­MEE-14-09-583 (Lucas et al.)

Responses to Referee's Comments

We thank both referees for their valuable and constructive comments. Please see our detailed response below. Line numbers refer to the revised manuscript unless otherwise stated. Citations in square brackets are to papers listed at the end of the current document.

Reviewer: 1  
  
Comments to the Corresponding Author  
It is rare that I have an opportunity to review such an potentially important paper  
  
My interest is in obtaining high quality monitoring data through large-scale citizen science. There are a number of challenges for bats and other taxa, but there have been some important and exciting developments in recent years for bats, including through other work by the authors here, that means that it is now possible to collect and analyse large volumes of acoustic data.  
  
With these data, an increasing number of projects are collecting such data, and there is challenge to do more with the information collected on bats passes, which are often used as a measure of relative abundance.   
  
For me, the most important development, would be to reliably infer true abundance from such data. This paper provides a novel approach to this problem.   
  
**Ref 1 Comment 1:** The main thing that I would like to see in this paper is discussion of other analytical approaches that could be applied to this problem. Practically, I would want to know whether the approach proposed here has significant advantages over other emerging alternatives. In particular, extensions of occupancy modelling have been applied to similar data where it is not possible to uniquely identify individuals, with the aim here as well of estimating true abundance, or at least to obtain a better understanding of relative abundance.  
  
Stanley & Royle 2005. Estimating site occupancy and abundance using indirect indices. Journal of Wildlife Management 69, 874-883.  
Guillera-Arroita & Morgan (2011). Species occupancy modelling for detection data collected along a transect. Journal of Agricultural, Biological, and Environmental Statistics 16, 301-317.

**Response:**

We agree that there is a large range of modelling options available to researchers, including occupancy models and its many extensions, and that choosing the correct analysis for your data is a vitally important stage in a study. We have therefore added lines 92-99 with some discussion o occupancy modelling and where it may be appropriate compared to the gREM. Occupancy modelling is a useful tool in the ecologist arsenal, however it includes a number of assumptions that may be difficult to justify and often throws away important information. The gREM directly estimates abundance and in this sense is simpler than occupancy modelling. Therefore we feel it is a better choice of model in many situations.

**Ref 1 Comment 2:** As discussed by the authors here, it would not be easy to field test how well this approach performs for species, such as bats, where this approach would be most valuable. I think that it is important to get this paper out now, but I would now like to see more extensive simulations next that do not assume an equal density across the area of interest, and make use of field data collected through tracking studies to consider how well the approach is likely to work in practice for different species. 

**Response: We agree that more extensive validation in the field and through simulations is an important next step for this method. However, specifically with respect to unequal densities, this should not have a strong effect as long as a number of sensors are being used and placed randomly in the environment (Hutchinson & Waser 2007).**

The only minor typo I can find it on page 13 (particularly).

**Response:** Line 353 changed accordingly.

Reviewer: 2

The paper presents a natural extension of the random encounter model (REM) (Rowcliffe

et al., 2008) and ideal gas model (Hutchinson and Waser, 2007) of animal encounters. Here,

the generalised random encounter model (gREM) is proposed to allow inference of absolute

density from passive acoustics and camera trap surveys. The incorporation of a variable

detection zone and directionality in animal signals is a useful development, especially for

analysis of acoustic survey data. However, the gREM does not account for uncertain de-

tection of animal signals (as other methods do) and assumes knowledge of mean animal

speed and directionality—requiring extra field work. Further, the gREM does not account

for possibly detecting the same animal multiple times, a common occurence with acoustic

surveys.

I think this paper provides a good step toward further generalising encounter models

to better reflect the reality to which they are applied. Yet, I also think, due to the method’s

limitations, that its applicability is still to be realised.

I have included some suggestions that I hope may help improve the paper.

General Comments

**Ref 2 Comment 1.** Increasing sample size improves precision: in lines 57–60, 290–295, 301–302 and 318–320, you describe how precision improves as the number of captures increases or the

signal/sensor width increases. For any reasonable estimator, one would expect its pre-

cision to improve as sample size increases; and so, could you make it clear that greater

precision for a higher number of captures is a familiar result? Furthermore, you say

that greater sensor/signal widths improve precision as if this were a seperate find-

ing, yet it again is due to the number of captures increasing—could this be explicitly

stated? The equivalency of the two results is implied in lines 371–372.

**Response:** We have added clarifications in lines 290-295 and 318-320 that greater sensor/signal widths improve precision because of their increased capture rate. We have added in lines 301-302 that the relationship between precision and number of captures is to be expected. “However, the precision was dependent on the number of captures across all four of the gREM submodels, where precision increases as number of captures increases, as would be expected for any statistical estimate”.

**Ref 2 Comment 2**. The effect of animal movement: in lines 60–61, you claim that different animal movement models have no effect on precision or accuracy of the gREM; however, this is

contingent on perfect knowledge of animal directionality and average speed. Further-

more, it has been shown that animals with highly tortuous paths reduce precision (Gu-

rarie and Ovaskainen, 2012). Could this claim be better qualified?

**Response: It is clear that, while tortuous paths can increase variance, they should not affect mean encounter rate (Hutchinson &Waser 2007, Gurarie and Ovaskainen, 2012). We have clarified this in lines 388-389. However, we think the reason this is not seen in our simulations is that we ran long simulations to test that, in the limit, tortuous paths do not bias results. We would expect higher variance in shorter runs.**

**@liz Really think this is begging the question “how do you know it's not biased with shorter sims. @Tim I will try to run some shorter sims to demonstrate this**

**Ref 2 Comment 3**. Double counting with acoustic detectors: in lines 388–395, you mention the possibility

of detecting the same animal multiple times and claim that this would not affect accuracy of the gREM. Multiple detections of the same animal is a common problem when estimating density from acoustic data. The gREM is derived assuming each detection is with a different animal, and so multiple detections of a single animal causes positive bias in the density estimate, as well as less precision. Not being able to account for multiple detections, gREM may not be applicable to many acoustic surveys, calling into question the claims made in lines 62, 318, 325–332. Could this limitation of the gREM be discussed in the paper? Could the model be improved?

**Response:** We agree that double counting is often a problem in acoustic surveys. However, the gREM is in fact modelling encounters per se, rather than number of individuals encountered, and so does not assume that each encounter is with a different individual (pg.340 in Hutchinson & Waser 2007). Another line of reasoning is to consider a population of one animal in a 1 x 1km square, with a sensor radius of 1km, animal velocity of 1km per minute and survey time of 1 minute. Then using the gas model equation (line 168), we would expect two encounters from the same individual. Conversely, if we experienced two encounters, we would predict an abundance of one. In this case, as the number of encounters is greater than the number of individuals, it is clear that the model is accounting for double counting. @marcus

**Ref 2 Comment 4**. Required knowledge of animal directionality and the detection zone: in lines 419–421, you state that perfect knowledge of animal directionality, animal speed, sensor width and sensor radius has been assumed. As such knowledge is often imperfect, it would be useful to know how misspecification would affect accuracy. The average profile can quickly change across boundaries (shown in Figure 4 of the paper) suggesting estimates would be sensitive to knowledge assumed. Also, you do not discuss how such measurements should be obtained as best survey practice. I think some practical advice would be useful if this method is to be applied.

**Response:** We assume the simplest case of perfect knowledge in our simulations. However, the average profile should not quickly change; although there are discrete boundaries, the function is actually smooth, with two models equalling each other across a boundary (see Figure 1). To confirm that the model is predictably sensitive to parameter estimates we have rerun the gREM on our simulations, with parameters that are 0%, 1% and 10% incorrect. A 10% inaccuracy in a parameter estimate gives a <15% error in the abundance estimate which we think is reasonable. Figures showing these results have been added to appendix S6.



Figure 1: The gREM evaluated on a 100 x 100 grid. Dark blues indicates values close to 2r while white indicates values close to 0. The smoothness of the function is apparent.

Best practices for parameter estimates are not trivial and will be parameter and system specific.

However we have added a paragraph (lines 399-411) that gives an overview of some methods and an entry into the literature.

@liz @kate really unsure about the paragraph I have added for this.

**Ref 2 Comment 5.**

**a)** Comparing gREM with existing methods: could other methods for acoustic data be better recognised within the paper?

**b)** Furthermore, could the comparison between gREM and existing methods be better explained? For example, in lines 87–100, existing methods are described as “require information that is often unavaliable”; however, the gREM also requires knowledge of mean speed and detection radius which may be as difficult to obtain.

**c)** Also, existing methods like distance sampling or existing capture-recapture allow for uncertain detection of animal signals whereas gREM assumes certain detection within the detection zone.

**d)** It would also be useful to include description of other current methods applied to acoustic data (Marques et al., 2013), for example, in lines 422–424; and to acknowledge the applicablity of these methods, for example, in lines 431–432 by saying gREM is another possible method one can apply instead of “gREM will make it possible”.

**Response:** We agree that there is a large range of modelling options available to researchers, including occupancy models and its many extensions, and that choosing the correct analysis for your data is a vitally important stage in a study.

**a)** We have added lines 92-99 with some discussion on occupancy modelling and where it may be appropriate compared to the gREM. This, along with the discussion of mark-recapture and distance sampling in lines 87-92, 132-136 and 437-477 largely covers the models discussed in (Marques et al., 2013) and abundance modelling more generally.

**b)** We note that there is a difference between the information required by gREM and that required by mark-recapture and distance sampling methods. The parameters in gREM need to be estimated only once. Therefore estimates from the literature can be used where appropriate. The information required by mark-recapture and distance sampling must be collected during surveys. We have noted in lines 87-88 that the information required for mark-recapture and distance sampling must be collected during the survey.

**c)** Detection probability is one of the important processes involved in estimating animal densities. The gREM does not ignore detection but it does deal with it in a different way to other methods which attempt to infer a detection probability from the animal count data. The gREM instead explicitly models some of the processes that lead to uncertain detection (i.e. even if an animal is present, it will only be detected if it is moving towards the sensor and will be missed otherwise.) We have added lines 371-377 that explain this difference and note that more detail could be added to account for other processes.

**d)** We have also clarified in line 456 that while there are other methods available, the different requirements of gREM mean it may be easier to apply than other methods rather than implying than it is the first and only method.

**Ref 2 Comment 6**. Wilcoxon signed-ranks test: in lines 256–258, 287–290, you use a Wilcoxon signed-ranks test to show that the gREM is accurate, however technically you only fail to reject

the null hypothesis that the median difference between the true and estimated density is zero, you do not accept the null hypothesis or prove it. I do not think this test is necessary. Is it not sufficient to report the estimated bias of the density estimator? A relatively small bias is indicative of an accurate estimator.

**Response:** We agree with this comment and have removed the Wilcoxon test.

We have therefore removed lines 256-258; 288-289; 299-300; 308-309; 311-312

**Ref 2 Comment 7**. Reported precision: in lines 302–303, 373–378, you state that the coefficient of variation falls to 10% for all submodels at 100 captures. This result is dependent on the simulation scenario considered and, further, it ignores the uncertainty in assuming average speed, signal width and sensor width. Could it be made clearer that in practice the coefficient of variation will be much higher due to non-linear animal movement, multiple detections of a single animal and uncertain knowledge of speed and directionality?

**Response:** In line 383 we have added an extra sentence to make clear that within live survey conditions it may take longer produce a precise result.

**Specific Comments**

1. Line 93: “gas model”— calling it the “ideal gas model” could be clearer and a citation,

useful. See (Hutchinson and Waser, 2007).

**Response:** We have called it the ideal gas model.

2. Line 160: “animals outside the zone are never captured”— could this be made clearer?

Animals outside that then move into the detection zone are captured.

**Response:** We have reworded this as “while outside this zone, animals are never captured.”

3. Line 228: what value does r take in the simulation? It would be useful to know for

reproducibility.

**Response: The radius of the sensor is 10 meters. This has been added to line 228 of the document: “A stationary sensor of radius $r$, 10m,”**

4. Line 237: “individuals were assigned 11 signal widths”— this sounds as if signal widths

were randomly allocated to each individual for every simulation; however, I think you

mean that a separate simulation was run for each signal width? Clarify?

**Response:** We have reworded as “11 signal widths α between 0 and π were used”

5. Line 242: σ d = vT10 — why was this standard deviation chosen? Is it because a normal

distribution was used to simulate a strictly positive parameter (distance)? Could a biological justification be given, as you do for the other simulation parameters chosen?

**Response:** σ d = vT/10 was chosen so that the standard deviation of the movement scaled with the speed of the movement. Line 242 has been changed to reflex this “standard deviation, σ d = vT/10 where the standard deviation was chosen to scale with the average distance travelled”

@Tim: I’m not sure about adding this to the MS, not sure that it makes sense

6. Line 243: “this is the largest day range”— here you refer to an average velocity while

day range is a distance, might be better to say average velocity was chosen based on a

day range of. . .

**Response:** Reworded in line with this comment.

7. Line 246: “or change direction (in a uniform distribution with maximum angle A)”— I

understand you are defining a correlated random walk, but this sentence could imply

you are sampling the new direction randomly from the interval (0, A). Clarify?

**Response: We agreed with your comments here and have changed line 246-247 to: “(where the change in direction has a uniform distribution with a maximum angle, A)”**

**@liz is something like “ change in direction has a uniform distribution in the interval [-A, A]) better?**

8. Line 249: Might be best to say it is a correlated random walk for (3) as you do later on

in the paper

**Response:** Reworded in line with this comment.

9. Line 251: “were counted as they moved in and out of the detection zone”— I assume

animals were only counted as they entered and not counted again as they left, also

animals initially inside the detection zone would also be counted.

**Response: We agreed that the wording here is confusing. Line 251 changed to “were counted as they moved into the detection zone”**

10. Line 253: “by assuming the number of captures per simulation” — Why would you

assume the number of captures? You obtain the number of captures from the simula-

tion. Clarify?

**Response: Assuming was a typo, and was meant to say “summing”, line 253 has been changed to reflex this.**

11. Line 256: “the density in the simulation”— better to say the true density to prevent

confusion with the density estimated from the simulated data?

**Response:** We have changed this to “by comparing the true simulation density with the estimated density” as suggested.

12. Line 266: “we calculated how long the simulation needed to run. . .” — do you mean

how long on average, as the formula applies to the expected number of encounters.

**Response: Line 266 changed to: “From a random starting point we ran the simulation until a range of different capture numbers were recorded (from 10 to 100 captures), recorded the length of time this took, and estimated the animal density for each of the four sub-models. “ Rather than run the simulation for a given time and calculate the number of captures, what we have done here is run the simulation for a given number of captures and calculate the amount of time it took.**

13. Line 269: “real density” — perhaps use true density for consistency?

**Response:** Edited to comply.

14. Line 271: “compare the precision between capture numbers” — I think more detail is

required: compare the precision of the density estimates from simulations with a differ-

ent expected number of captures.

**Response:** Edited as suggested.

15. Line 275: “using different amounts of time spent stationary” — should this not be the

time spent stationary on average? (This applies to all other instances of “time spent

stationary” in the paper.)

**Response:** Added 'average' in Fig.7 caption, line 275 and line 305.

16. Line 338: “the sum of the average animal velocity and the sensor velocity” — could be

clearer? It is the average animal velocity (averaged over all bearings) relative to a single

(animal or sensor) focal individual (Hutchinson and Waser, 2007).

**Response:** Hopefully made clearer by changing wording to “expanded for moving sensors by replacing $v$ as used here with the average animal speed added to the sensor speed”

17. Lines 388–395: you begin by saying accuracy may be affected by the interaction between the movement model and detection zone, then end saying the opposite, in brackets.

**Response: Line 388 have changed accuracy to precision. It is correct to point out that the accuracy of the model should not be affected by this interaction, however the precision of the model would be.**

18. Line 411: “entire world”— better to say study area?

**Response:** We agree and have changed to match this suggestion.

19. Line 416: “The distance travelled for an animal was assumed to be 40 km day −1 ”—

technically 40 km day −1 is a speed, also isn’t this the average distance per day?

**Response: Completely agreed with this as a comment. Line 416 changed to: “In the simulation animals moved at a speed of 40km day-1, equivalent to the largest day range** **of terrestrial animals”**

Editorial Comments

1. Line 167: Typo — “number of expected captures” should say expected number of cap-

tures.

2. Lines 174-176: this sentence does not make sense.

3. Line 226: perhaps better not to start a sentence with a number? Might be better to use

words: one hundred.

4. Line 228: “exact centre of the simulation”— does this mean the centre of the simulated

study area?

5. Line 241: better not to start a sentence with a mathematical symbol?

6. Line 245: Typo — At the end of each step

7. Lines 255, 258: perhaps better to not start a sentence with lower-case “g” in gREM?

8. Line 282: this sentence does not make sense.

9. Line 310: “pi” — use symbol π

10. Line 430: “which are important reservoir of infectious disease”— reword? For exam-

ple, which are an important reservoir of infectious diseases

**Response: We have corrected all these editorial mistakes.**

**Literature Cited**

Hutchinson, J.M.C. & Waser, P.M. (2007) Use, misuse and extensions of “ideal gas”

models of animal encounter. Biological Reviews of the Cambridge Philosophical Society, 82, 335–359