

PeerJ

Rebuttal: “Ungulates rely less on visual cues, but more on adapting movement behaviour, when searching for forage” by Venter et al.

Dear Editor

We thank the reviewers for their generous comments on the manuscript and have edited the manuscript to address their concerns in the rebuttal below.

Please do not hesitate to contact me if you need more information.

Best regards.



Dr Jan A Venter
Wildlife Ecologist, Lecturer & Researcher

1	Reviewer 1 is satisfied with the revised presentation but notes the inappropriate citation of a study whose conclusions are no longer considered valid. (This point might be addressed by also citing the critical subsequent article.	We removed Visvanathan et al. from the manuscript
2	Reviewer 2 is also basically satisfied with this version, but has several additional recommendations. My reading of the manuscript identified a number of issues, including some that overlapped with those of Reviewer 2. These include insufficient discussion of some conclusions and numerous problems with the presentation, including awkward, wordy or unclear sentence construction, errors in grammar and punctuation, and mistakes in the references. I have listed the non-grammatical issues below and have indicated the grammatical errors and potential alternative wording using highlighting and inserted	We worked through all the comments in the pdf. And corrected them.

	comments on the pdf.	
3	Regarding my comments below, you may treat them as a third review, making appropriate changes if my suggestions are valid and providing a clear rebuttal if they are not.	Noted
4	The conclusion that ungulates adapt their movement patterns to the demands of their foraging environment appears in your title, abstract, discussion and conclusions. However, I could not find any clear development of the evidence supporting this claim. The brief assertion regarding the value of random movement is not explicitly linked to your data, nor is there a discussion of possible alternative explanations for any randomness in the observed patterns. Is it possible that this conclusion is a residue from the previous version of your manuscript and needs to be limited to a paragraph discussing this as a possible explanation?	All three species used larger step lengths when moving to patches with unknown (unseen) quality. When success is considered it indicate that they could not anticipate success. This indicate that they did adapt their movement when moving to unknown quality patches and when they are in known patches they adapted again with having shorter step lengths. We added text in several places in the discussion to clarify this line of thought.
5	The conclusion that visual cues are unimportant to the discovery of new patches is supported by the shorter step lengths and lack of directionality when moving to visible patches. However, I think you need to summarize the evidence more explicitly and address any inconsistencies in the data and possible alternative explanations for the observed patterns, i.e., a more rigorous critical discussion.	We have done this now in the first paragraph and last two paragraphs of the discussion and also in the species specific paragraphs
6	Most of the discussion is devoted to a reasonable discussion of species differences. However, the conclusion (L264-266) that traits such as body size and morphology, feeding type, etc. play a role is overstated. While species differences are well supported, there is no rigorous analysis to show which characteristics influence movement patterns, nor can there be with only 3 species. As a major empirical finding of your study, a summary of the species differences ought to be included in the abstract.	We changed this sentence to: "In addition, it shows that different species search for forage in different ways, which could indicate that search strategies are linked to intrinsic traits such as body size, feeding type, digestive strategy and muzzle width". We added text on species specific results in the abstract
7	Success in finding a new patch appears in methods and results, but I did not notice a mention in the Introduction, predictions, or Discussion. What is the role of this measure?	We added: "We expected, if animals used visual cues, that there would be longer step lengths which are more

		directional when they move to better forage, because they could anticipate success. No difference in step length or directionality when comparing the outcome of movements (successful and not successful) would indicate that visual cues are not used at this particular scale because then the animal did not adapt the movement (walking straight towards a observed patch) to anticipated success or failure to find better forage. Due to the different intrinsic constraints different species of ungulates have to deal with, we expected that each species would approach its forage search strategy in different ways regardless of the use of visual cues or not or because one species could be using visual cues more than another.” To clarify this more
8	Check all references in text; sometimes the parentheses should be around only the year rather than the full reference (e.g., L124, 125, 178).	All these cases were corrected
9	It is reasonable to put quotation marks around "walk" at first use. After that, they are not needed, and your use throughout the text and figure captions is inconsistent.	This was corrected
10	L20. Define step length, even in the Abstract, because it may not be familiar to all readers and the expression is sometimes used for stride length, potentially creating confusion.	We defined step length in the main text but not in the abstract. We feel that it is unnecessary for the abstract because there is now a proper explanation in the min text. Length of abstract was also a consideration.
11	L51. Incomplete comparison: more optimal than what?	We changed the wording to: “In heterogeneous environments, adaptive

		<p>movement, at different scales of step lengths and directionality, e.g., a small-scale area-restricted search (within patches) mixed with a set of large more directional movements (between patches), can be a better search approach than an approach of using visual cues, especially when the forage resource is complex and in constant fluctuation.”</p>
12	<p>L63. This is a good place to define what you mean by both directionality and step length to avoid any confusion.</p>	<p>Yes agreed, we added the explanation here.</p>
13	<p>L64ff. Table 1 would be more appropriate at the start of the Discussion, rather than putting the results of your hypothesis test before you have even provided the methods. Also, this section needs a clearer justification of the predictions and an inclusion of the within-patch movement predictions.</p>	<p>We removed Table 1 and expanded on the predictions in the text.</p>
14	<p>L102. Rather than just refer to the existence of constraints, wouldn't it be a good idea to provide some details of what they are for each species and how they might affect foraging? Perhaps these details could be presented in the Introduction following L83. Indicate which herbivore species were selected for study and how they varied in ways important to foraging. The details of sexes of collared animals would remain in Methods.</p>	<p>Details of each species are now provided in the section as suggested.</p>
15	<p>L109-153. I found this critical section somewhat confusing. I think that the order of presentation could be improved for greater clarity. My proposal below is a suggestion that should indicate how I was confused, but still may not be the most logical order.</p> <ul style="list-style-type: none"> • Start by stating that the distance traveled between 30-min readings was considered a step and 20 consecutive steps during daylight hours was considered a walk. • Then, provide an explicit statement defining step length and direction and walk length (is it the sum of steps or distance between first and last locations). • You don't mention direction in this section, yet refer to it early in the analysis section; is walk direction also used? 	<p>Added text and clarified where needed, removed “landscape scale” and stayed with “habitat patch scale”. The starting points were randomly selected by day not by hour. We added text to clarify that. Yes correct it is 7 not 6 locations.</p>

	<ul style="list-style-type: none"> • Follow this with how you tested that 20 steps provided a suitable scale. This is unclear because you defined habitat patch scale in the Introduction (L60) and now introduce landscape scale. It is not clear whether you are using two terms for the same scale (as a reader might infer from the repetition of references) or whether you are trying to clarify whether they are in fact the same. <p>You refer to the last 3 h as 6 final locations (L135) whereas I would have expected 7 locations for 6 steps or 3 h.</p> <p>I don't understand the random starting point issue because random starting points are not possible for 20 consecutive steps within daylight.</p>	
16	<p>You need to join the information on visibility estimation with the information on their application to final patches given in the next paragraph. The sentence describing this classification (L48-51) is awkward and needs to be rewritten. Were final patches classified as visible or not from the starting point?</p>	<p>We moved the section on success lower down and connected the paragraphs on visibility.</p>
17	<p>The concept of successful and unsuccessful walks could be clearer. Did everything hinge on the 6-month burn criterion, so all patches were defined as good (<6 mo.) or poor (> 6 mo.) and walks were defined as successful if they switched from poor to good and unsuccessful if they switched from good to poor? Couldn't a search be successful if switched from good to good (for example, if the grass had been heavily cropped in the original patch?) Otherwise, an animal in a good patch could not make a successful move. L148-151. This sentence is not very clear and the order of classes does not match the way it was presented in the results. I suggest something like "The walks were then classified into different visibility classes: a) movements in which the end point was within the same patch as the starting location, b) movements in which the end point was a different patch visible from the starting location, and c) movements in which the end point was a different patch not visible from the departure point. Figure 3 should match this order. Note that I tried to use terms consistent with your previous definition of end point. Also, if movements within the same patch always have visible end points as implied by Fig. 3, you should state that here.</p>	<p>Yes your definition is correct. If there is no change in quality (whether is this good-to-good or bad-to-bad) the classification was no change. This is because it is linked to the predictions on visibility. Success is important here because that helps making the argument about animals using visual cues. We hope the better prediction around success help solving the confusion in this case.</p>
18	<p>L175. Confusing. Not sure what an 'error bar plot' is or what you are trying to say. Do you mean to say</p>	<p>'Error bar plot' removed, the text updated as suggested.</p>

	<p>something like 'Mean walk distances (detailed values) were similar to distances between patches (value), indicating that walks represented movements at a landscape scale'? Note also the confusion between habitat patch scale in the Introduction and landscape scale here and in the Methods noted above. Also, I don't think that you defined inter-patch distance in your methods. Is it the distance between patch centers or nearest edges? Finally, as I noted in my comments on the previous version, if you are going to use parametric (mean, SD) measures for your comparison, you should confirm that the data are normally distributed. Otherwise, use nonparametric measures.</p>	<p>We removed landscape scale and changed everything to habitat patch scale We changed to a non-parametric measure</p>
19	<p>L188. The Wald test was not mentioned in data analysis section of Methods.</p>	<p>We added “Wald test was used to determine whether variation in step length between individuals was significant and should be included as a random effect” to the Methods.</p>
20	<p>L190. Again, order of factors discussed should correspond in methods and results text, as well as table and figures for ease of understanding by readers. Several of your p-values approach significance, and I think this should be mentioned because it suggests a possible effect. The statement on the effect of visibility class is unclear. You did not clearly indicate that although the factor was statistically significant, though marginally, in the overall analysis, none of the two-way comparisons were statistically significant. Again, it may be important that two did approach significance, especially as there was an overall treatment effect.</p>	<p>We added marginally significant values to the text which now reads: “With search movement outcome, the difference between “no change” versus both “successful” and “not successful” were marginally significant (p=0.054 and p=0.074, respectively) (Table 2, Figure 4A). Zebra had significantly longer step lengths than red hartebeest (p=0.005) and approached significance for eland (p=0.06) (Table 2, Figure 4B). The difference between eland and hartebeest was not significant (p=0.69) (Table 2, Figure 4B). For visibility classes, step lengths in the “within visible” and “to visible” classes were not different (p=0.37), but the step lengths for both these categories were significantly shorter than step lengths to “not visible” classes (p=0.002 and</p>

		p<0.0005 respectively) (Table 2, Figure 4B).”
21	L214. As noted above, you need to provide a justification for your assertion that adaptation of movement to patchiness at a habitat patch scale is confirmed by your study. First, confirmation or 'proof' is a bit strong for normal philosophy of science. Second, a correlational study showing that relatively few 20-step sequences are directional seems to provide limited evidence for such a complex assertion. Given that a walk is expected to have a mix of directional and non-directional movements, what proportion of significant r-values would it require to reject this hypothesis?	Thank you we concur and take the point. We use the words “provide evidence” and “softened” the text throughout in order to indicate that it is only evidence indicating rather than solid proof
22	L229. You are referring to movement intensity and complexity, but I don't think you have defined these terms or demonstrated how they apply to zebras.	We removed these words and replaced it with step lengths and directionality
23	L240-241. The logic of using less and more nutritious patches in a similar way based on a comparison with zebra for within patch and to non-visible patch movements is unclear. This needs elaboration. The verb 'relates to' is too vague. How are these observations related?	Yes agreed. We removed the sentence and corrected the wording to “Red hartebeest, being the smaller ruminant (compared to eland), needing less, but better quality, forage to meet their nutritional and energy requirements (Demment & Soest 1985; Illius & Gordon 1992), used a strategy where they foraged using smaller and less directional steps (compared to zebra), whether they were moving within patches or to unseen visible patches, but increased their step lengths when moving to invisible patches, just like zebra and eland. The smaller step lengths could be explained by their tendency to move slower and spend more time in less nutritious patches that was observed by Venter et al. (2014a)”
24	L258. Did you explain what you mean by less complex movement and how that applies to eland?	We removed the use of “complex”

25	L261ff. What is evidence for adaptation of foraging mode to heterogeneity and quality? There is definitely no evidence for the effect of morphological traits and diet (with only 3 species differing in multiple traits, insufficient evidence to support role of any one or combination of traits).	We removed reference to quality
26	References need to be checked carefully. There are capitals that should be lower case in some article titles and the opposite in some book titles, some missing italics for scientific names, and a book title in which the publisher information is unclear.	Done
27	Fig. 1. I think that the figure would be strengthened by more detail. If it is a real as opposed to a hypothetical case, you could specify the species and date. A distance scale bar on the figure would also help. I only count 18 location points rather than the 21 I expected for 20 steps. If my expectation is incorrect, something in the methods may need clarification.	This is a hypothetical presentation of a walk. We indicated this in the heading now.
28	Fig. 2 needs some work. You don't need to interpret the results in the caption because that was done in the text. The caption is imprecise because it implies that the figure only shows the mean. I suggest "Mean +/- 1 S.D. (m) of inter-patch distances and distances moved in a 10-h walk by three species of grazing herbivore in Mkambati Nature Reserve)." You don't need the second x-axis label 'inter-patch distance and species'. You do need a hyphen for 'inter-patch' and to remove 'mean' from the y-axis label.	We made these corrections as suggested
29	Fig. 3. The caption is incomplete and somewhat confusing. I suggest the following. Also, note that for greater readability, you should have consistency in the order of end point types between the methods and caption/results. "Directionality of movement of three species of herbivore in relation to visibility of the final location in Mkambati Nature Reserve. Each point represents the r and associated p-value from a Rayleigh test for a single 10-h walk to locations in different patches that were not visible from the start (left column), to locations in the same patch that were visible from the start (middle column), and to locations in different patches that were not visible from the start (right column). Data are shown for eland (A,B,C), hartebeest (D,E,F) and zebra (G,H,I)."	We made these corrections as suggested
30	Fig. 4. I proposed some changes to refer to the relationship rather than effect because this is a	We changed the table to correspond to the figure

	<p>correlational study. Note that relating the figure to the text will be easier if panels A and B and the order of movement outcomes and visibility classes correspond to the order used in the results, Table 2, (and preferably the definitions in the methods as well).</p>	
31	<p>The revised manuscript is considerably better than the original submission, as it is free of misunderstandings about Levy walks, misunderstandings which are being perpetuated in the literature. In their rebuttal the authors disagree with me about the use of “step-lengths” when defined as being the distances between (arbitrarily defined) positional fixes, and cite several studies which have used this inappropriate specification. I will not labour the point but suggest that the authors (1) read Viswanathan et al. (1999) which they cite, and (2) take a look at the much-cited comprehensive review of Levy walks by Zaburayev et al. (Rev. Mod. Phys. 87, 483, 2015). The relevant subsection is “VI. Levy walks in biology. iii Levy walks vs Levy flights”. These leading experts conclude rightly that the misuse of step-lengths as defined above is partially responsible for causing the controversies surrounding Levy walks and does not add positively to the on-going debate about the biological relevance of Levy walks. I hope that the authors will take note of this in the future.</p>	<p>We thank the reviewer for drawing our attention to Zaburayev et al.2015. As we removed the mention of Levy walks we did not cite this work in the revised manuscript.</p>
32	<p>The citing of Viswanathan et al. (1999) is not really appropriate because the data analysis in that paper was overturned by Edwards et al. (2007).</p>	<p>Viswanathan et al. is now removed from the manuscript</p>
33	<p>The introduction is now much better and appropriate. However I am still missing some words about the predictions regarding the differences among species given that so much weight is given later to the differences among species. I understand that the inclusion of the first paragraph was meant to fulfil my request. However, this does not replace a specific prediction about the differences among species... the prediction does not have to be specific to the species involved necessarily, but if could deal with the expectations of different movements type according to species types.</p>	<p>We added “Due to the different intrinsic constraints different species of ungulates have to deal with, we expected that each species would approach its forage search strategy in different ways regardless of the use of visual cues or not or because one species could be using visual cues more than another. Demonstrating a difference in movement behaviour between visible and invisible habitat patches, and successful or not successful movements would enable an</p>

		<p>understanding of the importance of visual cues to different large herbivore species when moving between patches at a habitat patch scale.”</p>
34	<p>I am not entirely convinced about the response about the autocorrelation of missing values. I still think the autocorrelation of missing values or the relation of missing values to a certain habitat should be checked and mentioned at least in an appendix. I assume that if the missing values are biased per habitat or species, this could affect the results. If that there is no bias please justify/clarify in more detail.</p>	<p>I think I misinterpreted the initial question (in the previous review). The missing values that were removed were generally due to unit batteries going flat (at the end of data sets) or units failing for some reason. So these sections were removed. We rarely had missing data in the core of the data set. Mkambati has open habitat with not too much extreme topography. So we did not experience many issues with the GPS units not logging.</p>
	<p>Regarding the turning angles “problem”. I think that even though the authors corrected partially for it by eliminating the step lengths below 6 meters. I still would acknowledge this “potential bias” in the discussion to partially explain the potential influence of this “error” in the results.</p>	<p>We acknowledge a possible effect of GPS error on directionality add added the following paragraph to Discussion: “There is a certain degree of uncertainty whether walk directionality was affected by the step length. Hurford (2009) showed that GPS measurement errors might lead to reporting overly tortuous movement when the distances between locations were smaller than 20 m. Although we removed all distances smaller than 6 m from the analysis there is a chance that part of our turning angle measurements were affected by GPS error. For example, larger proportion of short steps in hartebeest might explain</p>

		why directionality in hartebeest movements was smaller than we expected.”
35	I personally do not understand the need to do the “Pairwise comparisons was done using a Bonferoni”. Using the fitted values from the LMM (figure 4). All combination of comparison can be done directly by comparing the the 95%CI of one category overlaps with the mean of the other category or not as a post-hoc test. Is this what the authors meant? This would be a more elegant option because it take into account the differences while controlling by the other variables included in the model.	We did not include interactions in the model (as they were not significant when included) and therefore we did pairwise comparison of the main effects. An explanation has been added to Methods: “We did not include interactions between the fixed effects as they were not significant when included in the model. Therefore, we used post-hoc pairwise comparisons with a Bonferroni correction to determine differences in the main effects” Since interactions were not included the p-values for the difference between species within different classes of visibility and success are the same as the main effects in Table 2.
36	The Wald test is first mentioned in the results but not in the methods. It should be included in the methods too or eliminated from the results.	The Wald test is added to the results.
37	The data collection and experimental collection are correct and the statistical analyses are much more appropriate now.	Thank you
38	The results are sound and robust although the discussion would benefit from highlighting the fact that the results sometimes did not support the hypothesis and then link to the explanations of "why" already included...	We tried to address this concern by adding numerous sections to correct this issue.