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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

Reviewer 1		
1	On reading the manuscript I had a strong sense of déjà vu and subsequently realized that in the summer of 2014 I had reviewed two earlier versions of it for Ecosphere. I did not retain copies of these earlier versions but I do still have my reviews. I can see that the authors have not addressed my primary concerns. I pointed out significant errors in technique, fact, calculation and interpretation.	Yes it is a small world indeed. We apologize if it seems that we are merely submitting to another journal because we are not getting our way with the first one. However the manuscript is in many ways different from the version that was submitted to Ecosphere two years ago. But unfortunately not adapted in the way the reviewer wanted. See below for further comments.

2	The manuscript tells a cohesive story in a concise, precise and easy to follow manner. The subject matter – effectively the relative merits of Levy walks and composite correlated random walks as models of complex movement patterns -- is topical and high profile, and is currently being played out in PNAS, Science and other top flight journals. The methods of analysis – maximum likelihood methods and the Akaike information criterion – are state-of-the-art and are well accepted by the research community. The presentation – the figures and accompany tables – are very clear and readily interpretable. The data set is extensive and impressive. There are, however, significant errors in technique, fact, calculation and interpretation. The hallmark of a Levy walk is a step-length distribution with a heavy power-law tail where a 'step' is a movement bout made between consecutive, significant turns (aka 're-orientation events'). The authors' analyses appear to be based on distances travelled between consecutive locational fixes made at regular time intervals that are set by the arbitrary data sampling protocol and so without biological significance. Such analyses cannot be used to test for the presence of Levy walks. Indeed, it has long been realized that turns should be used to define steps more generally; in, for example, the parameterization of correlated random walks of the type used by the authors (see Turchin's classic book- Quantitative analysis of movement: Measuring and modelling population redistribution in animals and plants, 1998). The problem with the authors method is readily understood. Suppose for simplicity that an animal walks in a perfectly straight line but walks with variable speed. If the speed variations are exponential, then the 'step' lengths (as defined by the authors) will be exponential-like and the movement pattern will be classified as being a correlated random walk. If speed is intermittent (the animal occasionally stops) then the steps will appear to be multiphasic and the walk will be classified as being a composite correlated random walk. An analysis based on turns would, however, correctly identify the movement as being a straight-line.	The reviewer response as stated to the left definitely has merit but we disagreed, see our response below (as per initial submission to ecosphere). Original response: "*The reviewer commented that in a Lévy walk context "a 'step' is a movement bout made between consecutive, significant turns". Indeed, some authors use this interpretation of a 'step'. However, in many studies a 'step-length' is interpreted as a move length between successive recorded locations – e.g. Austin et al. (2004), reanalysed by Sims et al. (2007) and Edwards et al. (2008) to name a few. De Jager et al. (2011) used the distance between subsequent points as well as two step length extraction methods and reported qualitatively the same results for all methods. This study is not centered on distinguishing between ballistic movement and Lévy walks with power-law exponent > 1 which would indeed require more frequent observations and more intelligent split of tracks into steps. We are not trying to explain in details what a movement pattern is. We ask the question "is there a difference in movement behaviour when moving to non-visible patch, visible patch or within the same patch?" We agree that*

		there are limitations to treating moves at 30 min interval as steps but we use a step length analysis in combination with analysis of directionality and path shape to make our conclusions." We still disagree with the reviewer on this matter but decided that will follow the second option (see below) given by the reviewer in order to conclude the research project.
3	The steps defined by the authors can be used to assess some differences in the movement patterns for the different visibility classes but these differences cannot, as the authors have done, be framed: in the context of Levy walks; expectations of Levy search theory and; the relative merits of Levy walks and composite correlated random walks (multiphasic walks) as models of the movement pattern data. The language adopted by the authors is highly misleading and will cause confusion. The authors' have a choice. They either re-do their analyses by determining steps in a way that allows them to properly test to Levy walks, composite walks etc. [the relatively coarse sampling may preclude this possibility]. Or they dispense with relating their results to such models and instead state their results more directly and simply, i.e., by stating that animals have longer, straighter movements when targets are not visible; and that foragers adapt to conditions encountered during searching by switching from an extensive to an intensive mode of searching upon detection of a patch…	We deliberated about this amongst the authors and have decided to follow the option highlighted in yellow and also suggested as an option by the editor e.g. "Note that PeerJ does not include 'impact' or 'importance' as a criterion for publication, so a comparative analysis of move speed and direction in relation to visibility of patches would still be potentially acceptable, even without the strong connection to search theory." This is not our preferred option but we feel this would be the easier way to conclude the work.
4	There are potentially two additional significant problems. First, a search ends when a patch is located. This truncation will give any step-length distribution a high exponential tail. This makes the detection of intrinsic search patterns, like Levy walks difficult, unless the patches are sparsely distributed so that intrinsic scaling extends over a large range of scales. This problem is compounded by the fact that the foragers could switch from an extensive Levy walk	This is not relevant when following option 2 (as per above)

	or extensive ballistic search to an intensive Brownian search upon entering a patch, making whole movement patterns resemble composite correlated random walks with multi-exponential step-length distributions. This is just the kind of the distribution found to best fit the movement pattern data.	
5	Second, the authors have pooled data for a number of different individuals. The resulting step-length distributions (which tend to be multi-exponentials) could reflect intrinsic variability that is displayed by all individuals, or reflect variability amongst individuals, or some combination of these two possibilities. The authors need to discriminate between these possibilities.	This is not relevant when following option 2 (as per above)
6	Some of the referencing and terminology are decidedly odd and suggests that the authors are not sufficient familiar with the relevant literature. Some examples:	This is not relevant when following option 2 (as per above)
7	L56 The authors state that they classify random movement behaviours (i.e., patterns) as being random walks (which is a tautology) or as being Levy walks. What the authors actually attempted to do was to classify the observed movement patterns as being either simple random walks, multiphasic random walks, or Levy walks. Moreover, the bracketed term “Brownian motion” is problematic because all movement patterns become Brownian at significantly long scales because of truncation at patches, at the boundaries of the home range, at topographical features etc.	This is not relevant when following option 2 (as per above)
8	L59 Viswanathan et al. 1999 is an appropriate reference for Levy walks but not for finite-specific random walks. Turchin’s classic book is an obvious reference.	This is not relevant when following option 2 (as per above)
9	L60 Edwards et al. 2012 iconoclastic paper is far from being an appropriate reference for Levy walks.	This is not relevant when following option 2 (as per above)
10	L60-63. This is too glib because the relative merits of any search pattern will depend on lots of factors, including the initial conditions of the search, i.e., whether searching begins close to a patch or midway between adjacent patches. See e.g., Viswanathan et al. 1999.	This is not relevant when following option 2 (as per above)
11	L65-74. Here the authors make much of the fact that composite correlated random walks can resemble Levy walks. This is true but it calls for an explanation	This is not relevant when following option 2 (as per above)

	because most composite correlated random walks will not resemble a Levy walks. The resemblance requires fine-tuning of the parameters in the multiphasic walk and this suggests selection for Levy walk characteristics. This in turn suggests that the arguments about the relative merits of Levy walks and composite correlated random walks are somewhat misplaced.	
Reviewer 2		
12	From the point of view of the language, this paper is well written. The overall structure is appropriate and the raw data is provided. However, there are a few points that could be modified to improve the reporting:	Thank you
13	I would recommend introducing in the introduction the concept of adaptive movement behaviour, to change the final part of the intro to put the hypothesis before the predictions, the results and methods should be slightly changed so that they relate more directly to the questions/hypothesis examined and table 4 is not necessary, so it could be taken out (see further details in comment to author).	In the introduction we added "African ecosystems are well known for their exceptional diversity of large mammalian herbivores, of which a large proportion are ruminant bovids with a few non-ruminant equids (Grange et al. 2004). The feeding type, body size and mouth morphology of large herbivores are intrinsic constraints on the habitat that they can effectively use, and provide an understanding as to how one species may be more or less constrained than another in a particular set of environmental conditions. Different species of large herbivores may use a range of different behaviours to enhance their foraging efficiency (Bailey et al. 1996; Beekman & Prins 1989)." Table 4 removed
14	The research is original in that it compares movement across different species of ungulates within the same area o study, and tries to depict the effect of visual cues to drive their movement. The data collection and	See further comments later

	selection are carefully done. The statistical analyses are mostly appropriate, although some improvements could be performed (see further details in comment to author).	
15	The results are valid, relate to the questions initially raised. The discussion is consistent with the results. The main weak point is the fact that the comparison among species (according to traits like diet, etc…) is not properly presented in the introduction.	We added text to improve on this in the first part of the introduction. See comments above
16	This paper presents and interesting comparison of ungulate movement among different visibility scenarios, trying to disentangle the effect of visual cues from other movement behaviours. The detail comparison of several ungulate species in the same study area is especially valuable and the analyses are appropriate. However, I would suggest the following changes before continuing with the publication process:	Thank you.
17	Line 22-23 from abstract, Brownian motion could/should be replaced by composite Brownian movement.	This is not relevant when following option 2 (as per reviewer 1 above)
18	Introduction: I think the introduction would benefit from introducing the “adaptive movement behaviour” concept as alternative or other alternative movement behaviours beyond the one relying on visual cues or memory cues.	Yes we agree it is a good idea. We added “An alternative behaviour to the use of visual cues would be adaptive search/movement behaviour (Benhamou & Collet 2015; Martin et al. 2015). In heterogeneous environments, adaptive 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 an optimal search approach (Benhamou 2007).” To the introduction
19	I missed hypothesis about the comparison among species. By reading the introduction on, doesn’t get the clear idea that later there will be so much time devoted to comparing the three species.	Se comments about text added in earlier comments above
20	Lines 84-86 seem like the hypothesis to me and I	This is not relevant when

	would suggest including them before the predictions (i.e. lines 82-83).	following option 2 (as per above)
21	I would recommend including the sections “study area”, “methods” (change to “data collection”) and “data analyses” all as subheadings of the heading “methods”.	We made these changes as suggested
22	In lines 127-129: the authors mentioned that they eliminated sections with missing values. Did they test for the special autocorrelation of these values? Are the always link to certain type of vegetation? If so specify.	We did not test for autocorrelation because of the way we extracted the data (sections of 10 hr movements, fragments of the data set). What we did then was to calculate the mean for each individual walk and used that in the linear mixed model as suggested later on by the reviewer.
23	Are radio-collared animals always females? Specify sex.	Added numbers of males and females to the description
24	Lines 156 – 159: are the “walks” classified considering the difference in patch between the start and end position? Clarify in the text.	Yes we added “When an animal, at the end of a “walk”, ended up in a a) better forage patch we considered the movement as successful; b) the same we considered it as no change; and c) worse patch we considered it as unsuccessful.” to the text
25	Line 165: if I understood well, what they are comparing here is the mean walk distance PER INDIVIDUAL for different species? If so specify.	We specify this in the text: “To confirm whether ten hours of movement were indeed within a realistic distance range for the landscape scale in ours situation, we calculated and compared the mean distance between patches as well as mean animal “walk” distances per species.”
26	Lines 184-191: I am not aware of the exact algorithms used to calculate “r”, but is this method considering the intrinsic correlation between step length and	"Yes, we are aware that GPS error might affect directionality. To reduce the

	turning angles in the case of GPS data. The existent of a measure error in GPS data leads by default to higher turning angles when step lengths are shorter than when they are longer. See for example (Hurford, A. (2009) GPS measurement error gives rise to spurious, turning angles and strong directional biases in animal movement data. PLoS ONE, 4, e5632.). This could explain the fact that Zebra has more directional steps (just because they are larger steps)). Did the authors take this into account?	effect of GPS error we removed all the step lengths below 6 m from the analysis. We based our decision on the values repeating themselves indicating that the measurement error was strong. Hurford (2009) suggests removing step length up to 20 m but comments that the particular threshold would be specific to the system. We think that 20 m is threshold is too harsh for our data and therefore we decided to keep the text and analysis as is for our study." We looked at the literature on the Reyleigh test (there are several post 2009) and could find no reference that indicates the potential problem occurs when using this test for the purpose we used it for in our study. We therefore decided to keep the text and analysis as is for our study.
27	The paper could benefit from ANOVA's being replaced by Linear mixed models in which the single walks could be used as variable response and "the individual ID" is introduced as random factor, to account for non-independence of the data. The "herd" could be also added as random factor to account for the case of the eland with several marked individuals moving together.	Thank you for this suggestion. We conducted this test and it was indeed the better one to use. We did not include herd as a random factor because only two eland cows out of the 17 study animals were in the same herd. It would not have made sense.
28	In general results should be adapted a bit more to the more direct answering of the questions raised in the introduction.	We did adapt the results and discussion (see track changes)
29	Line 205: do you mean figure 3?.	Corrected
30	Table 4 is not necessary, because all the information given here is already in table 5, so I suggest removing and highlighting in "bold" the preferred models in table 5.	This is not relevant when following option 2 (as per above)

31	Lines 221-226, add unnecessary length to the text. I suggest removing them.	Removed. This is not relevant when following option 2 (as per above)
32	Line 230 (do you mean figure?).	This is not relevant when following option 2 (as per above)
33	Lines 284-287: wouldn't that mean that animals have more directional movements in the case of moving to a non-visible patch? Unfortunately that was not the case in your results... maybe rethink this explanation.	We removed this section
34	In legend form table, the authors mentioned table 6.3, but I didn't find this table in the manuscript.	This is not relevant when following option 2 (as per above)
35	Table 5: for coherence sake the results of the different visibility scenarios, could be presented in the same order as in the other tables (first within patch,etc…)	This is not relevant when following option 2 (as per above)
36	Figure 5: replace "visable" by "visible".	Corrected