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ORIGINAL RESEARCH

How many sequences should I track when applying the random encounter model to camera trap data?

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Abstract

The random encounter model (REM) is a camera trapping method to estimate population density (i.e. number of individuals per unit area) without the need for individual recognition. The REM can be applied considering camera trap data only by tracking the passages of animals in front of the camera (i.e. sequences). However, it has not been assessed how the number of sequences tracked (i.e. trajectory of the animal reconstructed) influences the REM estimates. In this context, we aimed to gain further insights into the relationship between the number of sequences tracked and reliability in REM estimates to optimize its applicability. We monitored multiple species using camera traps, and we applied REM to estimate population density. We considered red fox Vulpes vulpes, roe deer Capreolus capreolus, fallow deer Dama dama, red deer Cervus elaphus and wild boar Sus scrofa as model species. We tracked from a minimum of 154 (red fox) to a maximum of 527 (red deer) sequences per species, and we then sampled the dataset to simulate different scenarios in which a lower number of sequences were tracked (20, 40, 80 and 160). We also assessed the effect of adjusting the survey period to the minimum necessary to record the desired number of sequences. Our results suggest that tracking around 100 sequences returns a precision level equivalent to the one obtained by tracking a considerably higher number of sequences and reduced and optimized the human effort necessary to apply REM. Tracking less than 40 sequences could result in low precise density estimates. Our results also highlighted the relevance of considering study periods of ca. 2 months to increase the number of sequences recorded and tracking a random sample of them. Our results contribute to the optimization and harmonization of REM as a reference method to estimate wildlife population density without the need for individual identification. We make clear recommendations on the cost-effective sample size for estimating REM parameters, optimizing the human effort when applying REM, and discouraging REM applications based on low sample sizes.

Introduction

The random encounter model (REM) is currently the most applied camera trapping method to estimate population density when monitoring populations in which individual recognition is not possible (Gilbert et al., 2021; Palencia et al., 2022). Briefly, the REM is based on modelling the process of random encounters (sequences) between the individuals in the population and the fixed detectors with which the population is been monitored (typically camera traps). Thus, accounting for the variables that affect the number of animal encounters (namely camera trap detection zone and average daily distance travelled by the individuals in the population, the day range), the REM scales the number of encounters to population density (i.e. the number of individuals per unit area) (Rowcliffe et al., 2008):

$$D = \frac{y}{t} \frac{\pi}{a \cdot s \cdot r \cdot (2 + \theta)} \tag{1}$$

where y is the number of encounters, t is the total survey effort, a is the activity level (proportion of time spent active), s is the travel speed (average speed of travel while active), r is the effective detection radius, and θ is the effective detection angle. Encounter rate is the ratio between the number of encounters

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and survey effort (y/t); day range is the product between activity level and speed $(a \cdot s, \text{Rowcliffe et al., 2016})$, and the detection zone is defined by the effective detection radius (r) and angle (θ) .

The REM was initially described by Rowcliffe et al. (2008). Since then, the REM has been broadly applied to estimate wildlife population density (Barroso et al., 2023; Kavčić et al., 2021; Pfeffer et al., 2018; Schaus et al., 2020; Wearn et al., 2022). Some studies have also focused on the statistical development of the method (Lucas et al., 2015; Wearn et al., 2022), the description of R packages and/or R function to implement REM analysis (Caravaggi, 2017; Palencia, Fernández-López, et al., 2021; Rowcliffe et al., 2011) and how to deal with the animal reaction to camera traps (Delisle et al., 2023). The reliability of REM was also compared with density estimates obtained using reference methods such as distance sampling and spatially explicit capture-recapture (Palencia et al., 2022), and the drivers determining the precision of the density estimates have been also explored (Henrich et al., 2022; Palencia et al., 2022; Rowcliffe et al., 2008). In this respect, it has been described that variability in the encounter rate (individuals detected per unit of sampling effort) is the main factor contributing to the final variability in the density estimate (Henrich et al., 2022; Palencia et al., 2022). In this respect, a relationship between population aggregation and precision, and 60 camera trap placements are recommended when monitoring highly aggregated populations to achieve acceptable precision (i.e. coefficient of variation below 0.20, Palencia et al., 2022; Rowcliffe et al., 2008). For lower levels of population aggregation, a lower number of placements could also result in coefficient of variation close to 0.20.

Other studies have been focused on assessing and describing accurate procedures to estimate REM parameters from camera trapping data (Hofmeester et al., 2017; Palencia, Fernández-López, et al., 2021; Rowcliffe et al., 2011, 2016). Briefly, to estimate travel speed (s) and the detection zone (r and θ) from camera trap data, it is necessary to reconstruct the trajectory of the individuals when crossing the field of view of the camera (hereafter track the sequence). From the tracked data, the location of the individual when the animal entered field of view is used to estimate the detection zone (Rowcliffe et al., 2011), and the length of the trajectory divided by the duration of the sequence is used to estimate the travel speed (Palencia, Fernández-López, et al., 2021; Rowcliffe et al., 2016). Despite the possibility of estimating the REM parameters from camera trap data increases the applicability of the method (Palencia et al., 2022; Rowcliffe et al., 2016), this also involves a great human effort in fieldwork (because it is necessary to calibrate the field of view of the cameras), and in the office (because it is necessary to track the location of the individuals recorded in each picture). However, it has not been assessed how the number of sequences tracked to estimate REM parameters influences the accuracy (how close the densities estimated are to their true value) and precision (how close the densities are to each other). Here and throughout the paper, we considered a sequence as a passage of an individual in front of the camera.

Considering all the above, the REM has been well received by the scientific community. The efforts focused on harmonizing the method as well as improving the estimation of REM parameters using exclusively camera trap data have contributed to its acceptance and growing number of applications. The REM is considered the reference method in a European initiative to monitor terrestrial mammal population density (Guerrasio et al., 2023). In this respect, two main practical limitations emerge when applying the REM: (1) the image processing; and (2) the human effort necessary to track the sequences to lastly estimate REM parameters. Regarding the former, it is a habitual limitation in any camera trapping study, but artificial intelligence has considerably reduced the human effort needed to process the pictures, and some models already classify pictures by species with accuracies higher than 0.95 (Beery et al., 2019; Rigoudy et al., 2023). Regarding the latter, further work is needed to better understand the relationship between the number of sequences tracked and precision or accuracy. The number of sequences tracked in published REM studies ranges from 6 to more than 400 (e.g. Barroso et al., 2023; Rovero & Marshall, 2009; Schaus et al., 2020). Tracking too few sequences could compromise precision and accuracy in density estimates, while tracking too many could reduce cost-effectiveness.

In this context, we aimed to provide further insights into the relationship between the number of sequences tracked and reliability in REM estimates to optimize its applicability. Our specific objectives were (1) to identify the most efficient number of sequences to be tracked in terms of human effort and precision; and (2) to evaluate if it is more appropriate to adjust the survey period to the minimum necessary to achieve the desired number of sequences, or to consider a longer survey period and track a random selection of the sequences recorded.

Materials and methods

Study area

The study was conducted in the Pyrenees, northern Spain (Lat: $42^{\circ}36'$ N, Long: $1^{\circ}16'$ W), where we monitored an area of 1000 hectares from 27 March to 26 June 2023. The area was characterized by a homogeneous forest of *Pinus uncinata* and *Pinus sylvestris*, with some *Quercus* forest at the lowest altitudes. We covered an altitudinal range from 940 to 2292 m.a.s.l.

Camera trap survey and image processing

Twenty-eight camera traps (Tetrao Spromise S308) were randomly deployed, placed heading towards the north, 50 cm above ground, and with the sensor angled parallel to the slope. Cameras were set to be operative 24 h per day, to record a burst of 10 consecutive pictures at each activation, with the minimum time gap between consecutive activations. Nocturnal pictures were illuminated with infrared flash (low glow). Cameras were checked once to check the status of the batteries and memory cards.

The pictures were filtered to discard false activations using Megadetector (Beery et al., 2019) and subsequently processed in the open software TrapTagger (https://wildeyeconservation.org/trap-tagger-about/) to classify the pictures by species. To

estimate the locations of the animals in the field of detection, we applied a photogrammetry approach (Palencia et al., 2023; Wearn et al., 2022). The photogrammetry approach describes the relationship between the size of the calibration object in the image (in pixels) and its actual size and distance from the camera; and the relationship between X-Y pixel position in the image and the angular distance from the camera's principal axis. To use photogrammetry, it is necessary to calibrate each camera deployment and the camera model. The camera model (here Tetrao by Spromise S308) was calibrated once by taking 15 images of the calibration pole (here a one-meter-length pole with marks at 20 cm intervals) at known distances from the camera (maximum 15 m) and from the centre to the laterals of the field of view. In the field, each camera deployment was calibrated by recording 15 pictures of the calibration pole across the field of view and spaces 1-2 m apart. We finally digitized the images to extract the pixel position of the animals in the open-source tool AnimalTracker (https://github.com/ lauraVzarco/animaltracker). To apply REM, we recorded the pixel position of all the individuals when entering the detection zone, and we also reconstructed the trajectory of those individuals that did not react to the presence of the camera. Pixel positions were later transformed to animal-to-camera distances and angles using the CTtracking package in R (https://github. com/MarcusRowcliffe/CTtracking).

Random encounter model parameter estimation

From the REM parameters described in equation 1, three of them (y, number of encounters; t, survey effort; and a, activity level) do not need to track the sequences for its estimation. The number of encounters (y) was measured by counting each time an individual entered the detection zone. Survey effort (t) was measured as the summation of all the days in which each camera was operating in the field. To estimate activity level (a), it is only necessary to capture the time of detection in which each individual was recorded by the camera. We estimated activity level using the 'activity' package in R and fitting circular distribution to the time in which animals were detected (Rowcliffe et al., 2014).

Tracking the animals recorded is necessary to estimate the effective detection zone (r and θ) and the travel speed (s). To estimate the effective detection zone, we used 'Distance' package in R and we fitted distance sampling models to the radius and angle in which each individual was first detected (Buckland et al., 2001; Rowcliffe et al., 2011). To estimate travel speed, we estimated the average speed by using 'trappingmotion' package in R (Palencia, 2020). Sequences in which the animals reacted to the camera (e.g. inspecting the camera and fleeing in response to being detected) were not considered in the speed estimation. Day range was estimated by multiplying activity level and average speed (Palencia, Fernández-López, et al., 2021; Rowcliffe et al., 2016). The R code to replicate the REM analysis can be found here: https://github. com/PabloPalencia/CameraTrappingAnalysis/tree/main/REM. The variance of the density was estimated incorporating the variance of all the parameters. Standard error of density was estimated by multiplying the mean density value by the square root of the squared coefficients of variation of each of the REM parameters. The coefficient of variation of density (standard error divided by the mean) and the 95% log-normal confidence interval of the density were also estimated.

Relationship between the number of sequences tracked and precision

Here and in the next section, we considered as gold reference the population density value estimated considering all the sequences tracked and the entire survey period ('golddensity'), a habitual procedure when optimizing camera trapping protocols (Kays et al., 2020). We considered as model species those with more than 150 sequences tracked, namely red fox -Vulpes vulpes-, roe deer -Capreolus capreolus-, fallow deer -Dama dama-, red deer -Cervus elaphus- and wild boar -Sus scrofa-. To evaluate the effect of the number of sequences tracked into the density precision, we sampled with replacement the data for each species. Specifically, we randomly selected 20, 40, 80 and 160 tracked sequences from the full dataset of each species, and we replicated each random sampling six, four, two and one times, respectively. The number of replicates decreases as the number of sequences increases to ensure independence among replicates. For instance, for a given scenario in which 200 sequences were tracked, two replicates of 20 sequences were independent, but two replicates of 160 sequences will not be independent. From these subsampled data sets, we estimated the speed (s) and detection zone (radius -r- and angle $-\theta$ -), and we then applied REM considering the entire data set of each species to estimate the encounter rate (y/t) and activity level (a), for which density ('subsample density') was estimated.

To assess the effect of the number of sequences tracked in precision, we fitted a linear model with Gaussian distribution and identity link function including the coefficient of variation of the density (CV) as response. The interaction between the number of sequences tracked and the species (as a factor) was included. We fitted four models in which the CV and/or the number of sequences tracked were log-transformed (i.e. Model 1: $CV \sim \log(n \text{ seq tracked})^*$ species; Model 2: $CV \sim n \text{ seq}$ tracked*species; Model 3: $\log(CV) \sim \log(n \text{ seq tracked})^*$ species; and Model 4: $\log(CV) \sim n \text{ seq tracked}^*$ species). The best model was selected based on R-squared value. The assumptions of normality, homogeneity and independence in the residuals were assessed following Zuur et al. (2010).

Relationship between survey length and REM estimates

Working on the results obtained in the previous section, we now explored if there were some differences between (1) reducing the survey period to the minimum necessary to record the desired number of sequences, and then tracking all the sequences recorded to estimate REM parameters; and (2) considering the entire survey period (83 days) for encounter rate estimation and activity level, and a random sample of the total number of sequences to estimate speed and detection zone. Due to the low sample size, no linear model was fitted, and these results were discussed considering point estimates and log-normal 95% confidence intervals overlapping.

Results

From the entire study period and all the sequences tracked, we estimated the population density of wild boar (6.58 ind·km⁻², 0.17 coefficient of variation -CV-), roe deer (7.85 ind·km⁻², 0.17 CV), red deer (6.48 ind·km⁻², 0.23), fallow deer (6.07 ind·km⁻², 0.32) and red fox (3.01 ind·km⁻², 0.33), with an average of 309 sequences tracked per species (min: 154 -red fox-, max: 527 -red deer-). A table including all REM parameters can be found in Appendix S1.

Relationship between the number of sequences tracked and precision

The best model was that included log-transformed CV and number of sequences tracked ($R^2 = 0.74$). The rest of the models have R^2 values lower than 0.65 (Appendix S1). We observed a strong negative relationship between the number of sequences tracked and the coefficient of variation (Fig. 1, Table 1). As the number of sequences tracked increased, the coefficient of variation decreased (i.e. precision increased). This pattern was especially noticeable when less than 100 sequences were tracked and was observed in all the species (Fig. 1, Table 1).

Considering all the above, 100 sequences could be the number of sequences to be tracked that did not compromise precision, but optimized the applicability of REM by reducing the analysis effort. **Table 1** Results of the linear model used to evaluate the relationship between the number of sequences tracked (n_seq_ tracked, logtransformed) and the species with the precision (measured as coefficient of variation, log-transformed) in random encounter model densities

| | Estimate | SE | t-value | P-value |
|--------------------------------|----------|-------|---------|---------|
| Intercept | -0.511 | 0.205 | -2.491 | 0.0156 |
| log(n_seq_tracked) | -0.121 | 0.054 | -2.245 | 0.029 |
| Red fox | -0.140 | 0.318 | -0.441 | 0.661 |
| Red deer | 0.050 | 0.269 | 0.185 | 0.854 |
| Roe deer | -0.117 | 0.276 | -0.423 | 0.674 |
| Wild boar | 0.346 | 0.281 | 1.231 | 0.223 |
| log(n_seq_tracked) x red fox | 0.030 | 0.086 | 0.347 | 0.730 |
| log(n_seq_tracked) x red deer | -0.043 | 0.070 | -0.615 | 0.541 |
| log(n_seq_tracked) x roe deer | -0.088 | 0.072 | -1.212 | 0.231 |
| log(n_seq_tracked) x wild boar | -0.181 | 0.074 | -2.460 | 0.017 |

The fallow deer was considered as the reference category. Bold highlight significant values.

Relationship between survey length and REM estimates

Based on the above results, we sampled our database to obtain independent periods in which ca. 100 sequences were tracked (hereafter periods). The number of periods and survey length depend on the species. While it was only possible to consider one period for red fox, five independent periods (about 15 days long) were considered for red deer. On average, we considered 103 sequences in each period considering all the species (Appendix S1). Alternatively, we also estimated densities considering the entire survey period but randomly selecting 100 tracked sequences to estimate speed and detection zone. Regarding precision, the results showed similar precision



Figure 1 Predicted values for the coefficient of variation in relation to the number of sequences tracked from the linear models fitted including the number of sequences tracked and the species as predictors. Shaded bands represent 95% confidence intervals.

between the gold reference (i.e. using all the sequences tracked and the entire survey period to estimate density) and the approach in which only 100 sequences were used to estimate speed and detection zone, and the entire survey period to estimate encounter rate and activity level (Fig. 2, Appendix S1). The difference in CV between both approaches was lower than 0.05 in all the species (Appendix S1). However, when defining the survey period to the minimum necessary to record 100 sequences. CVs were higher (i.e. lower precision) in comparison with the gold reference (Appendix S1). For instance, for red deer, the gold reference CV was 0.23, while the average CV for the subsampled periods was 0.35 (min: 0.29, max: 0.39). Similar patterns were observed in the other species. Regarding the consistency in the point estimate among approaches (proxy of accuracy), considering the entire survey period resulted in more similar density estimates in comparison with considering short periods (Fig. 2).

Discussion

Our results suggest that tracking ca. 100 sequences and increasing the survey period to consider a higher sample size for the estimation of encounter rate and activity level was the most cost-effective and reliable approach when applying the REM to estimate population density. On the contrary, monitoring periods shorter than 1 month could not be recommended (even when 100 sequences are recorded).

Previous studies have assessed the effect of sample size in the estimation of REM parameters, but the effect on density precision had not been assessed before. For instance, a minimum of 60–80 observations are recommended to fit distance sampling models (Buckland et al., 2001). Here, we have shown that tracking around 100 sequences returns a precision level equivalent to the one obtained by tracking a considerably higher number of sequences (Fig. 1, Table 1) and reduced the human effort necessary to apply REM. Regarding precision, we found that the coefficient of variation (CV) have an inflexion point when ca. 100 sequences were tracked, after which increasing the number of sequences tracked makes little difference (Fig. 1). This result could be explained considering the intrinsic variation in encounter rate. It is well established that most of the variance in REM is attributable to the variation in encounter rate between camera trap placements (Palencia et al., 2022; Palencia, Rowcliffe, et al., 2021; Rowcliffe et al., 2008). Thus, while tracking ca. 100 sequences optimized the precision in the detection zone and speed, any further improvement could be masked by the variability in the number of encounters among camera trap placements. The random designs necessary to apply REM imply an inhomogeneous number of detections on each placement, and the encounter rate is usually very aggregated (Palencia et al., 2022). Recent studies suggest that rotating the cameras to new placements during the survey period contributes to obtaining more precise encounter rates (Palencia et al., 2024). It is worth noting that we achieved CV ca. to 0.20 (min: 0.17, max: 0.33) sampling 28 placements. While a higher number of placements is usually recommended for this level of precision, the small size of our study area (10 km²) together with the low variability of habitats (continuous pine forest) could explain this result.

Regarding the survey period, reducing the survey length to the minimum necessary to record ca. 100 independent sequences could compromise REM reliability, resulting in low precision and potentially biased density estimates (Fig. 2). When monitoring abundant populations, 100 sequences could be recorded in relatively short survey periods (e.g. 2 weeks). The variability in density estimates when considering short survey periods can be explained by considering the minimum period necessary to obtain a reliable encounter rate. Kays et al., 2020 found that



Figure 2 Density estimates obtained (1) considering all the sequences tracked during the entire survey period (gold), (2) subsampling the survey period until the minimum necessary to record 100 sequences (green); and (3) considering the entire survey period but tracking 100 random sequences (blue). Error bars represent 95% log-normal confidence intervals.

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encounter rates were highly variable for the first 2 weeks of camera deployments, and from about 1 month onwards, estimates were within 10% of the estimate from the 60-day samples. Thus, when applying REM, the recommended protocol could be to increase the survey period to ca. 2 months, consider all the sequences for the estimation of encounter rate and activity level, and randomly select and track 100 sequences to estimate detection zone and travel speed (Fig. 2). The selection of the 100 sequences must be done randomly. On the contrary, selecting all the sequences from a single (or few) camera placement and/or a specific period (e.g. beginning of the survey period) could lead to biased REM parameters, and in consequence, biased densities. For instance, tracking 100 sequences in a camera placed in a grassland could lead to an over-sampling of the slow movements of herbivores while feeding (Palencia, Fernández-López, et al., 2021; Rowcliffe et al., 2016), and an over-sampling of long detection distances in comparison with those expected in a denser vegetation habitat (Hofmeester et al., 2017). We also do not recommend considering survey periods longer than 2-3 months because the variability in natural resources (e.g. primary production) and/or management or conservation actions (e.g. hunting season) could contribute to a variation in the true population density and/or spatial aggregation of the individuals.

Our results came from four ungulates species and one carnivore. Replicating the study by including species with different behavioural and ecological traits, such as rodents, could be appreciated. Similarly, independent and reliable density estimates could be useful to assess the effect of the number of sequences tracked in accuracy.

In conclusion, our results support the recommendation of tracking ca. 100 sequences when applying REM to estimate wildlife population density from camera trapping data. Ideally, the survey period could be ca. 2 months, and survey periods shorter than 1 month are not recommended. Similarly, applying REM when less than 40 sequences were tracked could not be recommended because low precise estimates are expected. Our results contribute to the optimization and harmonization of REM as a reference method to estimate wildlife population density without the need for individual identification.

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Author contributions

P. Palencia: Funding acquisition; conceptualization; data curation; formal analysis; writing – original draft; project administration. **P. Barroso:** Data curation; writing – review and editing.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability statement

The datasets generated during and/or analysed during the current study will be available in Appendix S1 after paper acceptance.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Tables with random encounter model parameters.