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Random encounter model is a reliable method for estimating population density of multiple species using camera traps

Pablo Palencia[1], Patricia Barroso[1], Joaquín Vicente[1], Tim R. Hofmeester[2], Javier Ferreres[1] & Pelayo Acevedo[1]

[1]Instituto de Investigación en Recursos Cinegéticos (IREC) CSIC-UCLM-JCCM, C/Ronda de Toledo 12, 13071, Ciudad Real, Spain
[2]Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, SE-90183, Umeå, Sweden

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Correspondence
Pablo Palencia, Instituto de Investigación en Recursos Cinegéticos (IREC) CSIC-UCLM-JCCM, C/Ronda de Toledo 12, 13071 Ciudad Real, Spain. Tel: 926295450 - Ext: 96015; Fax: 34 926 295 451; E-mail: palencia.pablo.m@gmail.com

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Abstract

Population density estimates are important for wildlife conservation and management. Several camera trapping-based methods for estimating densities have been developed, one of which, the random encounter model (REM), has been widely applied due to its practical advantages such as no need for species-specific study design. Nevertheless, most of the studies in which REM has been assessed against referenced methods have sampled one population, precluding evaluation of the circumstances under which REM does or does not perform well. At this point, a review of all REM assessments could be useful to provide an overview of method reliability and highlight the main factors determining REM performance. Here we used a combination of literature review and empirical study to compare the performance of REM with independent methods. We reviewed 34 studies where REM was applied to 45 species, reporting 77 REM-reference density comparisons; and we also sampled 13 populations (ungulates and lagomorphs) in which we assessed REM performance against independent densities. The results suggested that appropriate procedures to estimate REM parameters (namely day range, detection zone and encounter rate) are mandatory to obtain unbiased densities. Deficient estimates of day range and encounter rate lead to an overestimation of density, while deficient estimates of detection zone conducted to underestimations. Finally, the precision achieved by REM was lower than reference methods, mainly because of the high levels of spatial aggregation observed in natural populations. In this situation, simulation-based results suggest that c. 60 camera placements should be sampled to achieve acceptable precision (i.e. coefficient of variation below 0.20). The wide range of situations and scenarios included in this study allow us to conclude that REM is a reliable method for estimating wildlife population density when using appropriate estimates of REM parameters and sampling designs. Overall, these results pave the way to wider application of REM for monitoring terrestrial mammals.

Introduction

Together with occupancy and species richness, population density (i.e. the number of individuals per unit area) is a key state variable in wildlife management and conservation (Nichols & Williams, 2006). However, obtaining such information is particularly difficult in some wildlife species due to low detectability, usually associated with low population density, elusive behaviour and certain habitat features, among others (Kindberg et al., 2009). A plethora of methods (e.g. distance sampling or spatial capture–recapture [SCR]) have been developed to estimate wildlife population density (e.g. Borchers et al., 2002; Seber, 1982). Moreover, comparative studies assessing methods' performance and reviews of their applicability to different species have also been developed (e.g. Acevedo et al., 2008; ENETWILD consortium et al., 2019; Meriggi et al., 2008). In this connection, a recent review concluded that, in general, camera traps are an effective sampling tool when compared with alternative ones to collect data about medium-to-large ground-dwelling mammals and birds (Wearn & Glover-Kapfer, 2019). Camera traps allow highly standardized data collection on multiple species with minimal disturbance to wildlife, and do not require expert knowledge for their basic use. From camera trap data, a wide range of methods can be applied to estimate population density (Rovero & Zimmermann, 2016).

In this context, the use of camera traps has been firmly established in recent decades among the non-invasive tools available to support monitoring programmes for wildlife population density (Delisle et al., 2021). Initially, the estimation of population density from camera trap data was earlier limited to marked populations (i.e. those where animals can be identified individually by natural or artificial marks) when capture–recapture methods are applied (Royle et al., 2013). However, most wildlife species do not have natural marks that enable individual recognition (hereafter unmarked species). To monitor unmarked populations with camera traps, physical capture has been required for individual tagging, which greatly limits the applicability of capture–recapture methods. Some of its main limitations are as follows: (i) ethics committee approval is required for the capture of animals; (ii) highly qualified staff are needed (e.g. vets to anaesthetize the animals); (iii) the economic costs and human effort associated with the capture and tagging of animals are high and (iv) it defeats the non-invasive nature of camera traps and could harm the animals. Against this background, methods to estimate population density without the need for individual identification emerged (see Gilbert et al., 2020 for a review). Specifically, Rowcliffe et al. (2008) described the random encounter model (REM).

The REM is based on modelling random encounters between moving animals and static camera traps, taking into account key variables that affect the encounter rate (i.e. number of animals detected per sampling unit). These variables are camera detection zone, defined by its radius and angle, and the daily distance travelled by an animal in the population (hereafter, day range). The main advantage of REM is that individual identification is not needed, so then REM can be used to monitor both unmarked and marked populations without the need to capture and tag animals. Additionally, since the survey design is not based on target species (i.e. it is not needed that animals have a reasonable chance of being detected at more than one camera, so camera spacing is not determined by target species), more than one species can be potentially monitored during the same survey (Palencia, Rowcliffe, et al., 2021; Pfeffer et al., 2018). For all the above reasons, REM is one of the most widely used methods to estimate population density of unmarked populations today (Gilbert et al., 2020)' and has been recommended when tested against other methods. For instance, when problems related to burst mode performance in the camera are observed (Palencia, Rowcliffe, et al., 2021). In these scenarios, bias is expected in other methods such as camera trap distance sampling because some photos are not recorded at the predetermined snapshot moments (Howe et al., 2017).

The application of REM was originally limited because of the difficulties of estimating the parameters necessary to apply the method, especially day range (Nakashima et al., 2018; Rovero & Marshall, 2009). In recent years, however, procedures have been described for estimating all the parameters required considering camera trap data only (Hofmeester et al., 2017; Palencia, Fernández-López, et al., 2021; Rowcliffe et al., 2011, 2016). These studies clearly improved the applicability of the method and are increasing its use in wildlife monitoring (Palencia, Rowcliffe, et al., 2021; Pfeffer et al., 2018). Other studies have focused on the statistical development of the method and software development (Caravaggi, 2017; Jourdain et al., 2020; Lucas et al., 2015). The REM has been used in species with different behavioural and ecological traits, and c. 30 REM studies have been published so far. For instance, it has been compared against reference densities on gregarious and non-gregarious carnivores (e.g. lion *Panthera leo*, Cusack et al., 2015; red fox *Vulpes vulpes* Palencia, Rowcliffe, et al., 2021), ungulates (e.g. Grevy's zebra *Equus grevyi*, Zero et al., 2013; chamois *Rupicapra rupicapra*, Kavčić et al., 2021; moose *Alces alces* and roe deer *Capreolus capreolus*, Pfeffer et al., 2018), lagomorphs (e.g. European hare *Lepus europaeus* and Irish hare *Lepus timidus hibernicus*, Caravaggi et al., 2016) and Eulipotyphla (e.g. European hedgehogs *Erinaceus europaeus* Schaus et al., 2020), among others. Nevertheless, (i) most studies have monitored only a single species/population, precluding evaluation of the circumstances under which REM does or does not perform well (but see Rowcliffe et al., 2008; Pfeffer et al., 2018; Palencia, Rowcliffe, et al., 2021) and (ii) some of them have considered bibliographic data for some of the parameters required to derive densities which may introduce bias (Caravaggi et al., 2016; Cusack et al., 2015; Manzo et al., 2012). Broadly, most of these studies reported comparable results (Pfeffer et al., 2018; Rowcliffe et al., 2008; Schaus et al., 2020), but others reported considerable discrepancies (Chauvenet et al., 2017). Thus, a global overview of all the available comparisons between REM and reference densities is timely to provide further insights into which factors determine the performance of this method.

This study aimed to provide a comprehensive view of REM performance across a wide range of species/populations with different behavioural traits and a large range of densities and evaluate which factors determine REM reliability. We did this by comparing the densities obtained with REM with those obtained with other independent reference methods, mainly drive count, SCR and distance sampling (see below). We reviewed published studies on REM and sampled 13 populations. By discussing its strengths and weaknesses when monitoring wild populations, the results reported here allowed us to draw robust conclusions about the potential of REM for monitoring wildlife populations.

Materials and Methods

Review of published studies

We reviewed all applications of REM reported in published peer-reviewed studies. The results were retrieved in March 2022 by searching the Scopus, PubMed and Web of Science databases using “random encounter model”, “unmarked” and “density” as keywords. Of all the studies retrieved during the search, we were focused on those in which REM had been compared against a reference method. From these studies, we extracted the mean value of the estimated densities for both methods, the target species, the independent method considered and the number of camera trap placements sampled (see Appendix S1). Additionally, we evaluated the procedures used to estimate REM parameters (detection zone, day range and encounter rate). We considered two categories: appropriate and deficient. For instance, and considering the day range as an example, we considered as ‘deficient’ quality those cases in which day range values were imported from other populations, because of the expected variation in movement behaviour among populations. Moreover, those cases in which day range was estimated for the target population using telemetry data but without accounting for tortuosity were also considered as ‘deficient’ quality. Day range is expected to be underestimated (e.g. Marcus Rowcliffe et al., 2012). We considered as ‘appropriate’ quality those cases in which day range was estimated for the target population by (i) using telemetry data and accounting for tortuosity (Marcus Rowcliffe et al., 2012), (ii) applying the camera trap-based method (Palencia, Fernández-López, et al., 2021; Rowcliffe et al., 2016) or (iii) when observers followed animals and recorded the total distance covered (Cusack et al., 2015; Rowcliffe et al., 2008). Further details about the criteria considered for detection zone and encounter rate, as well as the qualification reported to each study are shown in Appendix S1. We did not consider precision in density estimates in the published studies because most did not adequately describe how they were estimated (e.g. whether or not they accounted for variance in all parameters) or reported explicitly that they had not considered precision in some of the measured variables (e.g. Balestrieri et al., 2016; Garrote et al., 2021; Pfeffer et al., 2018).

Field surveys

Study areas and target species

We sampled wild mammal populations at six sites in Spain. These included a protected area (site A), three fenced hunting estates (sites B, C and D) and two open areas where cattle farming and hunting were the main uses (sites E and F). Site A was located in southern Spain (Doñana National Park), sites B, C, D, E and F were located in two mountain chains in central Spain: the Montes de Toledo (B, C and D) and the Sistema Central (E and F). Although sites C and D are situated next to each other, we considered them as two independent study areas, because they were fenced off and separated by a road. Sites E and F were sampled over two consecutive years. Further details of the environmental characteristics of the sampled sites are given in Appendix S2.

For the target species, we sampled 13 wild populations (Table 1), including five species of ungulates (red deer *Cervus elaphus*; roe deer *C. capreolus*; fallow deer *Dama dama*; mouflon *Ovis musimon*; and wild boar *Sus scrofa*) and one lagomorph (Iberian hare *Lepus granatensis*). Each population was surveyed applying REM alongside an independent reference method (Fig. 1) for comparative purposes in terms of precision (coefficient of variation, CV) and consistency in average density values (see details below). Both surveys overlapped spatially and temporally.

REM: rationale and surveys

The REM models the encounters between animals and passive detectors (here camera traps) without the requirement for individual identification of animals (Rowcliffe et al., 2008). The REM equation is:

$$D = \frac{y}{t} \cdot \frac{\pi}{v \cdot r \cdot (2 + \theta)}$$

where y is the number of encounters, t is the total survey effort, v is the day range and r and refer to the effective radius and angle of the camera detection zone, respectively. To estimate encounter rate, we considered each time that an individual of the target species entered the detection zone of the camera trap as a new encounter. Day range was estimated following Palencia, Rowcliffe, et al. (2021) using the activity v.1.3.1 and trappingmotion

Table 1. Summary of REM surveys.

Site	Species	No. CT placements	Survey period	Survey length (days)	CT deployment height (cm)	Grid spacing (km)	CT brand	Reference method
A	Wild boar	24	September–November	21	50	1.5	BUSAT	SMR
	Fallow deer	24	September–November	57	50	1.5	BUSAT	TC
B	Iberian hare	30	May–July	93	20	0.75	BRW-SF	DS
	Roe deer	20	December–April	138	50	2	BUSAT	SCR
	Red deer	19	October	15	140	2	BRW-SF	DS
C	Mouflon	7	March–May	58	50	2	LTL	DS
	Red deer	7	March	25	50	2	LTL	DS
D	Mouflon	9	March–May	58	50	2	LTL	DS
	Red deer	9	March	25	50	2	LTL	DS
E_1	Wild boar	37	February–March	30	50	1.5	LTL	DC
E_2	Wild boar	17	November–December	44	50	1.5	LTL	DC
F_1	Wild boar	10	February–March	30	50	1.5	LTL	DC
F_2	Wild boar	14	November–December	44	50	1.5	LTL	DC

All the sites (study areas) are located on Spain. 'A' is a protected area, 'B', 'C' and 'D' fenced hunting states, and 'E' and 'F' two open areas where cattle farming and hunting were the main uses. $_1$ represents year 1 surveys and $_2$ represents year 2 surveys. REM, random encounter model; CT, camera trap; BRW-SF, Browning Strike Force HD Pro X; BUSAT, Bushnell Aggressor Trophy Cam; LTL, Little Acorn 5310 Series; DS, distance sampling; SCR, spatial capture–recapture; SMR, spatial mark–resight; TC, total count; DC, drive counts.

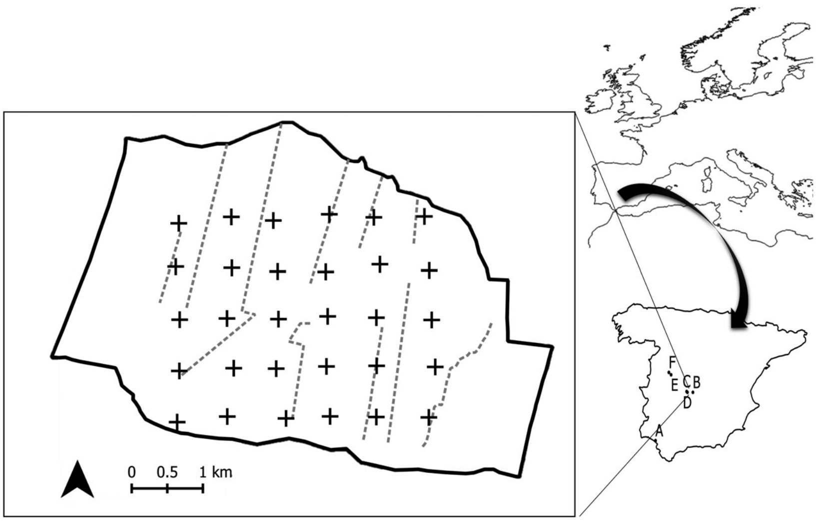

Figure 1. Example of the experimental design of one of the populations surveyed in this study (Iberian hare, *Lepus granatensis* – site B). Crosses represent camera trap placements for random encounter model application; the grey dashed line represents the line transects for distance sampling application (the reference method in this case); the continuous black line marks the boundary of the study area. Panels to the right represent the study area locations in Spain.

v.1.0.0 packages in R (Palencia, 2020; Rowcliffe, 2019). Briefly, speed was measured on each encounter by dividing the distance travelled by the duration of the encounter; we subsequently identified different movement behaviours based on the speed measurements. Second, we estimated activity level, following Rowcliffe et al. (2014). For each behaviour, we estimated the average speed and weighted the activity level, taking into account the proportion of time that the population spent on each behaviour. Day range was estimated as the sum of the product of the mean speed and the proportion of the activity level associated with each behaviour. To estimate detection zone, we recorded the position (radial distance and angle) of an animal when it first triggered the camera trap and then applied a distance sampling analysis to estimate effective radius and angle (Rowcliffe et al., 2011). The variance associated with the encounter rate was estimated by bootstrapping, resampling camera trap locations with replacements. The overall variance of density estimates was computed using the delta method (Seber, 1982) and the emdbook v.1.3.12 package in R (Bolker, 2019). The latter incorporated the variance of all the parameters (encounter rate, day range and detection zone). Log-normal confidence intervals were presented for density estimates because of the limited sample size and to prevent negative limits. In the roe deer population, only males were considered for estimation of encounter rate and speed, because we were only able to identify males individually for an independent estimate of density using the reference method (see details below). Since we did not expect differences in the effective detection zone between male and female roe deer, we also considered females for estimating the detection zone to increase the sample size and precision of the estimates.

With respect to field sampling, we used in all the populations a systematic design with random origin to meet the assumption of random camera placement relative to animal movement (Rowcliffe et al., 2013). Camera traps were deployed facing north on the nearest vertical feature (trees, poles and so on). Three different camera trap models were used: Browning Strike Force HD Pro X, Bushnell Aggressor Trophy Cam and Little Acorn 5310 Series, although the same model was used within each population (Table 1). Camera traps were configured to record a burst of photos at each activation, with the minimum time lapse between consecutive activations, which allowed us to record the entire passage of an animal. Cameras were set to be operational all day, recording nocturnal photos using an infrared flash. For the deployment of cameras in the field, we followed the procedure described by Palencia, Fernández-López, et al. (2021) and in the 10 m closest to the camera, natural markers such as rocks or branches were placed in the field of view of the camera at 2.5 m intervals using ground distance (i.e. accounting for inclination). In the case of the Iberian hare population, we also placed markers at 3.7 m from the camera. These markers were later used to locate the position of the animals in the field of view of the camera trap.

Finally, we evaluated the aggregation in encounter rates. It is well established that most of the variance in REM is attributable to the variation in encounter rate between sampling points (Palencia, Rowcliffe, et al., 2021; Rowcliffe et al., 2008), so a better understanding of the spatial aggregation in this parameter could be useful to provide future insights to improve precision. For that, we fitted Poisson and negative binomial distributions to the observed encounter rates (Appendix S3).

Independent density estimates from reference methods

We also sampled all populations using a reference method generally applied and recognized as reliable for wildlife population monitoring. All the populations, except for fallow deer, were monitored exclusively for this study (see details below). Briefly, we considered distance sampling for red deer, mouflon and hare populations (e.g. Acevedo et al., 2008), total counts (TC) for fallow deer (e.g. Grignolio et al., 2020), SCR for roe deer (e.g. Jiménez et al., 2013) and spatial mark–resight (SMR, an extension of SCR for partially marked populations) and drive counts (DC) for wild boar (e.g. ENETWILD consortium et al., 2019; Jiménez et al., 2017). Further details are shown in Appendix S2.

- *Distance sampling (DS)*: We performed line transect distance sampling to estimate the density of all red deer, mouflon and Iberian hare populations. A set of transects was distributed across the study areas, overlapping the areas sampled with the REM design (Fig. 1). We carried out the surveys in September (for red deer and mouflon populations) and April (for Iberian hare populations), beginning 1 h after sunset from a vehicle moving at an average speed of 10 km·h^{-1}, using a handheld 100 W spotlight to search a 180° arc in front of the vehicle. We repeated the surveys over five consecutive nights. When an animal/group of animals was detected, radial distance between animal(s) and observer, and the angle between animals and transect were measured with a telemeter (Nikon Laser 550AS) and a compass, respectively. We used Distance Sampling 6.2 software to analyse the data (Thomas et al., 2010). Data were right truncated when the probability of detection was lower than 0.15; half-normal, uniform and hazard rate detection functions were fitted to the data using cosine, hermite polynomial and simple polynomial adjustment terms. The best model was selected according to the AIC (Buckland et al., 2001).
- *TC*: Total counts were performed as part of the Doñana National Park monitoring program (http://icts.ebd.csic.es/monitoring-data) and were applied to estimate fallow deer density at site A. During the rutting season, two gamekeepers simultaneously sampled open areas and grassland in a single afternoon (2 h before sunset). The survey was carried out from a vehicle at an average speed of 10 km·h^{-1}. When a group of animals was detected, the size of the group and the sex and age classes of individuals were recorded. We estimated density by dividing the number of animals observed by the total size of the study area. Since only one survey was performed, it was not possible to estimate precision of density. This method assumes perfect detection (i.e. all the individuals in the population are detected). To increase the reliability of this assumption, we carried out the count in the period of higher detectability of the species (i.e. rutting season) and at the peak of the activity pattern during the day (i.e. sunset). Additionally, based on telemetry data from fallow deer tagged in the study area (Triguero-Ocaña

et al., 2020), we designed a targeted survey, and we surveyed those areas used by the species.

- *SCR*: To estimate roe deer density at site B, we sampled with the camera traps 17 artificial feeding points for 3 months, designed exclusively for roe deer and distributed throughout the study area. Since we were only able to identify individuals based on the antlers (size, shape, length, curvature and number of points), we discarded females and calves and estimated the density of males (Jiménez et al., 2013). Data were analysed with SCR using the oSCR v.0.42.0 package in R (Sutherland et al., 2019). We tested the performance of both M_0 (which assumes constant baseline detection probability, $p0$) and M_b (where $p0$ is allowed to vary depending on the previous capture). We tested M_b because we used baited sampling points, animals might respond positively (trap happiness) and they might be more likely to be captured subsequent to their initial capture. We also run three models including factors affecting density. In one of them, we included habitat (open areas and dense vegetation areas), in the second we included region (north and south, because of the natural density gradient reported in previous studies; Jiménez et al., 2013) and in the third model we included statistical interaction between habitat and region. We also tested a model in which region was included as factor of $p0$. Models were compared on the basis of AIC values (Royle et al., 2013). As the study area was fenced, we restricted the state space to the fenced area.

At site A, to estimate wild boar density, we captured and ear-tagged seven wild boar. Two of these individuals were also tagged with GPS-GSM collars programmed to acquire one location every 10 min. As it was not possible to recognize all the wild boar, we applied SMR. Specifically for the SMR method, we deployed 61 cameras with a 500 m inter-camera spacing in two regular grids (5×5, 6×6) representatives of the study area. We analysed the photographic captures of both marked and unmarked wild boar using an extension of SMR model with incomplete identification: the generalized SMR model (genSMR-ID, Jiménez et al., 2019). This approach solved two common problems in SMR studies: the difficulty of reading all the marks and recognizing individuals, and equal encounter rates in marked and unmarked animals. We fitted the null model and included telemetry data to allow inferences about the posterior distribution of σ, and considered a survey period of 25 days to avoid the effect of transient animal movement.

- *DC*: We applied DC to estimate wild boar densities at sites E and F. An average of four drives of 229 ± 54.90 ha (SE) in different scrubland zones in the study areas were surveyed on separate days. Observers were placed at fixed locations with an open field of view (e.g. firebreaks). The DC started at 11:00 and lasted for 4 h. While the observers were in their positions, beaters with dogs moved across the area. An experienced beater (J. Ferreres) supervised all the DC, collected all the information and minimized the likelihood of double counting. Assuming that all animals were detected, we estimated densities by dividing the number of observed animals by the surveyed area. Multiplying these densities by the area covered by scrubland, we estimated the total number of wild boar. It was assumed that at the time of the DC, all the wild boar were in the scrubland areas, and animals in the open grassland zones were ignored. Finally, by dividing the total number of individuals by the total area of the population, we estimated the density.

Comparison of density results

To identify the factors that determine the reliability in REM, we run a linear mixed-effects model using the bias as response variable. Bias for each population was estimated as the difference of the REM-density minus the reference-density, and this value was divided by the reference-density. Thus, negative values indicate an underestimation of REM, positive values overestimation of REM, and 0 correspondence between the densities obtained with REM and reference method. At this point we would like to highlight that because of the absence of reliable precision of densities reported on literature, it was not possible to include uncertainty in the response variable, that can lead to an overestimation of the precision in the model parameters (Behney, 2020; Cressie et al., 2009). As explanatory variables we considered the number of camera trap placement $\log_{10}$-transformed as continue, the reference method as a factor with five categories (distance sampling, DC, dung count, spatial explicit capture–recapture and TC), the species taxonomic group as a factor with six categories (Artiodactyl, Carnivora, Diprotodontia, Eulipotypha, Lagomorpha and Rodentia), and the quality of the estimation of the REM parameters (i.e. day range, detection zone and encounter rate) used as a factor each one with two categories (appropriate and deficient). All these variables were included as predictors in a full model. The study was included as a random effect factor. Raw data for these variables are found in Appendix S1. The assumptions of normality, homogeneity and independence in the residuals were assessed following Zuur et al. (2010).

Results

In the review of the existing literature, we found 34 studies in which REM was applied to a total of 45 species. Reported REM densities ranged from 0.07 individuals·km^{-2}

(cougars *Puma concolor*, Loonam et al., 2021) to 468 individuals·km^{-2} (wallabies *Macropus rufogriseus*, Rowcliffe et al., 2008) (Appendix S1). In 25 of these studies, REM estimates were compared with a reference method, generating a total of 77 REM-reference method comparisons (Fig. 2).

In the populations surveyed in this study, the densities obtained using REM ranged from 0.44 individuals·km^{-2} (males in roe deer population at site B) to 60.55 individuals·km^{-2} (red deer population at site D) (Fig. 3 and Table 2).

With respect to the LLM, the results did not show an association of the reference method, the number of placements sampled and the species taxonomic group with the bias (Fig. 4). We observed an effect of the quality of REM parameters (appropriate/deficient) in density bias (Fig. 4). Deficient procedures for the estimation of day range and encounter rate led to an overestimation of density when applying REM; while an underestimation in density was observed when deficient procedures were applied to the estimation of detection zone (Fig. 4). We also reported a tendency to overestimate density when appropriate procedures were applied to estimate detection zone (Fig. 4). The model has an R^2 of 0.51, while the R^2 associated with the random effect (here the 'study') was 0.26.

With respect to precision, we observed overdispersed encounter rates in all the populations surveyed in this study, where parameter k ranged from 0.04 (fallow deer

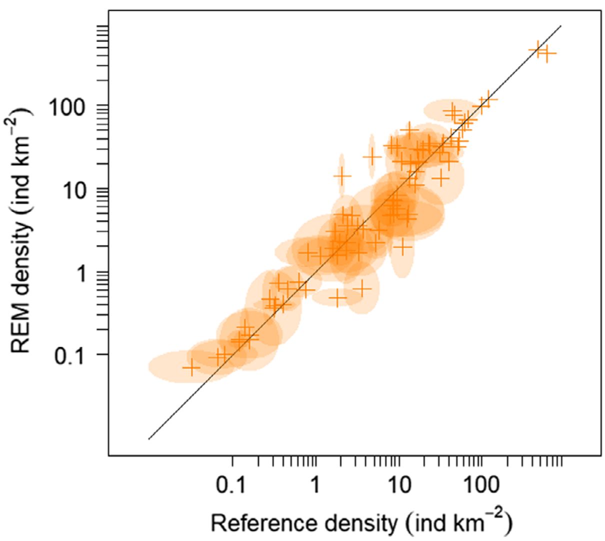

Figure 2. Densities plotted in a pairwise comparison between random encounter model (REM) and reference methods reported in published studies. Crosses represent mean density values; translucent ellipses represent 95% log-normal confidence intervals. Those populations without ellipses are those which did not report variance values in the original study. A detailed list of references and density values can be found in Appendix S1. The diagonal line is the line of equality.

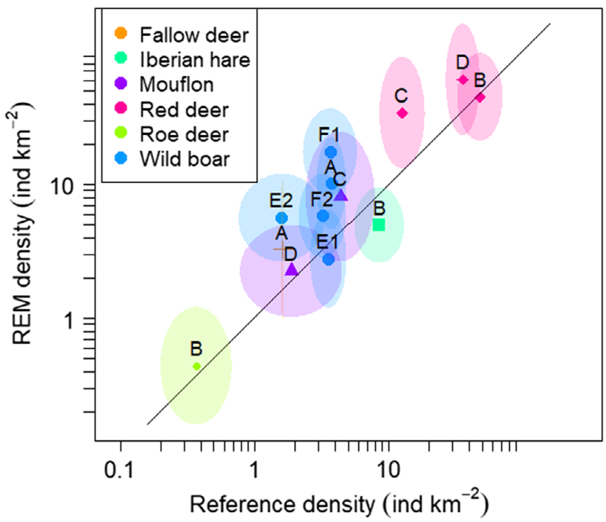

Figure 3. Densities plotted in a pairwise comparison between random encounter model (REM) and reference methods for populations surveyed in this study. Symbols represent mean density values, and translucent ellipses, 95% log-normal confidence intervals. Note that species are grouped according to colour and symbol type. The diagonal line is the line of equality. Capital letters above the symbols represent the populations at the different sites.

population at site A) to 1.39 (wild boar population at site F_2). The mean CV was 0.47 in the REM estimates, ranging from 0.34 to 0.75. In contrast, the mean CV of the reference methods was 0.25, ranging from 0.13 to 0.47. The REM achieved lower precision than the reference method in all populations, except for the mouflon population at site D (REM-CV = 0.42, reference method-CV = 0.47) and the wild boar at site E_2 (REM CV = 0.40, reference method CV = 0.39), in which reference methods were distance sampling and DC, respectively. Based on this result, we included in Appendix S3 a brief simulation to evaluate the survey design needed for a given level of precision considering the high levels of aggregation observed in the populations sampled in this study.

Discussion

The development of new methods to estimate population densities without the need for individual recognition has improved the applicability of camera trapping for wildlife monitoring. However, comparative studies surveying more than one population and assessing methods reliability are scarce. This study, based on a combination of reviewed and empirical data, shows the potential of REM for estimating population density, as well as what factors determines its reliability.

Broadly, we found a strong equivalence between REM and reference densities (Figs. 2 and 3). These results are

Table 2. Estimated random encounter model (REM) parameter values for each population, where *y/t* is the encounter rate; *v*, the average distance travelled by an individual during a day (day range); *r*, the radius of detection; and , the angle of detection.

Populations		Parameters			
Site	Species	y/t (ind·(cam·day)$^{-1}$)	v (km·day^{-1})	r (km)	θ (rad)
A	Fallow deer	0.203 (0.194)	5.776 (1.596)	0.0088 (0.0004)	0.733 (0.083)
	Wild boar	0.600 (0.270)	15.770 (1.931)	0.0080 (0.124)	0.733 (0)
B	Iberian hare	0.144 (0.040)	4.069 (0.752)	0.0059 (0.0005)	0.911 (0.121)
	Roe deer	0.012 (0.005)	6.644 (2.436)	0.0049 (0.0003)	0.733 (0.238)
	Red deer	0.670 (0.254)	4.020 (0.420)	0.0046 (0.0001)	0.959 (0.0001)
C	Mouflon	0.181 (0.056)	6.112 (1.213)	0.0049 (0.0003)	0.959 (0.083)
	Red deer	0.317 (0.039)	1.840 (0.446)	0.0045 (0.0002)	0.641 (0.049)
D	Mouflon	0.063 (0.026)	6.112 (1.213)	0.0049 (0.0003)	0.959 (0.083)
	Red deer	0.995 (0.714)	4.383 (0.472)	0.0045 (0.0002)	0.641 (0.049)
E	Wild boar$_1$	0.063 (0.013)	7.097 (2.086)	0.0034 (0.0004)	0.380 (0.052)
	Wild boar$_2$	0.149 (0.063)	6.482 (1.465)	0.0034 (0.0004)	0.380 (0.052)
F	Wild boar$_1$	0.280 (0.091)	6.326 (1.345)	0.0030 (0.0001)	0.582 (0.050)
	Wild boar$_2$	0.135 (0.059)	7.753 (1.960)	0.0029 (0.0006)	0.582 (0.050)

Data represent means (±standard error). All the sites (study areas) are located on Spain. 'A' is a protected area, 'B', 'C' and 'D' fenced hunting states, and 'E' and 'F' two open areas where cattle farming and hunting were the main uses. Subscripts: $_1$: year 1, $_2$: year 2.

in agreement with most of the studies that have assessed REM, most of which reported comparable results (Pfeffer et al., 2018; Rowcliffe et al., 2008; Schaus et al., 2020), although others reported discrepancies (Chauvenet et al., 2017). In this respect, our results suggested that biased REM densities are obtained when REM parameters (namely day range, detection zone and encounter rate) are estimated applying deficient procedures (Fig. 4). First, should be mentioned that, considering the number of REM and reference method comparisons (N = 90), we are going to discuss the observed effect (point estimate) in the statistical model, since the absence of significant differences in some factors could be due to the wide intervals obtained likely related with limited sample size (Amrhein et al., 2019). Focusing on encounter rate, we observed that some studies applied not random (i.e. targeted) designs by setting cameras in placements in which the presence of animals such as dung piles, footprints or wildlife trails were observed (e.g. Rahman et al., 2017; Rovero & Marshall, 2009; Soofi et al., 2017). Additionally, other studies have considered regular grids, but the placement selected around the predefined point was based on the presence of wildlife signs (Pfeffer et al., 2018; Zero et al., 2013), so the camera trap placement is not random. Targeted designs when applying REM could lead to an increase in encounter rate, and this could explain the tendency to overestimate density observed (Fig. 4). Regarding the day range, we also reported a tendency to an overestimation in REM densities when applying deficient procedures to estimate day range. Looking into the bibliography (Appendix S1), we observed that most of the deficient procedures to estimate day range are those in which tagged animals with GPS collars were used to estimate day range without accounting for tortuosity (e.g. Caravaggi et al., 2016; Garrote et al., 2021; Massei et al., 2018; Rovero & Marshall, 2009; Zero et al., 2013). It is well described that estimate day range assuming straight-line distances between consecutive fixes notably underestimate day range, and some studies concluded that more than 5 fixes·min^1 would be required to get tolerably accurate estimates (Marcus Rowcliffe et al., 2012; Sennhenn-Reulen et al., 2017). If day range is underestimated, densities are overestimated when applying REM. Finally, an underestimation of density when applying REM using deficient procedures to estimate detection zone was observed. Looking into literature (Appendix S1), we observed that habitual practice is to determine the dimensions of the detection zone by a series of trials in which the camera was approached by a person from varying directions (e.g. Cusack et al., 2015; Garrote et al., 2021; Loonam et al., 2021; Massei et al., 2018; Rowcliffe et al., 2008). In this respect, some studies have evidenced that detection zone is determined by different factors such as environmental conditions and camera trap settings (Palencia, Vicente, et al., 2021; Rowcliffe et al., 2011). More relevant, other studies have described a positive relationship between species body mass and detection zone dimensions (Hofmeester et al., 2017). Thus, if detection zone is estimated using human trails, an overestimation is expected because target species are usually shorter and smaller than humans. If detection zone is overestimated, REM densities are underestimated. Additionally, other habitual practices for the calculation of detection zone are to use the values reported on

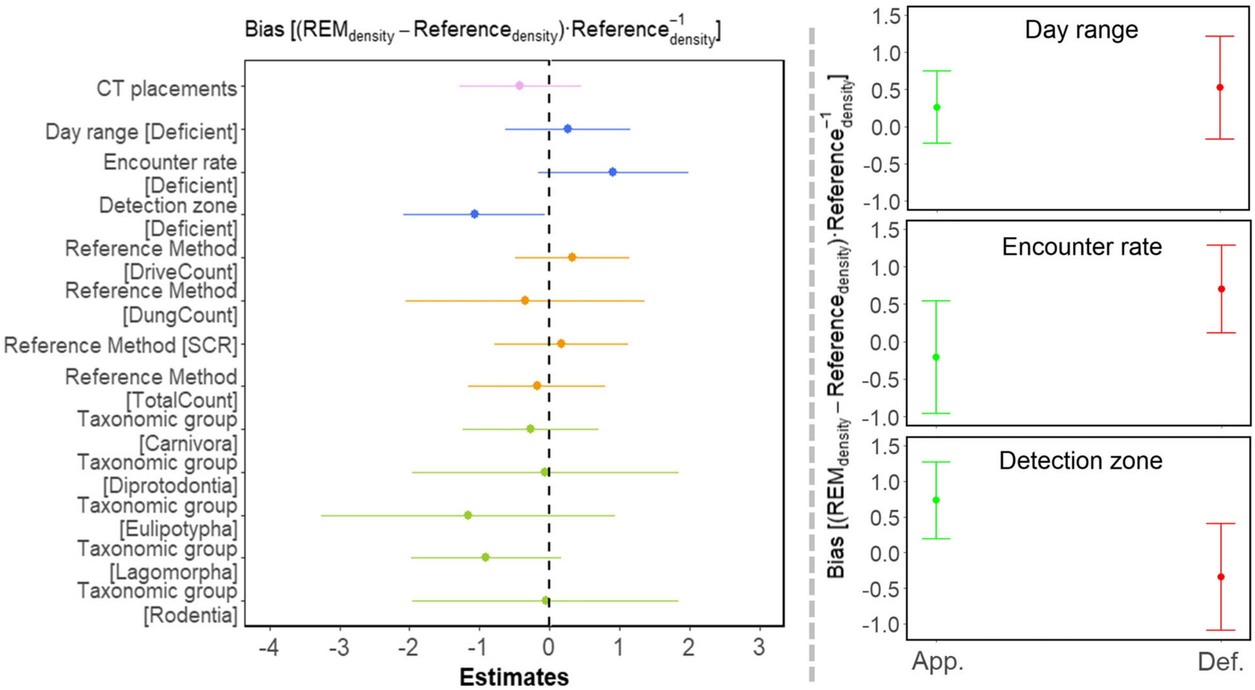

Figure 4. Left panel: coefficients for the predictors included in the LLM model to valuate REM reliability. Bias was estimated as the difference of the REM-density minus the reference-density, and this value divided by the reference density. Colours represent different levels of the same factor. The reference categories for day range, encounter rate and detection zone quality were "appropriate", for reference method was "distance sampling" and for taxonomic group was "Artiodactyl". Right panel: predicted values for day range, encounter rate and detection zone considering two categories (app.: appropriate and def.: deficient) according to the quality of the procedures applied to estimate these parameters. Error bars represent 95% confidence intervals. REM, random encounter model.

manuals (e.g. Pettigrew et al., 2021; Popova et al., 2019) or to take reference values from literature (e.g. Soofi et al., 2017; Zero et al., 2013); both approaches could lead to biased detection zones, and consequently, biased densities. On the other hand, underestimation of detection zone could lead to overestimation of density. Theoretically, detection zone size is estimated accurately using detection distances and applying distance sampling if detection probability is certain for at least some distance from the camera (Rowcliffe et al., 2011), which can be achieved by setting the cameras at shoulder height of the target species (Palencia, Vicente, et al., 2021). Thus, future studies in which appropriate procedures are applied to estimate all the parameters are necessary to confirm that, under these scenarios, accurate REM densities are estimated. Broadly, deficient procedures for the estimation of REM parameters will be lead to biased densities. Thus, a best practice guide for the application of REM should include the estimation of all the parameters for the target population applying reliable procedures (see Appendix S1) together with random camera placements relative to animal movement (Rowcliffe et al., 2013). Additionally, variance in all the parameters should be considered when estimating density precision. Random designs can lead to low sample size but increasing the sampling effort by increasing the number of cameras or survey length should be always considered, rather than using attractants or targeted designs.

Regarding the number of camera trap placements, the reference method and the species taxonomic group, we did not observe relevant relationships (i.e. values for the estimate close to 0, Fig. 4) with bias in density estimations from REM. With respect to the reference methods, we acknowledge that there are relevant differences among them, for instance, in the estimation of probability of detection. However, other practical reasons usually determine which method is applied in monitoring programmes, so we decided to include all of them in the comparisons, and not only the robust ones (Borchers et al., 2002). Regarding the species taxonomic group, the most relevant patterns were associated with Eulipotypha and Lagomorpha. Both groups showed a slight tendency to underestimate REM densities. Considering the low number of studies that sampled these groups, further comparisons in these taxonomic groups are still necessary.

After estimating all REM parameters for the target population, the Spanish surveys demonstrated their reliability in ungulates and Iberian hare in different environmental scenarios and a wide range of densities (from 0.44 to 60.55 individuals·km^{-2}). This range of densities covers the vast majority of the population densities reported in wildlife monitoring programmes (Fig. 2). We also surveyed gregarious (e.g. fallow deer, mouflon) and non-gregarious (e.g. Iberian hare) mammals and the results showed a high degree of equivalence between REM and reference densities (Fig. 3). For REM application, it is not needed that animals have a reasonable chance of being detected at more than one camera, which means that multispecies studies can be considered. Here, we surveyed red deer and mouflon populations at sites C and D in parallel, while previous studies have surveyed the ungulate and carnivore community (Palencia, Rowcliffe, et al., 2021; Pfeffer et al., 2018). Thus, in addition to the advantages of REM discussed above, we would like to highlight the potential of REM for monitoring more than one species using the same survey design. This is less common in other reference monitoring methods. Distance sampling surveys, for example, should be conducted during the season of highest detectability when target species activity is at its peak (Buckland et al., 2001). On the other hand, when using SCR methods, the distance between traps depends on the home range of the species (Royle et al., 2013). Home range and activity periods are usually species specific.

A potential point of concern is that our REM estimates showed relatively low precision (Figs. 2 and 3). The low precision of REM estimates has been reported before (ENETWILD consortium et al., 2019; Palencia, Rowcliffe, et al., 2021). Although we considered variance in all estimated model parameters, most of the final density variance was attributable to the variation in encounter rate between sampling points (Table 2), and it has been described in other studies (Howe et al., 2017). The distribution of animals is not uniform but aggregated, and usually overdispersed (i.e. the variance is greater than the mean). In this study, for example, we monitored highly aggregated populations (maximum k of negative binomial distribution for encounter rate was 1.4) throughout the study area. In highly aggregated scenarios (e.g. $k = 0.05$), when applying REM, a minimum of 60 camera trap placements (sampling locations) should be sampled to obtain a CV of <0.2 (which is a rule of thumb for monitoring programmes; Pollock et al., 1990) (Appendix S3). The human effort and cost associated with sampling more than 60 placements would not be feasible in some management programmes, which may limit the applicability of REM for wildlife monitoring (but CV of <0.2 may not always be necessary'). In this respect, some studies have shown seasonal variation in encounter rates (Kays et al., 2021; Kolowski et al., 2021), so a general recommendation when applying REM could be to survey populations when low aggregation is expected. This could help to optimise human effort. Considering all the above, future advances in REM should be focused on optimizing surveys design to improve density precision.

In addition to the advantages highlighted above, we would also like to highlight that previous studies evaluating the costs associated with REM and reference methods have concluded that REM is cost-effective in the long term despite the high start-up costs (Cusack et al., 2015; Pettigrew et al., 2021; Rovero & Marshall, 2009; Schaus et al., 2020; Zero et al., 2013). The REM is recommended particularly when the assumption of population closure is violated (i.e. density is expected to change during the survey), since it provides an average density across the sampling period, but not biased results. It should be mentioned that violation of closure is common, for instance, when monitoring game species during the hunting season (ENETWILD consortium et al., 2019). The REM could also be recommended for well-defined areas (such as forests surrounded by agricultural lands or fenced hunting areas). On the other hand, a significant limitation is that REM estimates average density over the entire study area and survey period, which limits its potential to identify spatial variation in densities (Caravaggi et al., 2016; Rowcliffe et al., 2008).

In conclusion, our results showed that REM could be a reliable alternative for monitoring wildlife populations and is highly recommended when parameters (day range, encounter rate and detection zone) are adequately estimated, and survey effort, in terms of camera trap placements, is appropriate to obtain precise estimates. Since it was first described, the REM has been well received and widely applied by the scientific community (c. 30 applications) and even included in citizen science projects (Schaus et al., 2020). It has also been proposed as a reference method for monitoring certain species at European level (ENETWILD consortium et al., 2019). Here we provide strong evidence of the reliability of REM, highlighting the priority aspect of estimating REM parameters properly and using appropriate survey design. These results, along with the practical recommendations for improving precision, and its methodological advantages relative to other methods described above, allow us to conclude that REM could be recommended for monitoring wildlife population density, especially managers and partitioners responsible for monitoring wildlife populations.

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Data Availability Statement

Data available via Zenodo https://zenodo.org/record/6784645#.Ytaw47bP07E. The R code, working data and vignette to run a REM analysis are available on https://github.com/PabloPalencia/CameraTrappingAnalysis/tree/main/REM.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Summary of random encounter model published studies.

Appendix S2. Study areas and reference methods details.

Appendix S3. Assessing improvements in precision.