Associate Editor

This is an interesting article making great use of the tracking data to evaluate the extent of wild dogs' dispersal corridors are protected. Both reviewers provided extensive comments that will help to improve the manuscripts and attention is needed regarding analytical methods used. I added a few minor comments that the authors should consider when revising the manuscript.

OUR ANSWER:
We would like to thank the associate editor for the positive feedback and the suggestions.

The authors should consider how would the findings from this tracking study, confined to a relatively small distribution range of wild dogs, may / may not apply to other wild dog populations.

OUR ANSWER:
We added a paragraph in the discussion commenting on the applicability of our findings to other ecosystems (lines 310-317).

Abstract – point #4, if I followed properly it is more a correlation rather than causation.

OUR ANSWER:
We adjusted the wording accordingly. It should now be much clearer that our observations are based on correlations and not causalities (see abstract point #4).

Line 42 – “appropriate” – please explain.

OUR ANSWER:
We have adjusted the wording and replaced “appropriate” with “large spatial scales” (line 41).

Line 98 – please summarise the “criteria” here if possible.

OUR ANSWER:
We added a summary giving more detailed information on the selection criteria (lines 98-101). These are, among others, individual age, number of siblings, pack size.

Line 102 – some details on the collar type (model name, manufacturer's name), weight and weight in relation to the wild dog, attachment method would be useful.

OUR ANSWER:
We now describe the weight of the GPS devices, their weight in relation to the dogs, and the attachment method (lines 103-105). We also indicate the model name and manufacturer on lines 101-103.

Line 112-114 – somewhere in the text, perhaps at the beginning of the result section, a descriptive summary of the dispersal process would be useful. Report how long does this last? and also how far do they disperse. I could see the answers provided in appendix but would be nice to have a one-sentence summary mean+-SD in the results.

OUR ANSWER:
We added a brief summary at the beginning of the results section (line 199-202). We also added the corresponding Mean+-SD to Table S1 in the Appendix.

Line 244-255 – it's great that the approach is not limited to the species studied nor the study area, however, to make this approach more broadly applicable, I would encourage the authors to share the codes (or at least the key parts) used in this study for future uses on dryad, in addition to the GPS relocation data.

OUR ANSWER:
To showcase the steps required to produce a connectivity map, we prepared an R-script containing a simple theoretical example. The script also contains some references to other tutorials that will help with integrated step selection analysis. The script will be made available through GitHub (line 382).

Line 317 – “to” instead of “t”.

OUR ANSWER:
Thanks, we corrected the mistake (line 359).

Figure 2 – bottom right panel’s legend, consider “short” to “long” instead of “low” to “high” for distance.

OUR ANSWER:
Thanks, we amended the legend (Figure 2, bottom right panel).

Reviewer 1

General Comments (Email)

Overall, I found your paper to be excellent. Please see my detailed comments in the attached file, and please don’t hesitate to reach out for clarification if needed [Journal note: please ensure all communication related to peer review is directed through the journal’s Editorial Office].

OUR ANSWER:
Many thanks. We are glad to hear you enjoyed the reading.

General Comments (Separate File)

I find this paper very interesting. Movement data can (and should) be used to evaluate both existing and proposed protected areas, but to date, this is approach is very underutilized. The authors make good points about the importance of using the movements of dispersing individuals to estimate dispersal connectivity, and they have an excellent dataset for examining the questions that they are interested in. In my opinion, they also chose the ideal analysis to examine their question, integrated step selection analysis, and they were able to implement it following a recent advance that allows the inclusion of random effects in iSSA, accounting for within-coalition dependency. I have a few comments about the implementation of the iSSA that I’d suggest addressing, but that I do not see as major flaws in the analysis. Overall, this is an excellent paper.

OUR ANSWER:
Thank you very much for the encouraging feedback. Please find below the answers to your comments, including references to line numbers of the new version of the manuscript.

Specific Comments

Line 4: the use of utmost here is a little awkward for me. Perhaps, “a task of utmost importance,” would work better.

OUR ANSWER:
We modified the text according to your suggestion (line 4).

Line 20: I would change “randomly selected locations” to “available locations”, since the assumption that those random locations are actually available to the animal is critical.

OUR ANSWER:
Thank you for the suggestion. We changed “randomly selected” to ”available” (line 21).

Lines 108 – 109: I’m sure you realize that NSD is the Euclidean distance squared, but since you’re going to define it, you should be careful to say that it is squared.

OUR ANSWER:
Thank you for spotting this. We corrected the wording to clarify that distances are squared (line 113).

Lines 110 – 112: How did you segment the NSD time series? Did you do it by visual inspection, or did you use an algorithm?
OUR ANSWER:
It was a combination of visual inspection of the NSD time series and field observations (line 111-113).

Line 126/Appendix A.3: I must say, you did an excellent job explaining how you processed the covariates, something that I find is typically insufficiently described in most publications

OUR ANSWER:
Thank you for the kind comment.

Lines 143 – 144: I try to avoid using the word "preference" to describe the betas of a habitat selection function. I think a better term for them would be "relative selection strength", e.g., "To estimate relative selection strength for each habitat (i.e., the betas), we used..." For more on relative selection strength, see Avgar et al. 2017 (Avgar, T., Lele, S. R., Keim, J. L. & Boyce, M. S. 2017. Relative Selection Strength: Quantifying effect size in habitat- and step-selection inference. Ecol. Evol. 7, 5322–5330).

OUR ANSWER:
We adjusted the wording throughout the manuscript (lines 17, 66, 122, 140, 153, 154).

Line 148: You used a Gamma distribution to sample available steps. Under the Gamma distribution, you need parameters for both the step length and the log of the step length in the iSSA to update the selection-free movement kernel. I'd say this is an optional step, since you are not making any inference on the selection-free movement kernel, and log(sl) is probably sufficient to account for the movement process in the habitat selection coefficients.

OUR ANSWER:
Many thanks for the clarification. For completeness and correctness, we decided to rerun the models including both, the step length and the log of the step length (lines 158-162). Estimates remained largely unchanged and the coefficient for sl was insignificant in the final model. Using the new model, we reran all subsequent steps (e.g. model validation, permeability surface, corridors etc.), yet results remained unchanged.

Lines 157 – 158: Step selection analyses are conditional on the start location of a step, and therefore you should not technically use them to unconditionally predict across the landscape, i.e., the way you calculated w(x) for each raster cell was unconditional. This is likely to overestimate w(x) for some cells, especially far from suitable habitat. You did cite Signer et al (2017) in your discussion when you (correctly) pointed out that it would be possible to simulate corridors from an iSSA that captured a more mechanistic model of dispersal. However, that same citation also demonstrates the bias that comes about when not using simulation to estimate the UD from a fitted (i)SSF. However, Signer et al (2017) did not categorically dismiss the approach that you took, and it would be a major computational task to simulate a steady-state UD from the iSSF. Your least cost path analysis is subsequently modeling transitions on a scale more appropriate for the iSSA, but the w(x) raster that you use to estimate permeability is still at least somewhat biased. At a minimum, I would suggest adding a brief discussion that this method could possibly overestimate connectivity. I'd applaud you for choosing to redo the UD surface using a simulation approach (and perhaps it would be worth comparing the difference it would make to such a complex question on a real landscape, as opposed to the simpler simulations run by Signer et al.)

OUR ANSWER:
Many thanks for pointing this out. We have explored the possibility of using simulated utilization distributions and ran some simulations but simulating movement on such a large extent has so far proven computationally very challenging. As suggested, we included a cautionary note in the discussion explaining the slight bias introduced by predicting permeability unconditionally (lines 351-358).

Lines 188 – 189: I don't think you've interpreted the coefficients for the movement parameters correctly. Under the iSSA, your initial Gamma distribution was a proposed distribution, which you can then update to the true selection-free movement kernel by adjusting the shape and scale parameters using the betas from the sl and log(sl) parameters. Your initial Uniform distribution is really a von Mises distribution with concentration parameter of 0, and again, the beta for cos(ta) can be used to update that distribution. So rather, they do not "select" for longer steps, but instead the simulated available steps were on average too short and the turning angles were not directed enough. Put another way, your dispersing wild dogs would take longer and straighter steps than your Gamma and Uniform distributions suggested if all habitat was uniform. However, your betas were small, so your proposal distributions were fairly close, so I wouldn't be worried about your inference. Just remove the suggestion that the wild dogs "selected" a step length or turn angle.

Thank you very much for pointing this out. As suggested, we removed the sentence to avoid confusion.

General section 3.1: You didn't report on the variance of the random effect. Were there large differences between coalitions?

OUR ANSWER:
We give details about the random effects in the results section (212-214) and we added a plot of the random effects in the appendix (Figure S7). Except for "DistanceToWater", random effects revealed little variation between coalitions.

Lines 205 – 207: I just want to reiterate here that using the "naïve" (sensu Signer et al 2017) method for estimating w(x) probably overestimates the edges of the UD, which makes these relationships even more difficult to interpret.

OUR ANSWER:
We added a statement pointing out the weaknesses of this approach in the discussion (lines 351-358).

Lines 208 – 210: In contrast to my previous comment, I like this statement and it offers an explanation of why the country differences appear.

OUR ANSWER:
Thanks!

General section 3.3: I'm wondering what the least cost paths analysis gives you that the least cost corridors does not. I prefer the least cost corridors, so you could potentially cut the LCP out. If there's a benefit to the LCP analysis, could you please make that explicit (maybe in Methods explain why both)? If not, perhaps present the LCC analysis alone?

OUR ANSWER:
There are two reasons why we decided to include LCPs in the results. First, we needed to illustrate the location of source points and corresponding protected areas (plotting them on top of the LCC plot was not feasible). Second, LCPs are a discrete representation of potential corridors, which allowed us to calculate how many unique paths traversed a given pixel. With LCC this was not possible because their representation is continuous. We added a corresponding statement on lines 194-195.

Lines 252 – 255: Very interesting point about a multispecies assessment. I hope to see someone work on that!

OUR ANSWER:
Thank you, we hope to expand this research by involving colleagues working on other species.

Lines 260 – 263: Good point here. I think it might be worth making the point that habitat selection is use vs availability, and that animals can only choose from what is available to them. You've shown that when they have the choice, they'll avoid humans, and that isn't necessarily at all incompatible with the findings from South Africa. (Actually, you make great points throughout this paragraph. Well done.)

OUR ANSWER:
Thanks! We have added a sentence to highlight that our model compares use and availability (line 279-285).

Lines 280 – 282: Interesting point. I think you see support for this because your point estimate for your distance to water is relatively far from 0, but the CI is very wide, perhaps because they're often forced to switch behavior due to biotic interactions. Might want to point that out.

OUR ANSWER:
We now point out explicitly that these considerations could explain the large confidence interval surrounding the coefficient for "Distance to Water" (lines 305-306). We were rather surprised to find that distance to water was not highly significant and we are curious to understand why. Hopefully, we can incorporate biotic interactions in the future.

Line 317: Missing the "o" in "to" ("can be used to identify")

OUR ANSWER:
Thanks, we have corrected the error (line 359).

Figure S1: Misspelled "classified" in the caption ("calssified")

OUR ANSWER:

Thanks, we have corrected the mistake (Figure S1).

Table S4: In the model names you have “HB5”, but it doesn’t appear in the key at the bottom. Is that the human influence index?

OUR ANSWER:
Thank you for the catch. We replaced HB5 (HumansBuffered5000m) with HI (Human Influence) in Table S4.

Reviewer 2

General Comments

I have read with great interest the manuscript by Hofmann et al. titled “Bound within Boundaries: How Well Do Protected Areas Match Movement Corridors of Their Most Mobile Protected Species?”. The Authors address a very important topic in large carnivore conservation, and dispersal ecology in general by modelling landscape connectivity for a species with mobile dispersers, and assess the coverage of most likely dispersal routes by a network of protected areas in a vast landscape in Southern Africa.

They modelled landscape permeability to dispersal movement using an integrated step-selection function (iSSF) fitted to a tremendous dataset of African wild dog (AWD) dispersal movement in the Kavango-Zambezi transfrontier conservation area (KAZA-TFCA) region. They then modelled least-cost corridor (LCC) to identify the most likely dispersal routes for AWD in this landscape. They found that dispersing AWD avoided water and human-impacted areas, and that permeability was higher within the boundaries of the KAZA-TFCA than beyond, and that most dispersal corridors where situated within this landscape, too with only little minor routes remaining outside protected areas. While I found the paper well written and the analyses they have carried out well done, I believe that a LCC approach is fundamentally flawed in the context of dispersal, and does not do justice to the quality of the movement data collected. While the Authors do sort out one recurrent problem with identifying dispersal habitat empirically by fitting a habitat selection model directly to dispersers’ movement data, they do not take advantage of the movement data further, and fall back onto the least-cost modelling unrealistic assumptions in the context of animal movement and dispersal in particular. Dispersing individuals do not have perfect knowledge of the landscape, nor a preconceived destination they are headed to, and therefore a start-and-end-point modelling approach limits our ability to identify movement corridors between areas we do not predefine as dispersal start and destination points. While the Authors do acknowledge these limitations and mention the potential for simulated dispersal movement in identifying dispersal routes more realistically (L304-316), they somehow restricted themselves a priori, arguing that their data set is too limited for such an approach. In the contrary, I believe that this is an excellent opportunity to use their fitted iSSF based on GPS tracked dispersers at regular intervals to simulate movement trajectories in this landscape, despite what they feel is a limited sample size. I doubt anyone else will get so much AWD dispersal movement data at this resolution any time soon and taking such an individual-based movement model (IBMM) simulation approach would truly advance our understanding of landscape connectivity for mobile, large carnivores.

I strongly encourage the Authors to model dispersal corridors using a movement simulation approach and potentially compare the results to what they have currently done and demonstrate how an IBMM improves (or not) our understanding of dispersal corridors and related management recommendations in this landscape.

There is also a lot of important information regarding the methods that is buried in the Supplementary material, which hinders clarity. I suggest giving more (not all) information in the main text itself.

I give some more specific comments below that I hope are constructive and will help the Authors in improving their manuscript.

OUR ANSWER:
We thank the reviewer for the positive feedback and the suggestions. We have replied to single comments further below; we here summarize the more important aspects raised and how we addressed them.

1) We do agree with the reviewer that dispersers do not have a preconceived destination they are headed to. Therefore, a start-to-end-point modelling approach has some conceptual limitations (lines 341-350). We would like to list some of the main considerations we made, which may help to understand the decision for a least-cost modeling approach and to stress that an individual-based movement model (IBMM) has some limitations that are yet to be overcome.

a. In general, we are of the opinion that least-cost analysis and IBMMs are complementary and not mutually exclusive approaches. Least-cost analysis is well established and therefore easily accessible. The method has also undergone substantial improvements in the past (e.g. Pinto and Keitt 2009; Panzacchi et al. 2016). At the opposite end, while maximizing "realism", IBMMs typically sacrifice generality and may therefore preclude a more holistic view of connectivity (Diniz et al. 2019).
b. Using an IBMM to simulate dispersal from a known starting point to an unknown end point is computationally very demanding, particularly when modeling interactions between the movement and habitat kernel (Signer 2017) and when simulating over a large extent. We have run some simulations (please also refer to reply to reviewer 1) but the exercise has proven very challenging.
c. Simulations (and derived maps) are highly sensitive to selected source points. This is especially true if one is interested in the transient (i.e. non-stationary) utility distribution (Avgar et al. 2016, Signer et al. 2017). We have investigated this in our simulations and moving a starting point by only a few kilometers can make a huge difference. Least-cost analysis is more "robust" in this regard.
d. Furthermore, IBMMs are highly sensitive to the selection of environmental covariates, which, given the large spatial extent of our study area, are only an approximation of detailed conditions on the ground
e. Lastly, IBMMs are sensitive to the duration of simulated dispersal events (i.e. the number of steps simulated). We have not yet found a biological meaningful way to cap a dispersal event.

2) We do share the reviewer's opinion, that a meaningful selection of source points is crucial, regardless of the modeling approach chosen. In this regard, we would like to stress that least-costs approaches are less sensitive to the exact location than an IBMM.
    a. Our selection of starting and end points was within protected areas, unarguably the only portion of the KAZA-TFCA that can sustain source populations of large carnivores (see below).
    b. We did not adopt an Okavango Delta-centered approach. Each location was linked to all other locations within KAZA, yielding 2'278 unique linkages.
    c. To confirm the robustness of our approach, we followed the reviewer suggestion and applied the proposed omnidirectional approach to our data (start and end points located at the periphery and not within the KAZA-TFCA). Results remained qualitatively similar, underlining the reliability of our conclusions.
    d. To keep the manuscript accessible to the broad readership of Journal of Applied Ecology and due to the limited word count, we suggest focusing on the approach presented in the original manuscript, but we will surely consider adding this additional map (omnidirectional approach) should the reviewer and the editor feel strong about it.

3) We thank the reviewer for appreciating our sample size, the quality of the data, and the effort required to collect such data. We are continuing to develop our analysis in the direction pointed out by the reviewer. The development of a robust IBMM and a comparison with least-cost analysis is our intention but (also for the difficulties listed above) outside the scope of the current manuscript.

Specific Comments

ABSTRACT

The end of the last sentence is a bit strange. Couldn't it read as: "Furthermore, observed regional differences in landscape permeability highlight the need for a coordinated effort towards maintaining or restoring connectivity, especially where transboundary dispersal occurs"

OUR ANSWER:
Thank you for the nice suggestion! We modified the sentence accordingly (Abstract, last sentence).

INTRODUCTION

L24-25 also see Abrahms, B., Sawyer, S. C., Jordan, N. R., McNutt, J. W., Wilson, A. M., & Brashares, J. S. (2017). Does wildlife resource selection accurately inform corridor conservation? Journal of Applied Ecology, 54(2), 412-422.

OUR ANSWER:
We have cited Abrahms et al. 2017 elsewhere in the manuscript but we failed to do so here, thank you for pointing this out. We have now added this citation (line 26).

L28 This introduces severe biases -> this can introduce bias. For some species, residents' habitat can be predictive of dispersal movements. In such instances, in the absence of dispersal data, a friction model based on empirical resident data would likely still be preferable to an expert-based model.

OUR ANSWER:
Thank you for pointing this out. We have modified the sentence and acknowledge that, in some cases, habitat use during residence can be informative about habitat use during dispersal (line 23-24).

METHODS
L118-122 It is not clear how you dealt with categorical landcover data. Did you use them as categorical/dummy variables or did you turn them into continuous variables as a proportion (and at which grain)?

OUR ANSWER:
We realized that we moved too much information into the Appendix (see Appendix A3 and A5). We now give a more detailed explanation of the covariates in the methods section (lines 122-137).

L121 human "influence' is too vague – what is it?

OUR ANSWER:
Thank you for pointing this out, this was a mistake. We should have called the layer differently. We modified the text accordingly (lines 122-124). Human influence refers to another layer that combines human influences stemming from human density, roads, and agriculture (lines 129-131 and Appendix A.3.3.).

L155 Unclear how this is different from a spatial projection of the iSSF.

OUR ANSWER:
It is not. The permeability map is a spatial projection of the iSSF. When inverted, the same layer is often referred to as "resistance surface". Because we did not convert predicted values to "resistance", the term "permeability" appeared more appropriate.

L159 In my opinion, this is quite a problematic aspect of your analysis (or at least unclear). The water regime in the KAZA region is very dynamic, and as far as I understand you collapsed the water dynamic to a single layer of 'water' to project the iSSF spatially. This is because your aim was in the end to produce a single layer of dispersal corridors in this landscape. I suggest that you rather project the iSFF monthly (as per your Fig. S6) and run the corridor analysis on each. Then, you would be able to identify which sections of these corridors persist year-round in this landscape by overlapping the monthly output layers, and identify potentially corridors that exist only in the dry vs the wet season, adding to your recommendation regarding protected area coverage.

OUR ANSWER:
The flooding regime of the Okavango Delta is highly dynamic and may influence dispersal locally. However, the extent of the Delta covers only 5 % of the entire KAZA. Hence, a dynamic representation of water and subsequent corridors would be confined to a relatively small area and is outside the scope of the present manuscript, which focuses on processes at a much larger spatial and temporal scale. We feel that ignoring seasonality in our large-scale predictions does not introduce substantial biases in connectivity across the entire KAZA. Nonetheless, using dynamic flood maps was crucial to reliably estimate habitat selection for those dogs moving in its vicinity.
We agree with the reviewer that investigation of which corridors persist year-round and which change across the year depending on different flood levels will be very interesting and definitely worth exploring for conservation and management interventions at a local scale.

L187 As you have subset AWD movement trajectories to these types of steps (that define dispersal, fig. S1), would you expect to find other movement parameters? I think that saying "showed that dispersing wild dogs moved in a directional and fast manner" is quite circular, here.

OUR ANSWER:
We categorized AWD trajectories based on the net squared displacement (lines 111-115), not based on step characteristics. How dispersers moved (i.e. step characteristics) between the time of emigration and the time of settlement (i.e. during transience) is an outcome of the analysis. As suggested by reviewer 1, however, we removed the statement about directionality and speed from the main text (see reviewer 1 comment to lines 188-189). This because we only included movement metrics to more reliably estimate selection for environmental characteristics, while they are not the focus of this study.

RESULTS

L228 I really think that this an artefact because you have (quite logically) centered your modelling extent on your study area: you modelled more corridors between the central dot and other destination points than between any other pair. Also, this area is highly suitable dispersal habitat as per the projection of the iSSF (Fig. 4). I suggest that you consider an approach that is more omnidirectional and uses the permeability surface as a go-through between pairs of nodes placed at the periphery, as in Koen et al. 2014 and applied by Pitman et al. 2017 on another large African carnivore (that said, this approach also has limitations and tends to identify high density of permeability at the edge the study area).

OUR ANSWER:

We may have not been sufficiently clear in the approach that we followed, and we rephrased to clarify (lines 180-196). We did not model more corridors through the central source point. Each source within the KAZA-TFCA was equally connected to all other locations. You are correct that the central area is more suitable to dispersal as per Fig. 4. This is not an artifact of the methodology, but the result of the geographic location as well as favorable conditions. We highlighted this at lines (320-322).

We read the proposed papers and we understand the reviewer's concern with respect of the selection of source points. We are confident that source points located in protected areas are biologically meaningful in our case. Wild dogs, like many other large carnivores, mainly reside within protected areas (Woodroffe & Ginsberg 1998, 1999; Balme et al. 2009; Van der Meer et al. 2014; Loveridge et al. 2017) which can indeed be considered as true source points for our least-cost analysis. We considered the suggested omnidirectional go-through approach and applied it to our system. The output is reported below. The new map (b) is a "stretched" version of the original map (a), but corridors remain largely the same. Overall, map values correlate by 0.87, suggesting that the location of source points has little influence on our conclusions. Because of the biological relevance (i.e. source populations within protected areas), we prefer the alternative with source points located in protected areas but would consider including (b) in the Appendix if the reviewer and editor feel strong about this.

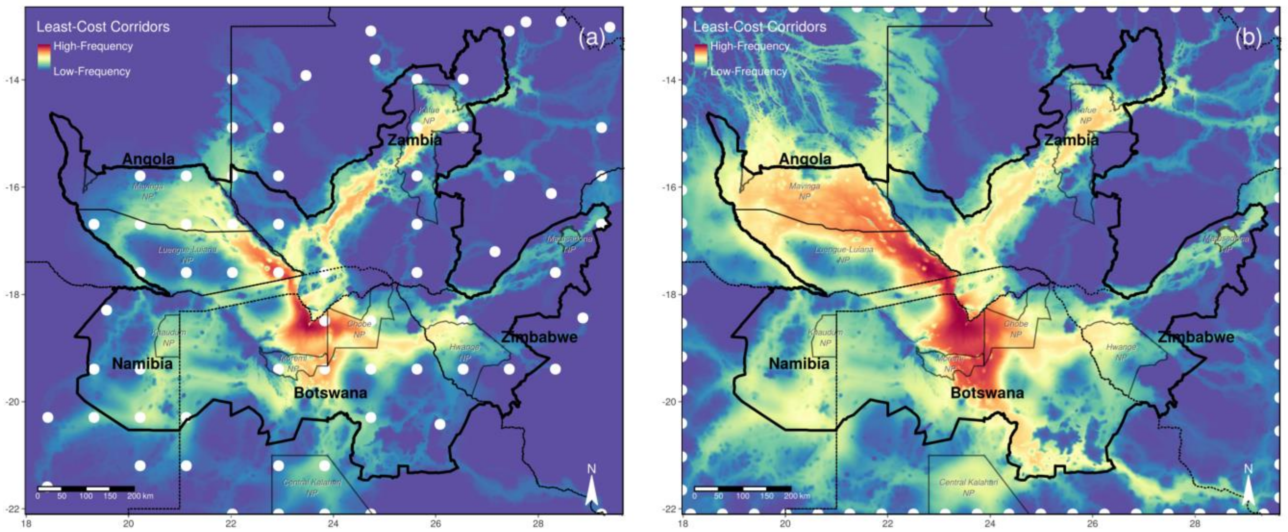

Figure 1: Comparison of connectivity maps resulting from two different approaches of sampling source points (white circles). (a) Source points located within protected areas. (b) Source points distributed along map boundaries. In both cases a total of 68 source points were used.

L230, L234, L236 This is clearly expected by the lack of suitable habitat in these areas as per Fig. 4, that makes dog disperse over longer Euclidean distance, in an arc-shaped route to link two dots, via a stretch of suitable habitat. This is an expected behaviour in the case where functional connectivity corresponds to structural connectivity, i.e. dispersers follow suitable habitats to disperse (e.g. Fattebert et al. 2015, Masenga et al. 2016, Hauenstein et al. 2019, Zeller et al. 2020). I think these aspects (structure = function) needs to be discussed further; at the moment your discussion hardly touches on this.

OUR ANSWER:

Thank you for these considerations. We discuss your observations on arc-shaped routes on lines 323-327.

We are not sure what the reviewer means by "structure = function". As defined by Taylor et al. 2006, structural connectivity, "*ignores the behavioral response of organisms to landscape structure and describes only physical relationships among habitat patches.*" Functional connectivity, on the other hand, "*increases when some change in the* *landscape structure increases the degree of movement or flow of organisms through the landscape"*. Because we consider movement data of dispersers and model how dispersers react to environmental features, our manuscript focuses on functional connectivity.

L233 This is one more evidence that the LCC output is biased towards the input destination points. For example, in Angola you would likely draw a corridor west of the protected areas if you placed a node in the suitable habitat (based on Fig. 4) outside the PA. If one of your key questions is to assess the coverage of dispersal corridors by the PA network, I feel this is one more argument for using a go-through approach (see my comment above on L228), or, better yet, a dispersal trajectory simulation approach, since you do have the necessary empirical data.

OUR ANSWER:
We have considered protected areas > 700 km^2 as meaningful source points because any smaller protected area cannot host viable wild dog populations and viable populations cannot survive outside PAs (Van der Meer et al. 2019). We added a corresponding statement on line 188-190. We have nevertheless applied the proposed omnidirectional approach to our system (see our comment above), yet corridors remain largely the same. The main difference is an increase of corridors along the edges, particularly in the corners, which as the reviewer also suggests, is partly an artifact of the selection of the source points along the edges.

DISCUSSION
L259 While the dispersers recorded in Davies-Mostert et al. 2012 likely dispersed through unprotected areas, that study recorded only net dispersal events, and was therefore unable to identify the structural suitability of the habitats the dogs dispersed through (e.g. a game farm, while the risk of mortality from persecution is likely high, is not unsuitable habitat (structurally), and not human-dominated either, in terms of infrastructure or landcover changes. I suggest that you rephrase this. At the moment, your analysis is biased towards linking protected areas (your start and end points are only in protected areas as per Fig. 5a, and not suitable habitat patches (as per Fig. 4) that can also lie outside protected areas – see my comment below on Fig. 5.

OUR ANSWER:
We thank you for these considerations. You correctly point out that Davies-Mostert et al. only observed straight line dispersal distances. We have added a corresponding statement in the discussion, and we highlight the fact that our approach compares use vs. availability (lines 279-285). We also agree that wild dogs may find suitable habitats outside protected areas. However, to the best of our knowledge these populations are very rare and their viability questionable. Wild dogs require vast natural habitats (Woodroffe & Ginsberg 1999; Pomilia et al. 2015), which is also why they are most vulnerable to habitat fragmentation. Consequently, the bulk of dispersing individuals move from one protected area into another, which is why we limited our focus on protected areas large enough to sustain viable wild dog populations.

L304-316 Do it. You have all the necessary data (see my comment above on L233).

OUR ANSWER:
We thank the reviewer for their enthusiasm on the topic. As we mentioned in the main text, we share the reviewer's opinion that a simulation-based approach will likely represent the dispersal process more accurately than a start-to-end approach. As a result, we have already invested a lot of time and effort in this direction. This approach is, however, not as trivial as it may appear. We have outlined some of these weaknesses in our response to the general comments (see reply above).

L317 t -> to

OUR ANSWER:
Thanks, we have corrected the mistake (line 359).

TABLES AND FIGURES
Fig. 4 This is a detail, but I feel it would be more intuitive to flip your legend around, to get low at the bottom and high at the top.

OUR ANSWER:
Thank you for the suggestion. We flipped the legend in Fig. 4, as well as in Fig. 5.

Fig. 5 This is a major limitation of the study based on LCP modelling: you defined destination points that forced PA to be linked (the algorithm will always give you an computational answer to the least costly path, even if it is costly; especially given the fact that you did not cap the ecological distances). For example, you gave a destination point in the PA at the north-eastern most corner of the study area in Zambia. This is not dispersal habitat according to your model Fig. 4, and I doubt dogs would use these corridors and reach there. You did not allow dispersers to target any structurally suitable habitat patches outside of PA (e.g. west of the KAZA in Angola, Fig. 4) – it biased your answer to the "how much is under PA or not" question towards PA. To answer this question, it seems simpler to quantify how much dispersal habitat in Fig. 4 is formally protection or not. Are these points all in PA where dogs actually are? Are you modelling connectivity between known breeding population? What is the spacing – it looks regular. Are these dots in 'good' habitat pixels at least?

OUR ANSWER:
To select biologically meaningful source points, we placed points within protected areas, regularly spaced 100 km apart (183-186). Only for those protected areas > 700 km^2 for which no point on the regular grid existed, we added a source point in its center (lines 186-188). A very similar approach has been applied by Elliot et al. (2014), who conducted least-cost path analysis for dispersing lions within the KAZA-TFCA.
Because we did not assess habitat suitability for resident individuals, we could not make any statements about the actual or likely location of resident packs outside protected areas. Nevertheless, past research strongly suggests that carnivores in general, and wild dogs in particular, hardly survive outside protected areas (Woodroffe & Ginsberg 1998, 1999; Balme et al. 2009; Van der Meer et al. 2014; Loveridge et al 2017). For instance, Woodroffe & Ginsberg (1999) found that wild dogs outside protected areas are very prone to persecution, poisoning, roadkill, and diseases, which is why no viable populations exist outside of large reserves. In result, most wild dog populations outside PAs have been extirpated or serve as sink populations at best (Woodroffe et al. 1999; Van der Meer et al. 2014). We therefore believe that our selection of source points within protected areas truly represent breeding populations.
The reason we did not cap ecological costs is that one would need to set an absolute cost threshold. This goes against the idea of relative selection behavior (as pointed out by reviewer 1). For instance, a wild dog originating from an area surrounded by humans may still move through human dominated landscapes if there are no alternatives, even if this is considered costly.

Fig. 5b shows that you have an Okavango delta-centric approach of dispersal (emigration) – but what about a population somewhere else sending dispersers out to the Delta region (immigration)? This unnecessarily limits the scope of your paper to where can dog from the Delta disperse to, vs a broader scope identification of the dispersal landscape in the KAZA and beyond. This relates to my comment above on L228. You might want to take a go-through approach (Koen, Pitman) or a simulation, IBMM approach (Zeller, Hauenstein).

OUR ANSWER:
We did not follow a Delta centric approach; each point was equally linked to all other points, resulting in 2'278 linkages (line 190-191). We placed source points within protected areas across the entire KAZA landscape (lines 183-188). We did not use the Delta as a source location from which dispersers may or may not reach other locations. For example, we linked Kafue NP in Zambia to Matusadona NP in Zimbabwe, and as our results show, a direct link is very unlikely (no obvious corridors) suggesting that the boundary of KAZA is not missing out a potential corridor.

Literature Cited

Avgar, Tal, Jonathan R. Potts, Mark A. Lewis, and Mark S. Boyce. 2016. „Integrated Step Selection Analysis: Bridging the Gap between Resource Selection and Animal Movement“. Methods in Ecology and Evolution 7, No. 5: 619–30.

Balme, Guy, Matt Rogan, Lisa Thomas, Ross Pitman, Gareth Mann, Gareth Whittington-Jones, and Neil Midlane. 2009. „Big Cats at Large: Density, Structure, and Spatio-temporal Patterns of a Leopard Population Free of Anthropogenic Mortality“. Population Ecology 61 (3): 256–67.

Brennan, A., P. Beytell, O. Aschenborn, P. Du Preez, P.J. Funston, L. Hanssen, J.W. Kilian, G. Stuart-Hill, R.D. Taylor, and R. Naidoo. 2020. „Characterizing Multispecies Connectivity across a Transfrontier Conservation Landscape“. Journal of Applied Ecology 57, No. 1: 1700-1710.

Diniz, Milena F., Samuel A. Cushman, Ricardo B. Machado, and Paulo De Marco Júnior. 2019. „Landscape Connectivity Modeling from the Perspective of Animal Dispersal“. Landscape Ecology 35 (November): 41–58.

Elliot, Nicholas B., Samuel A. Cushman, David W. Macdonald, and Andrew J. Loveridge. 2014. „The Devil Is in the Dispersers: Predictions of Landscape Connectivity Change with Demography“. Journal of Applied Ecology 51, No. 5: 1169–78.

Loveridge, Andrew J., Marion Valeix, Nicholas B. Elliot, and David W. Macdonald. 2017. „The Landscape of Anthropogenic Mortality: How African Lions Respond to Spatial Variation in Risk“. Journal of Applied Ecology 54 (3): 815–25.

Muff, Stefanie, Johannes Signer, and John Fieberg. 2020. „Accounting for Individual-Specific Variation in Habitat-Selection Studies: Efficient Estimation of Mixed-Effects Models Using Bayesian or Frequentist Computation“. Journal of Animal Ecology 89, No. 1: 80–92.

Panzacchi, Manuela, Bram Van Moorter, Olav Strand, Marco Saerens, Ilkka Kivimäki, Colleen C. St. Clair, Ivar Herfindal, and Luigi Boitani. 2016. „Predicting the continuum between corridors and barriers to animal movements using Step Selection Functions and Randomized Shortest Paths“. Journal of Animal Ecology 85 (1): 32–42.

Pinto, Naiara, and Timothy H. Keitt. 2009. „Beyond the Least-Cost Path: Evaluating Corridor Redundancy Using a Graph-Theoretic Approach“. Landscape Ecology 24 (2): 253–66.

Pomilia, Matthew A., J. Weldon McNutt, and Neil R. Jordan. 2015. „Ecological Predictors of African Wild Dog Ranging Patterns in Northern Botswana“. Journal of Mammalogy 96, No. 6: 1214–23.

Signer, Johannes, John Fieberg, and Tal Avgar. 2017. „Estimating Utilization Distributions from Fitted Step-Selection Functions“. Ecosphere 8, No. 4: e01771.

Taylor, Philip D., Lenore Fahrig, und Kimberly A. With. 2006. „Landscape Connectivity: A Return to the Basics“. In Connectivity Conservation, herausgegeben von Kevin R. Crooks und M. Sanjayan, 29–43. Cambridge: Cambridge University Press.

Van der Meer, Esther, Hervé Fritz, Peter Blinston, and Gregory S.A. Rasmussen. 2014. „Ecological Trap in the Buffer Zone of a Protected Area: Effects of Indirect Anthropogenic Mortality on the African Wild Dog Lycaon Pictus“. Oryx 48, No. 2: 285–93.

Woodroffe, R., and Joshua R. Ginsberg. 1998. „Edge Effects and the Extinction of Populations Inside Protected Areas“. Science 280 (5372): 2126–28.

Woodroffe, Rosie, and Joshua R. Ginsberg. 1999. „Conserving the African Wild Dog Lycaon Pictus. Diagnosing and Treating Causes of Decline“. Oryx 33 (2): 132–42.

Zeller, Katherine A., Kevin McGarigal, and Andrew R. Whiteley. 2012. „Estimating Landscape Resistance to Movement: A Review“. Landscape Ecology 27, No. 6: 777–797