5$) with the greatest number of other species when looking at connectivity across the entire study area (Table 1). Together, spotted hyaena and African wild dog were also correlated with a complementary set of species, representing all species except female elephant and roan antelope. Overall, female elephants demonstrated the weakest correlations with other species (Table 1).

We identified a large area of contiguous high current flow (top 10% of connectivity values) for female elephants between Sioma Ngwezi and Mudumu national parks (Figure 5). Within this corridor there was evidence of concentrated flow for male elephants, buffalo and African wild dog, as more than 75% of the current values was >1 *SD* from the mean (Figure 5; Figure S2-3). While there were smaller areas of concentrated current flow for spotted hyaena and female and male lions, a majority of the current flow was diffuse suggesting few barriers and multiple pathways for movement (Figure 5). Normalized current values within the elephant corridor were statistically significantly higher than current values within 5- and 10-km corridor buffers for all species except roan antelope.

4 | DISCUSSION

Connectivity assessments are commonly centred around a single focal species, often with the assumption that it will also act as an umbrella species to support the connectivity needs of co-occurring species. This assumption is rarely tested, however, in which case connectivity conservation plans may poorly conserve multispecies connectivity. African elephants, for example, are often the focal species of connectivity assessments as a strategy to bolster elephant-specific conservation (e.g. KAZA TFCA Secretariat, 2014; Naidoo et al., 2018; Roever et al., 2013), because they are considered an umbrella species for conservation (Epps et al., 2011; Roever et al., 2013). However, in our examination of connectivity across the landscape, female elephants were found to be only weakly correlated with the five other species in our study. Spotted hyaena and African wild dog, in contrast, were strongly correlated with the greatest number of species (Table 1). They also appeared to be complementary surrogates (i.e. they were correlated with different species), in which case combining their connectivity models could further extend the relevancy of connectivity conservation plans to other species. Thus, as both species are also charismatic, wide-ranging species of conservation concern, they may represent good umbrella species for connectivity in the KAZA region.

Although female elephant connectivity at the landscape scale was poorly correlated with other species in our study, the female elephant corridor nevertheless encompassed the areas of high connectivity value for all species in our study except roan antelope (Figure 5). This corridor also overlapped with an area of concentrated current flow in the multispecies connectivity maps (Figure 4), suggesting that while elephants may not be good surrogate species for connectivity across entire landscapes, they may still be effective as a surrogate at local scales where they can help protect local movement pathways or stepping-stone habitats for other species. This female elephant corridor, which aligned with a multispecies hotspot, also directly follows a high-priority elephant dispersal pathway recognized by local communities and KAZA leadership (KAZA TFCA Secretariat, 2014; Naidoo et al., 2018). Therefore, the results of our study verify the importance of this corridor for multispecies connectivity in the region and showcase how our methods using wall-to-wall connectivity models can help to identify important movement pathways within conservation landscapes.

Another locally and regionally recognized elephant dispersal pathway in our study area is located in Botswana and Namibia, along the Kwando River from the eastern edge of Nkasa Rupara National Park northwards into Angola (Figure 4; KAZA TFCA Secretariat, 2014; Naidoo et al., 2018). We also found this dispersal pathway to be a multispecies hotspot of concentrated current flow, with strips and patches of channelled current flow. Similar small multispecies hotspots of channelled flow were also dispersed throughout many of the national parks and other protected areas in our study (Figure 4; Figure S2-2), potentially representing pinch points or vital stepping stones for movement. These smaller hotspots may add to the connectivity value of larger multispecies hotspots, such as those found within and around Sioma Ngwezi National Park in Zambia, by helping to create more complete linkages between critical habitats. Additionally, animal movements and ecological patterns and processes occur at multiple scales (e.g. as with elephants moving between local habitat patches versus moving between national parks: Buchholtz et al., 2019; Roever et al., 2013), and thus it can be important to identify and assess both small and large areas of connectivity in tandem. Wall-to-wall omnidirectional connectivity methods provide a framework to do this.

We found that across all species in our study it was the natural and anthropogenic barriers that had the greatest effects on movement and connectivity patterns (Figure 3). For female elephants, the veterinary fences acted as an absolute barrier to movement and the dominant factor affecting their broad-scale connectivity patterns (Figure 4). These connectivity patterns demonstrate how border fences separate female elephants in Namibia and Botswana, and suggest that female elephants constrained by fences in Botswana may be largely disconnected from the rest of the region. Fence effects, as well as road effects, on elephants in our study mirrors the findings of other elephant movement and connectivity research in the region, further supporting the broad-scale negative effect of these barriers on populations and regional connectivity (e.g. Loarie et al., 2009; Naidoo et al., 2018). Confining elephant movement via barriers could increase elephant densities which has been linked to significant habitat degradation and landscape transformation (van Aarde & Jackson, 2007). Research in other parts of the world has also highlighted the disruptive effects of fences and roads on large mammal movement and connectivity (e.g. Proctor et al., 2015; Squires et al., 2013) and demonstrated a substantial decline in wildlife movement where the footprint of human activities is high (Tucker et al., 2018).

Using fine-resolution movement data, we were able to demonstrate how connectivity patterns can differ among species and scales, thus highlighting the importance of making these considerations when planning for connectivity conservation. Examining multispecies connectivity across other large landscapes would lend to our understanding of how connectivity requirements differ among species and whether there are any patterns that emerge, for example, within or across ecoregions, wildlife communities or types and levels of human disturbances (e.g. different agricultural management regimes). Multispecies models could also be used in KAZA and elsewhere to evaluate the efficacy of habitat restoration projects as well as the impacts of different infrastructure development scenarios. Because species respond to human disturbance and fragmentation differently, future multispecies connectivity research should evaluate approaches to weighting species based on vulnerability to connectivity loss and other criteria (as in Early & Thomas, 2007; Pliscoff et al., 2020). This could help to prioritize conservation of pathways or other areas where maintaining connectivity is most critical.

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AUTHORS' CONTRIBUTIONS

A.B., R.N., R.D.T. and G.S.-H. conceived the ideas; A.B. and R.N. designed methodology; P.B., O.A., P.D.P., P.J.F., L.H. and J.W.K. collected the data; A.B. analysed the data; A.B. and R.N. led the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data have not been archived due to sensitive data revealing the locations of species vulnerable to poaching.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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