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Do anthropogenic and natural features act as barriers to African elephant (Loxodonta africana) space use?

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Title: Do anthropogenic and natural features act as barriers to African elephant (*Loxodonta africana*) space use?

By Kristy Robertson

External Examiner Comments

Examiner 1:

1. The Kruger National Park is an unusual shape for a game reserve, with major fencing along the east and west boundaries and minor fencing on the northern and southern boundaries. This is worthy of comment and whether or not the models ignore or compensate for this factor
   The models do not compensate for the fact that the Kruger National Park is an unusual shape for a game reserve, being extremely long with major fencing along the east and west boundaries and narrow with minor fencing on the northern and southern boundaries. This might have affected results from the models with regards to fencing (see correction on page 48).

2. What is the status of the fencing on the Mozambique border and have all the intermediary fences between APNR and KNP been removed? This needs to be clarified.
   It can be seen in the first map showing fence line in Appendix 1 that some of the northern fence line between KNP and Mozambique has been dropped. This map also shows that all fences between APNR and KNP have been removed. But I have added a paragraph in Methods: Page 17, Paragraph 1, lines: 5-7.

3. I would have liked to see a map or two of the elephant home ranges and how they overlap. I realise that this is a moving target but it would give the reader a sense of the distribution of the animals under observation at least at one moment in time.
   Yes, there were many home ranges for each male and female elephant for each season, and each of the wet and dry seasons were divided into 3, making a total of 6 different seasons (over the three year period). But I can show an example or two. I added Appendix 1: Page 66.

4. Figure 2 and title need to be reunited on the same page
   Corrected.

5. I found the question of female use of basalt or granite a very confused one. On page 30 it is stated that fewer granite areas were used and yet on page 31 the Fig 16 shows the reverse and the sentence there claims the reverse...that males use basalt more than females. Please clear up this confusion.
   Corrected.
   Pg. 30: last sentence: For females, fewer basalt areas were used and more granite areas were used in both seasons (Figure 16).

6. The use of symbols to depict male and female elephants and wet and dry season have been standardised throughout yet this is not true for Fig. 19 and Fig. 20 which leaves the reader highly confused. It would help if the standard symbols for the sexes were used here too.
   Corrected.
7. P.63 Strelitzia has been spelt incorrectly. Please correct here and elsewhere.
   Corrected.
8. P. 64 and elsewhere Kangwana, K. – where all editors in other references have their initials first.
   Corrected.

Examiner 2:

General Comments:

1.1. I would suggest that the author add in additional Appendix that contains a map (or maps) of the home ranges of the different elephants monitored in the study. This will provide the reader with reference as to where these different home ranges are found, and thus help with the interpretation of a number of different findings. For example, were the females used in the study found in the North of Kruger and thus had very little contact with railroads? Did the male and female home ranges overlap? This does not seem to be the case judging from statements made in the discussion (see points below). Furthermore, as it is stated briefly that most of the females are found in the APNR (page 51), this has implications as to the furthest distance to any one feature and where random points should be put. My guess is that these two things are grossly over-estimated. For example, if the females are restricted to APNR, there were random points placed around Punda Maria or Pafuri? If so, then is this realistic? I wouldn't think so.
   I provided an example of one female and one male home range. The female elephants in the study were found to select areas in the APNR, yes; however the females could have selected any space within the study site. For example: Punda Maria or Pafuri. So I think it is realistic and therefore I placed random points within the entire study area (wherever they could have chosen).
   Please see added Appendix on page 66.

1.2. One key concern about the statistical analysis is the breaking apart of the data and analysing it separately by sex and season. Quite simply, this is wrong and leads to Type I errors. There is no problem generating log-odd ratios as they have been done. However, all the factors need to be included in the Generalized Linear Mixed Effects Model. If the literature suggests the factors will affect sexes differently, then you should get a significant result in the analysis. This, however, does not provide an acceptable reason to spilt the data and analyse parts separately. Ultimately, this may change some of the findings and thus require some re-writing and re-interpretation.
   I disagree. The data set was far too large to run all the factors in the Generalized Linear Mixed Effects Model; I did attempt this. Therefore I decided analysing the data like I did was acceptable.

Specific comments:

Introduction:

1. Page iii, Line 14: Did elephants 'use the features' (e.g. railways, fences, habitats) or rather 'respond to features'?
   I agree with 'use of features'. The elephants used roads with regards to the space available in their environment.
2. Page 2, Paragraph 1, lines 7-8: The idea that impacts will be diluted is a scale issue. As elephants, or any herbivore for that matter, don't use space uniformly, impacts will still be concentrated in specific habitats/areas. Thus, increasing the total area will only reduce impacts if the area increased comprises the preferred habitats.
   Acknowledged.
3. Page 2, Paragraph 3, line 2: Please provide examples of geological features pertinent to this study. This will help the reader.
   This is explained this later on in methods (Page 17, Paragraph 1, line 2), not in the research questions section.
4. Page 3, Paragraph 1, line 11: the correct spelling for 'Imfolozi' is 'iMfolozi'.
   Corrected.
5. Page 3, Paragraph 3, lines 3-4: Also see Owen-Smith & Chafota (2012) J. Mammal. 93: 698-705.
   Added in.
6. Page 5, Paragraph 2, lines 4-6: the key thing about dispersal is that animals do not return. If they did, that would likely be considered migration.
   Corrected.
7. Page 6, Paragraph 1, lines 4-6: Rhinos cannot cross deep rivers.
   Added the word 'some'.
8. Page 6, Paragraph 2, lines 1-2: Provide a couple of examples of anthropogenic features as this will help the reader. In addition, can these features be beneficial to animals (e.g. artificial waterhole?)
   I do give examples later on in the paragraph (Page 6, Paragraph, lines: 10-12).
9. Page 6, Paragraph 2, lines 12-13: Of these four features are villages found in the study area? Do you mean camps?
   Yes.
   This is discussed on Page 7, Paragraph 4.
10. Page 6, Paragraph 3, lines 2-4: Need to define 'edge-effect'.
    Provided on Page 6, Paragraph 3, lines: 2-4.
11. Page 7, Paragraph 1, line 1: Need to be consistent with the use of '*et al*.'. In this sentence it is written as '*et al*', but later in paragraph four it is written as '*et al*.'. Please check throughout the document.
    Corrected.
12. Page 7, Paragraph 4, line 8: Does this 'food' comprise crops, trees or both?
    Added in.
13. Page 8, Paragraph 2, lines 4-6: See also Wall, J., Douglas-Hamilton, I. & Vollrath, F. 2006. Elephants avoid costly mountaineering. *Current Biology,* 16, 527-529.
    Added in.
14. Pages 9-10, Resource selection functions: Shouldn't this section be moved to the Methods?
    Disagree, Resource Selection Functions need to be introduced to the reader.

15. Page 11, Paragraph 1, lines 2-4: This is because elephants are water-dependent species. See Western, D. 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. *East African Wildlife Journal,* 13, 265-286.
    Added in.
16. Page 12, Paragraph 2, lines 1-5: The author needs to provide examples of the 'geological features' found in the study area. For example, I'm not aware of mountains and deep v-shaped valleys being features of Kruger. Do you mean soils? If so, then why not just say 'soil type'? In addition, how are these features influenced by seasonality? Mountains, hills and valleys don't change over the course of the year. Do you mean that the use of these features varies? Please explain.
    I do provide clear examples of pertinent geological features in the introduction: Page 8, Paragraph 3. Mountains are geographical features (Page 8, Paragraph 2) where as basalt/granite are geological features. Basalt/granite are not a soil type, they are a geology type. I think I do state throughout my report that the use of the features varies by season.
17. Page 12, Paragraph 2, lines 5-9: It would be good to mention that the reason females don't make long trips is due to small calves found in breeding herds.
    Added in.
18. Page 12, Paragraph 2, lines 11-13: If this is the case then how can you tease apart these two factors?
    I understand what the examiner is saying. But a specific geology type (such as basalt) has a variety of vegetation types that can occur on it. Therefore you can separate these two factors.
19. Page 12, Paragraph 3: I think this is the world's longest sentence. It can easily be cut into four sentences. This would make it easier to read.
    Corrected.
20. Page 12, Paragraph 3, lines 3-6: If the reason that females don't travel as far is related to their young, then the large movements of males have nothing to do with their large body size. See also page 54, Paragraph 1.
    Please see revised sentence: Page 12, Paragraph 3, lines 3-6.

Methods:

21. Page 14, Paragraph 2, line 3: Were the 6 females from separate herds? Let the reader know here.
    Page 15, Paragraph 1. I mentioned that one female represents a group of individuals/herd.
22. Page 14, Paragraph 2, lines 4-8 & Table 1, Page 15: If abnormal movements related to collaring is of concern, then why use individuals that were recently collared (e.g. 0-2 months)? It would be better to remove these individuals from the analysis, and thus remove the possible effects of collaring. This would then leave you with a sample N=12 males and N=5 females.
    Acknowledged, but we were mandated by our funders to use as many elephants as possible that fall within the 3 year study period. And no abnormal movement behaviour was noted.
23. Page 15, Paragraph 1, lines 3-6: It is not clear why you consider the six females represent an equal number to the 15 males. Please explain.
    I explained this adequately.

24. Page 15, Paragraph 1, lines 4-5: Why wasn't musth considered in the analysis? As males in musth are generally looking to breed, you would expect them to seek out an oestrus female and then move with her. Thus, their movement patterns during this study period will likely match a breeding herd's movements and not reflect a 'normal' male movement pattern. I would remove these periods, so that the data better reflect 'normal' ranging behaviour.
    Musth wasn't considered because we did not have the exact dates of males in musth. The table simply points out which males were in musth sometime during the study period which could have influenced results.
25. Page 15, Paragraph 1, lines 5-8: What analysis are you talking about? Specify. This is not a convincing or legitimate justification for splitting the analysis. Why not just put sex in as a factor? This will then allow direct comparisons (via interactions) to be made. Moreover, analysing the data separately leads to Type I errors.
    That was the original plan. But this was not possible during statistical analysis therefore I had to separate sex.
26. Page 16, Paragraph 1, line 1: Again, why do this and which analysis? Just put season into the analysis. That way, you can see the combined effects of season and sex. Type I errors! If I am off base here, then this needs to be better explained and justified in more detail so as to make things clear and convincing for the reader. As it stands, I'm not convinced.
    Please see added sentence: Page 15, Paragraph 1, line 8 to Page 18, Paragraph 1, line 3.
27. Page 16, Paragraph 1, lines 1-4: What were the long term averages for the wet and dry seasons? Please provide in the text.
    Not relevant.
28. Page 16, Paragraph 2, lines 6-8: Now here you talk about combining the data into one analysis. This is correct. So I don't understand the need to do separate analyses on sex and season.
    This ANOVA was done to detect which factors were significant. This was a simple model that could accommodate both sex and season.
29. Page 16, Paragraph 2, line 6: Railways are a pretty rare feature in the study area (see Appendix 1) and can be up to 200km away from anything. With this in mind, is it a reliable/important factor to include in the analysis.
    Yes. One of the main points of my project was to determine the influence of railway lines on elephant movement.
30. Page 17, Paragraph 1, line 2: There is a problem that you'll need to consider/explain. Some of the vegetation types are associated purely with a specific soil (geological) feature (e.g. granite lowveld, Mopane Basalt shrubland; Appendix 1). Thus, they covary. How will you be able to tease apart what is influencing preference or avoidance of these habitats? It might be better to drop soil from the analyses and just discuss potential impacts. Something to think about.
    Thank you, acknowledged. But one of the main reasons of the project was to investigate how elephants are using the geological features which I think was accomplished.
31. Page 18, Paragraph 1, line 1: Shift the figure caption to page 17 so that it is under Figure 2.
    Corrected.

32. Page 18, Figure 3: It would be clearer to add in the fence (e.g. black line) in the colour 'distance to fence' portion of the figure.
    I think it was quite clear that the fence line is where the yellow colour is. This is provided in the Appendix.
33. Page 19, Paragraph 1, lines 11-12: Was this/these Generalised Linear Mixed Effects Model(s) done for the combined seasonal data for both males and females? This would make the most sense. However, it is not clear from what is written.
    No. I state on this on Page 19, Paragraph 1, lines: 11-12.
34. Page 19, Paragraph 2, lines 3-4, and Appendix 2: How were these distance categories determined? Please explain.
    Added in. Please see if sentence is ok: Page 19, Paragraph 2, lines 4-7.

Results:

35. Page 20, Figure 4: I would add in an 'a' above the male bars and 'b' above the female bars. This would then indicate that there were sex differences, but not seasonal differences. (It is interesting that you didn't find seasonal differences). You could then just put 'a' above all the bars in Figure 5 showing lack of difference in sex and season. This would make things easier for the reader.
    Disagree. The graphs adequately represent the data.
36. Page 22, Paragraph 1, lines 3-4: Please provide the distances (mean±SE) in the text. Do this also for roads, railways, infrastructure, and rivers (pages 24-29).
    This is not the point of the study. My study considered the location of elephants on the landscape in relation to potential barriers. The mean values are subjective and do not consider individual GPS points and the feature which will vary considerably. It is therefore not possible to generate mean values.
37. Page 26, Paragraph 1, line 1: Could this apparent preference of being close to railroads possibly be an artefact of where the home ranges of the elephants used in the study were located? For example, were any of the home ranges in the far North of Kruger? Reading further on it seems not.
    Yes, I state this in my discussion.
38. Page 32, Paragraph 1: Provide the total number of habitats used by males and females in the two seasons (i.e. males N=10 in dry and N=9 in wet). This is important and interesting information. From Figure 18, it looks like females use fewer habitats than males. From here, you can discuss which habits were preferred, etc.
    Added in. It is actually: males N=10 in dry and N=10 in wet; females N=6 in dry and N=7 in wet.
39. Page 32, Paragraph 4, lines 1-2: In total (according to Figure 18) males used 10 habitats in the dry season and 9 during the wet. Within these habitats, the difference in the males' selection was only one habitat (i.e. 3 vs. 2), and thus not very convincing. What is interesting is that they preferred two habitats throughout the year and incorporated Sand forest in the dry season. Females used five in the dry season and six in wet, but selected 6 in dry (not sure how this is possible as they only fed in five habitats according to Figure 18) and three habitats during the wet season. These three habitats were selected in both seasons and thus they incorporated 3 new habitats in the dry season. Present this type of information for both male and females as biologically it is important and interesting. As a writer/scientist, it is

your job to present this information to the reader and not rely on them to have to figure this out for themselves.

Added in. Please see Page 32. Paragraph 3, lines: 2-3 and lines: 5-6.

40. Page 33, Figure 18: The colours for Tshokwane-Hlane Basalt Lowveld and Phalaborwa-Timbavati Mopaneveld are too similar. In addition, are the availabilities of the last six habitats (Nwambyia-Pumbe Sandy Bushveld to Sand Forest) so minor that they don't feature in the figure?

    Corrected.

41. Figures 19 & 20: Use the same symbols (i.e. circle=male, triangle=female) and colours (green=wet, brown=dry) as in Figures 7, 9, 11, 13, 15, and 17. This will be easier for the reader to follow. Also, delete "Veg" before each habitat type on the x-axis.

    Corrected.

42. Page 38, Paragraph 1, lines 2-4: As with the 2nd order analysis, you should rather just include sex and season into the model.

    I have explained already why I could not do this.

43. Page 38, Paragraph 2, lines 4-5: Could this be due to the females having smaller ranges and thus being found in a smaller proportion of the study area?

    Provided in the discussion. Page 51, Paragraph 1, lines 4-6.

44. Page 39, Paragraph 1, lines 2-3: Were there fences found within the cores of the female's home ranges?

    Reason for this is provided in the discussion. Page 49, Paragraph 1, lines: 6-9.

45. Page 40, Figure 23: Vertical lines?

    Added in.

46. Page 41, Figure 25: Vertical lines? Category 'C'? You could provide all the categories to further highlight that the females did not use areas far away from railway lines. Moreover, this would make the figure more similar to Figure 24.

    Vertical lines added in. There is no category C.

47. Page 43, Paragraph 1: It would be beneficial to present these data with reference to what habitats were selected in the total home range. For example, for males, during the dry season sand forest isn't even found in the core, yet it is selected in the total home range. Make these links for the reader. I see you present the broad-scale comparisons in Table 5, but these specific habitat comparisons are missing yet are interesting.

    In the discussion, I discuss more about what the elephants preferred and compare these between sex and season.

48. Page 46, Paragraph 3, lines 2-4: These home range sizes need to be presented in the Results.

    Added in.

49. Page 47, Paragraph 1, line 1: What do you mean by 'neophilic'? Ability to adapt? Short attention span? I'm not sure how do these things fit into this sentence?

    The meaning of neophilic is known in the behavioural literature.

50. Page 47, Paragraph 3, lines 7-8: It seems that the elephants are acting like typical water-dependent species. To highlight this, it would be better to make the comparison to other water-dependent herbivores (e.g. kob, zebra, wildebeest). You'll likely find that elephants are not that different. Especially as you discuss water not being limited, and thus elephants do not have to move.

    Acknowledged.

51. Page 49, Paragraph 1, lines 4-9: Does this suggest an increase of long-range excursions from the core during the dry season.
    Yes, I stated that throughout.
52. Page 49, Paragraph 3, lines 3-9: This is one possibility, but what about others. For example, were there fewer fences in the female's home ranges?
    Added in. Page 49, Paragraph 3, lines: 9-10.
53. Page 51, Paragraph 1, lines 2-4: If most of the female home ranges are in the APNR (N=?), then surely this has an impact on greatest distance possible from any feature? You do not have data/home ranges for every female in Kruger/APNR. Thus, this small sample (N=6), coupled with the fact that they are restricted to a small portion of the study area (i.e. APNR) tells you things only about elephants living in this small area. Thus, it would be better to limit the random points to the APNR so as not to over-estimate potential areas that could be used by these elephants. For example, is the furthest distance from fence or road really ~35km for females in this area? Unlikely.
    Same as comment 1.1 by Examiner 2.

    The female elephants in the study were found to select areas in the APNR, yes; however the females could have selected any space within the study site. For example: Punda Maria or Pafuri. So I think it is realistic and therefore I placed random points within the entire study area (wherever they could have chosen).

54. Page 52, Paragraph 2: This is a strange way to interpret the data with regards to rivers. The reason elephants are close to rivers during the dry season is likely not because they are no longer a barrier (i.e. water levels have dropped), but rather because elephants are water dependent and thus focus their foraging and space use around water points (e.g. rivers, permanent pans) during this time period. In the wet season when surface water is prevalent across the landscape, elephants can forage more wildly and thus move away from permanent water sources. A better way to interpret rivers as being a barrier would be to see whether the elephants are restricted to one side of the river during the wet season (i.e. cannot cross it), compared to the dry season where they are found on both sides (i.e. are able to cross it). You could use the GPS points to indicate this.
    Added in. Please see: Page 52, Paragraph 2, lines 9-11.
55. Page 3, Paragraph 1, lines 3-5: Again, if the females' HR's used in the study are restricted to APNR, it is not surprising that they preferred granite as all of APNR is granite.
    Acknowledged.
56. Page 53, Paragraph 2, lines 1-3: As stated previously, if soil type determines habitat type, how do you tease these two factors apart?
    Please see comment 18.
57. Page 55, Paragraph 2, lines 3-4: If males do not have railroads in their home ranges, then is this a good factor to include in the analysis? In addition, from reading between the lines, it seems that many differences found between the sexes may purely be due to the fact that their home ranges are found in completely different areas. If this is the case, then it is likely that the availability of factors ultimately differ (e.g. railroads, soil type, roads). Thus, results are not biologically driven, but rather an artefact of the experimental design. This really needs to be looked at, and discussed up front, not buried in the discussion.

I disagree. The examiner implies that the elephants location is accidental but the position of the elephants could be a matter of choice. The male elephants chose to have their home ranges where they want to. I did this study to establish whether railways influence where they choose to have their home range. And clearly males choose areas away from railways.

58. Page 57, Paragraph 1, lines 4-7: You assume proximity equals breaking into the camps. The question is, do you have examples/reports to back this up? You mention this one instance, but what about Kruger itself? If so, do these break-ins happen during the dry season? This sort of information would back up your assumption, without it, it is pure speculation and thus not something that management decisions should be based on.
    Yes I do have examples as backup. Please see Reference: McCagh 2008. There are several examples in this report.
    I could not find literature about season and infrastructure.
59. Page 57, Paragraph 1, lines 7-9: The data collected does not indicate that rivers acted as barriers. Movement across rivers during the wet season being prevented supports this claim. Movement away from rivers in the wet season is a very standard movement response for water-dependent species.
    Acknowledged.
60. Page 57, Paragraph 2, lines 1-7: As you have a small sample size that does not reflect all of the herds across the total study area, this conclusion is likely wrong. As stated, the females were restricted to APNR and thus restricted to granite soils. If males used in the study were predominantly limited to the basalt area, then these results are driven by experimental design and not biology. This needs to be considered, critically evaluated and explained.
    No. The females were not restricted to the APNR. The boundary fences were taken down. The females were located there, possibly out of choice. The females could choose to leave but remained in the APNR for whatever reason. Therefore I do not think my conclusion is wrong.

References:

61. Page 59, Boyce 2006: Single author papers should go before the same author's papers with co-authors (i.e. move this before Boyce and McDonald 1999). Do the same for Vanleeuwe 2008 on page 65.
    Corrected.
62. Page 60: DeVilliers & Kok (1997) is in the text but not in the reference list.
    Corrected.
63. Page 64: Rosenberg & McKelvey (1999) is in the reference list but not the text.
    Corrected.
64. Page 65: Zambatis (2003): is in the reference list but not in the text.
    Yes it is, see page 13, paragraph 1, line 9!