

RESEARCH PAPER

# Population assessment without individual identification using camera-traps: A comparison of four methods



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## Abstract

The use of camera traps to estimate population size when animals are not individually recognizable is gaining traction in the ecological literature, because of its applicability in population conservation and management.

We estimated population size of synthetic animals with four camera trap sampling-based statistical models that do not rely on individual recognition. Using a realistic model of animal movement to generate synthetic data, we compared the random encounter model, the random encounter and staying time model, the association model and the time-to-event-model and we investigated the impact of violation of assumptions on the population size estimates.

While under ideal conditions these models provide reliable population estimates, when synthetic animal movements were characterised by differences in speed (due to diverse behaviours such as locomotion, grazing and resting) none of the model provided both unbiased and precise density estimates. The random encounter model and the time-to-event-model provided precise results but tended to overestimate population size, while the random encounter and staying time model was less precise and tended to underestimate population size. Lastly, the association model was unable to provide precise results. We found that each tested model was very sensitive to the method used to estimate the range of the field-of-view of camera traps. Density estimates from both random encounter model and time-to-event-model were also very sensitive to biases in the estimate of animals' speed. We provide guidelines on how to use these statistical models to get population size estimates that could be useful to wildlife managers and practitioners.

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**Keywords:** Camera traps; Abundance estimation; Time-to-event; REST; Population monitoring; Association model; Random encounter model

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## Introduction

A reliable estimate of population density for medium- and large mammal species is crucial to develop population dynamic and distribution models, and to implement conservation and management programs (Williams, Nichols, & Conroy, 2002). Moreover, precise and unbiased population density estimates are fundamental to conserve rare and vulnerable species. According to the IUCN criteria, knowledge of the population size is an important criterion to establish the appropriate level of threat of a wild species. Currently, the IUCN red list (<https://www.iucnredlist.org/>) reports that for 127 medium and large terrestrial mammal species data is deficient, so that population size cannot be assessed. Obtaining a reliable population assessment is necessary to verify the efficacy of policies for controlling invasive or alien species. The assessment and monitoring of population size and population density by means of affordable and reliable methods are therefore key tools for developing fact-based management.

Several methods exist to estimate population abundance, ranging from traditional survey methods such as point counts or distance sampling, to spatially explicit capture-recapture techniques (e.g. Borchers & Efford, 2008; Royle & Young, 2008). Recently, there has been a growing number of studies proposing analytical methods to estimate density based on camera traps (CTs) data. As technology has improved, wildlife biologists and animal ecologists have increasingly used CTs to monitor animal communities because they are non-invasive, relatively inexpensive tools, with extended operating times (days/weeks or months, depending on the trigger protocol and battery used), saving labour of field assistants and allowing animal monitoring at day and night (Burton et al., 2015; Rovero et al., 2013; Trolliet et al., 2014).

The precision of the estimates, usually reported as coefficient of variation (CV), is key for practical applications, for example to effectively evaluate animal population response to management actions (Engeman, 2005). Thus, the precision of an estimate is fundamental to reduce sampling errors to *a-priori* defined levels (Focardi et al., 2020). Skalski, Ryding, and Millspaugh (2005) suggested that a coefficient of variation (CV) lower than 0.2 is appropriate for the estimates to be meaningful for management purposes.

Over the last decade, several analytical methods have been proposed to estimate density from CT data for non-individually recognisable species. Some of these methods have been derived from Hutchinson and Waser's (2007) seminal paper, which assumes that animals may be treated as "ideal gas" molecules and that methods stemming from statistical mechanics can be useful to evaluate their density. Accordingly, Rowcliffe et al. (2008) developed the random encounter model (REM). The amount of animals  $y$  crossing a detector (assumed circular of radius  $r$ ) is given by:

$$y = 2rtvD \quad (1)$$

where  $v$  is the speed of animals,  $t$  is time, and  $D$  is the density to be determined. The appropriate formula for  $D$  when CT have a field of view (FOV), i.e. a sector of actual visibility by CT within a circle with angle  $\theta < \pi$ , reads:

$$D = \frac{\pi y}{tvr(2 + \theta)}. \quad (2)$$

Such a model is strictly deterministic and assumes that the number of encounters is observed without error, and that the values of  $r$ ,  $\theta$ , and animal movement speed  $v$  are known (Rowcliffe et al., 2008). Since speed is considered in the Eq. (2) as a static parameter, its overestimation can cause an underestimation of density, and vice versa. For a given number of detections, using REM can lead to estimate a smaller population if animals move faster than average during the sampling period. This is simply because we assume that animals that move faster have more chances to be detected. The inverse is true as well: the slower the animals move, the less likely to be detected they are. Therefore, the same given number of detections could lead REM to estimate a greater population size for a sample of slower moving individuals. To overcome this bias, corrections to the method to estimate the area traversed by animals during any single day (*day range*) based only on CT data have been developed (Palencia et al., 2019, 2021; Rowcliffe et al., 2016b). With REM, precision is usually estimated using bootstrapping and the delta method (Rowcliffe et al., 2008), although more recently Jourdain et al. (2020) developed a maximum likelihood estimator version of REM.

An approach similar to REM has been developed by Nakashima, Fukasawa and Samejima (2018): the random encounter and staying time model (REST). For REST, the amount of time an animal remains in the field of view (FOV) of a camera ( $T$ ) has to be known. In this method, density  $D$  can be estimated as:

$$D = \frac{E(y)E(T)}{sH} \quad (3)$$

where  $s$  is the area surveyed and  $H$  the duration of the study,  $E(y)$  is the expected number of encounters, and  $E(T)$  is the expected staying time. This formulation stresses that the model presents a full-likelihood formulation and so the standard error (and hence CV) can be directly estimated.

Campos-Candela et al. (2018) proposed a different model, the Association Model (AM), which supposedly overcomes some limitations of the previous methods. In this latter method, density  $D$  can be estimated as:

$$D = \frac{\sum_i^C \sum_j^F n_{ij}}{CFA} \quad (4)$$

where  $C$  is the number of camera traps,  $F$  is the number of photographs,  $n_{ij}$  is the number of animals observed in camera  $i$  and photograph  $j$  and  $A$  is the area covered by the FOV of each camera. These authors validated the AM by

simulations of the movement of animals characterised by a home range. Unfortunately, their approach presents several shortcomings as shown by [Abolaffio, Focardi, and Santini \(2019\)](#), and assumes perfect detection within the field of view (see also [Campos-Candela et al., 2019](#)).

Other interesting methods to estimate population density were proposed by [Moeller, Lukacs, and Horne \(2018\)](#). Amongst these, the time-to-event model (TTE) seems promising as it performed well both in [Moeller et al. \(2018\)](#) simulations and field study, such as recent work by [Loonam et al. \(2020\)](#) and [Loonam et al. \(2021\)](#). This model does not originate from the ideal gas theory, rather it is rooted in sampling theory and uses observations of the time between an arbitrary starting moment until the first detection of an animal. A key assumption of this method is that animals are Poisson distributed across camera grid cells. This assumption allows to assume an exponential distribution of the time until a detection occurs at a camera. In order to measure this exponentially distributed time until a detection, the survey is divided into occasions (e.g., days) and each occasion into periods (e.g., hours), assuming that the number of animals  $N_{ijk}$  visible to camera  $i$ , on occasion  $j$  and period  $k$  is Poisson distributed:

$$N_{ijk} \sim \text{Pois}(\lambda) \tag{5}$$

where  $\lambda$  is the average number of animals visible to a camera. Thus, if  $T$  is the distribution of *periods* of first detection, then:

$$T = \exp(\lambda) \tag{6}$$

We can estimate overall density ( $D$ ) by dividing the estimated  $\lambda$  by the mean area  $a$  of a camera’s FOV:

$$D = \frac{\lambda}{a} \tag{7}$$

The authors warn that TTE may provide biased population estimates, but [Looman et al. \(2020\)](#) showed that TTE can perform comparably to existing methods for estimating abundance in unmarked species that live at low densities (such as the cougar *Puma concolor*).

Despite evident differences, all these methods share a common number of assumptions which are:

(1) Camera traps must be placed randomly with respect to the spatial distribution of animals, so that all individuals are at risk of being captured and the inference obtained from the sample can be unbiasedly extended to the rest of the population. Usually, this is done using a random grid of CTs or a stratified random sampling. This assumption excludes the use of baited CTs or to set CTs on trails or other special locations ([Durbach et al., 2020](#)). See [Garrote et al. \(2021\)](#) and [Cusack et al. \(2015\)](#) for useful examples of deviations from random placement.

(2) CTs must detect the animals with certainty inside an area measured with negligible error (detection area). This area can be identical or different amongst the set of CTs used in a specific survey, e.g., in dependence on technological differences amongst camera traps (such as triggering sensitivity, or lens quality, etc.; [Rovero et al., 2013](#)) or obstacles that reduce the FOV of a given CT.

(3) Population is closed during the study period: no birth, death, net immigration or emigration are expected to occur.

(4) Animal movement and behaviour are not affected by CTs, which means that instruments should neither attract nor repel; the encounter with a CT should not influence the detection probability by any other CT deployed in the same sampling scheme.

Only if these general assumptions, as well as other general and method-specific ones ([Table 1](#)), are met, the output of analytical methods is meaningful. We summarise the assumptions and the effects of their violation in [Table 1](#).

**Table 1.** Summary of the assumptions upon which the four methods we tested are based. We also list some likely outcomes of violation of the assumptions in relation to accuracy and precision (see [Palencia et al., 2021a](#); [Gilbert et al., 2021](#)). Legend: camera Traps (CTs), Association model (AM), random encounter model (REM), random encounter and staying time model (REST), time-to-event model (TTE).

Assumption	AM	REM	REST	TTE	Likely effects of violation of the assumption on	
					Accuracy	Precision
CTs are placed randomly with respect to animals	X	X	X	X	Positive bias when the CT is placed on trails and preferred locations	
Certain detection	X	X	X	X	Negative bias	
Closed population	X	X	X	X		Low
Animal movement and behaviour are not affected by CTs after first detection	X		X		Direction of bias depends on whether the animal is attracted or turned down by the CT	
Independent detections	X	X	X		Positive bias in REM	
Certain detection at zero distance	X	X		X	Negative bias	
Certain animal recording inside focal area			X		Negative bias	
False detection	X	X	X	X	Positive bias	
Instantaneous detection	X			X	Negative bias	
Unaffected by inactivity periods	X		X	X	Negative bias	

The analytical methods presented above have been validated using synthetic data and/or applied to populations of known size, but using different simulation approaches, so that it is difficult to compare their relative performance. Rowcliffe et al. (2008) did not simulate movement trajectories, but generated trapping data by drawing random numbers of photographs from a negative binomial distribution. Nakashima et al. (2018) approximated the movement of simulated animals using a biased correlated random walk with step intervals of 15 min. In a later contribution, Nakashima (2020) approximated home range behaviour via an Ornstein-Uhlenbeck process. The model proposed by Campos-Candela et al. (2018) used a biased uncorrelated random walk, while Moeller et al. (2018) and Chauvenet et al. (2017) also used uncorrelated random walks. All these movement models miss important components of realistic animal movement. First, the models assume homogeneity of behaviours along the trajectory, whereas alternative behaviours (e.g., resting, feeding) occur. Second, in most cases, synthetic animals are characterised by diffusive unbounded movements which are unrealistic.

In this work, we fill this methodological gap by comparing the performance of these methods (namely REM, AM, REST and TTE) using an identical set of simulations and allowing for complex behavioural phases of the surveyed animals. First, we used a unique simulation model characterised by the presence of home ranges and by a variable degree of path tortuosity, with animals that may alternate different behaviours, each characterised by a specific rate of displacement (Abolaffio et al., 2019). Secondly, we developed a synthetic CT survey using variable sampling efforts and CT settings for known population of animals characterised by home range behaviour (moose *Alces alces*). We initially compared the models' performance under simplistic conditions, then introduced a further level of complexity in the behaviour of synthetic animals. We also tested the impact of a variable FOV on all models' performance, and of the accuracy of speed estimation on REM and TTE models.

## Materials and methods

### Animal movement model

In this paper we used the moose (*Alces alces*) as species of reference (cf. Appendix S2 in Abolaffio et al., 2019, for further information). The coordinates of the home range centers were randomly assigned. In the model, the animal moves in a 2-dimensional space and is characterized by a maximum of three different behavioural patterns: displacement or fast movement, grazing with slow movement and resting. The fractions of time spent in movement and grazing are denoted  $p_{graze}$  and  $p_{move}$ , respectively, while  $(1 - p_{graze} - p_{move})$  is the resting time.

Our model falls under the class of correlated velocity models (Gurarie et al., 2017), also known as continuous time movement models (Calabrese, Fleming, & Gurarie,

2016), as opposed to the more popular discrete-time movement models, such as correlated random walks. However, our model shows two major differences with respect to those described in Gurarie et al. (2017): (i) in our model the speed is correlated only in magnitude and not in direction, giving the animal the desired mean speed in magnitude and (ii) the mean turning acceleration is pointing toward the centre, creating the desired home range behaviour.

Coherently with a large body of literature on animal movement patterns, our model displays these main features: i) correlation of movement that determines the direction of successive steps, i.e. the turning angles are correlated (Turchin, 1998); ii) assumption that the distribution of distances between the animal's position and the home range centre, of coordinates  $X_c$ , is bivariate normal and homogeneous (Okubo, 1980); iii) characteristic movement velocity of relocation  $V_a$ .

Beyond these main features, we explicitly accounted for different types of movement for each animal: fast movements, grazing, and resting. These stages are included in the model as follows.

**Fast movements.** The displacement  $X(t)$  of the animal is given by:

$$X(t + \Delta t) = X(t) + V(t)\Delta t \quad (8)$$

where the vector  $V(t)$  denotes the velocity and  $\Delta t$  is the time interval.  $V(t)$  depends on the sum of three terms:

$$V(t + \Delta t) = V(t) \frac{V_a + (V(t) - V_a)e^{-\Delta t/\tau}}{V(t)} - K(X - X_c)\Delta t + R_t \quad (9)$$

The first one brings the module of velocity  $V(t)$  close to the characteristic speed  $V_a$ . When  $V(t) > V_a$  the fraction is  $< 1$  while when  $V(t) < V_a$  it yields values  $> 1$ . Note that  $\tau$ , measured in seconds, is a characteristic time scale of auto-correlation (see Gurarie et al. 2017).

The second term of Eq. (9) represents an acceleration towards  $X_c$ , while the third component of Eq. (9) is a random noise  $R_t$  (m/s), with variance  $\varepsilon^2\Delta t$  assumed identical in the two axes. Note that in Gurarie et al. (2017),  $R_t$  is denoted  $\beta d\omega_p$ , where  $\beta$  is equivalent to our  $\varepsilon$  (m/s<sup>3/2</sup>). Gurarie et al. (2017) also defined  $1/\tau = \alpha.K$  (1/s<sup>2</sup>) is a parameter which represents the intensity of centripetal component of movement. If  $K = 0$ , in the limit of  $\tau \rightarrow 0$  and  $\varepsilon=0$ , the animal performs a ballistic motion. The case of  $\tau \gg 0$ , cannot be dealt with analytically, but numerical simulations have showed that there is not a large discrepancy with the case  $\tau \rightarrow 0$  (cf. Appendix S1 in Abolaffio et al., 2019). When  $K > 0$  and  $\varepsilon>0$  the animal performs a home range behaviour which reduces to deterministic orbits around  $X_c$  when  $\varepsilon=0$ . In case of  $\tau \rightarrow 0$  it is possible to compute the home range size  $S_{HR}$  as:

$$S_{HR} = c_1 V_a \sqrt{\frac{1}{2K}} \quad (10)$$

where  $c_1$  is a constant which depends on the definition of home range. For a 95% home range,  $c_1 \approx 2.45$ . Since the home range size and  $V_a$  are usually known, one can use Eq. (10) to estimate the value of  $K$  to be used in simulations to develop the survey design for the species of interest. Note that the velocity  $V(t)$  has a module correlation time  $\tau$  and angular correlation time given by  $\frac{V_a^2}{v}$ . The home range size was set to 26 km<sup>2</sup>, which is the average home range size computed for over 300 moose from several Scandinavian populations (Allen et al., 2016), and considered identical for all simulated animals, with a mean daily speed of 0.03 m/s (Vander Vennen et al., 2016).

**Grazing.** The animal performs a uniform uncorrelated Brownian motion on a small scale, with mean absolute displacement *per minute* equal to 0.5 m.

**Resting.** The animal stands or lays still.

For the appropriate range of parameters and at a large scale, the model looks similar to an Ornstein–Uhlenbeck process in that there is a diffusion term coupled with a movement bias towards the home range centre (Preisler et al., 2004), but here we introduced a term for aligning the velocity to the typical speed of the species of interest. For a similar Ornstein–Uhlenbeck foraging model, see also Fleming et al., (2014).

During each day of simulated movement, there was a variable number of activity phases, and in each phase the different activities alternate as moving, grazing and resting, using the proportion established for the whole day.

### Simulating camera trap sampling

To generate simulated CT surveys, we hypothesized an idealized squared study area of 10 × 10 km with periodic boundary conditions, within which we placed a squared grid of equidistant cameras. We used four grids with 25, 49, 100, 225 CTs with 2.00, 1.43, 1.00 and 0.67 km distance amongst CTs, respectively. We simulated five different animal densities, i.e. 0.25, 0.5, 1.0, 2.5 and 5.0 animals/km<sup>2</sup>.

Moving animals were recorded when they entered the detection area of the camera. Each camera was assumed to have a maximal detection radius equal to 9 m and a FOV of 45°, unless otherwise specified. Here we assumed that all the animals entering the FOV were recorded, and that there were no obstacles that could affect detection which, of course, is not always true in the case of actual CTs (Trolliet et al., 2014). To assess the effect of variability in camera detection radius (e.g., due to physical obstacles) we produced a set of simulations where the effective detection distance of each camera was randomly extracted from a uniform distribution bounded between 5 and 15 m. This set of data was then analysed under two different scenarios: 1) the effective detection distance was unknown, in which case the maximum detection distance (15 m) was used in the density calculations; 2) the effective detection radius was known,

with its average value across the set of CTs being used to estimate animal density.

### Simulation scenarios and data analysis

We simulated two different movement scenarios. In the first one, each animal moves at constant speed ( $p_{move} = 1$ ), without any grazing or resting period. This rather unrealistic scenario was used because previous studies implicitly or explicitly assumed constant speed. In the second scenario, we assumed  $p_{graze} = 0.3$ ,  $p_{move} = 0.1$ , and the remaining being resting. For the moose, the activity budget was derived by Van Ballenberghe and Miquelle (1990). To be consistent across the two scenarios, the speed of the animals in scenario 2 was calculated to obtain the same overall mean speed as in scenario 1. The simulated surveys lasted 30 days, a duration that can reasonably allow to meet population closure assumption for a range of mammalian species. Cameras were set to be turned on for 24 h/day, and the recording of animals entering the field of view occurred without error and no delay.

For REM we developed our own code based on Caravaggi et al. (2016). For AM we used the code developed by Abolaffio et al. (2019). Estimates for the TTE model were obtained using the R code provided by Moeller et al. (2018). Note that this code produces idle error messages which were ignored (A. Moller pers. com.). The critical point in TTE is that the duration of the *period* should be carefully set to the time necessary for the animal to cross the FOV. In the absence of clear indications in Moeller et al. (2018) we took as *period* the time necessary to cross the field-of-view at the maximum distance during moving, which turned out to be 225 s, for a total of 384 *periods* per each occasion of 24 h. Note that the number of *periods* per occasion does not impact results (A. Moeller, pers. com.). For REST, the estimation of parameters was performed within a Bayesian framework using a JAGS code, kindly provided by Y. Nakashima. Posterior samples of parameters were obtained by the MCMC method using JAGS software (Plummer, 2003). The activity proportion was known without errors. A uniform prior value from 0 to 100 was used for the parameters of staying time and the dispersion parameter for trapping rate. Following Nakashima et al. (2018) a gamma distribution with shape (0.1) and rate parameters (0.1) was used as the prior distribution for animal density. Each set of simulated data was run using four different distributions for staying time (exponential, gamma, log-normal and Weibull), and the model yielding the lowest DIC value was selected (Spiegelhalter et al., 2002).

We used semi-logarithmic funnel plots of the ratio of the estimated density to true density which yields 1 in case of perfect matching. We also reported upper and lower log-normal 95% confidence limits as a function of the true population size (0.25, 0.5, 1.00, 2.50 and 5.0 animals per km<sup>2</sup>) per survey effort.

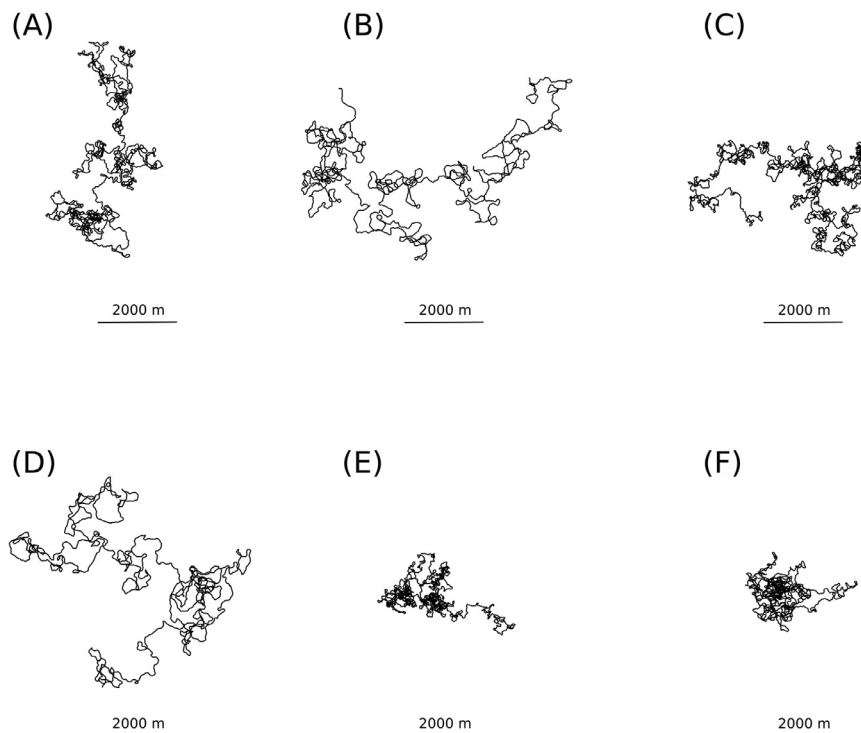
## Results

Six examples of 30-day trajectories, using different parameter assignment values, are reported in Fig. 1. As suggested by this plot, by varying motion parameters it is possible to change the size and the shape of the simulated home range. The home range size is determined by  $K$  (Eq. (6)): when  $K$  increases (as in Fig. 1E, F) the home range size decreases.

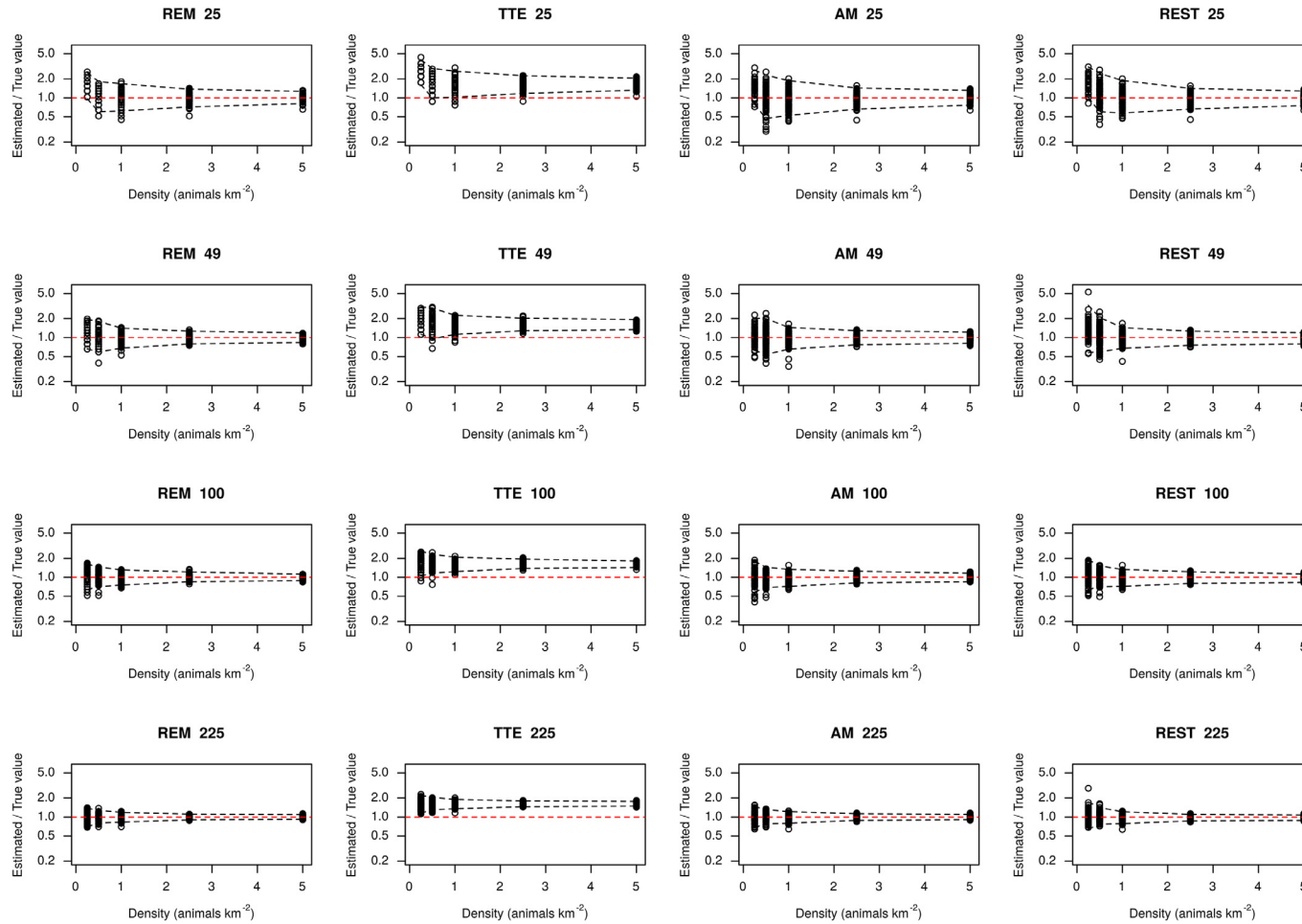
The analysis of the performance of the four estimators for the case where model parameters are perfectly known, and the simulated animals perform a continuous movement at constant speed, is reported in Fig. 2 (see also Table S1 for the numerical values displayed in Fig. 2). We present results relative to four levels of effort (25, 49, 100 and 225 CT) and five values of animal density. To give the reader an idea of the sample size, around 20 detections were collected for the smallest density and effort, while for the largest ones around 200 detections were recorded. The variability was generated entirely by the stochasticity in animal movement and by the initial random positioning of home ranges. For all models we observed a reduction of sampling variance as a function of density and sampling effort. At small sampling effort (25 CTs) and low density (0.25 animals/km<sup>2</sup>) the range of variation was around 200% for all methods and attained values

around 80% at high density (5 animals/km<sup>2</sup>). Using the largest sampling effort (225 CT) at the highest density the range of variation was lower, i.e. around 20–30% for all the four methods. REM, REST and AM were asymptotically unbiased, since there is no systematic deviation from 1, and precision improved with sample size. On the contrary TTE appeared to be systematically biased high.

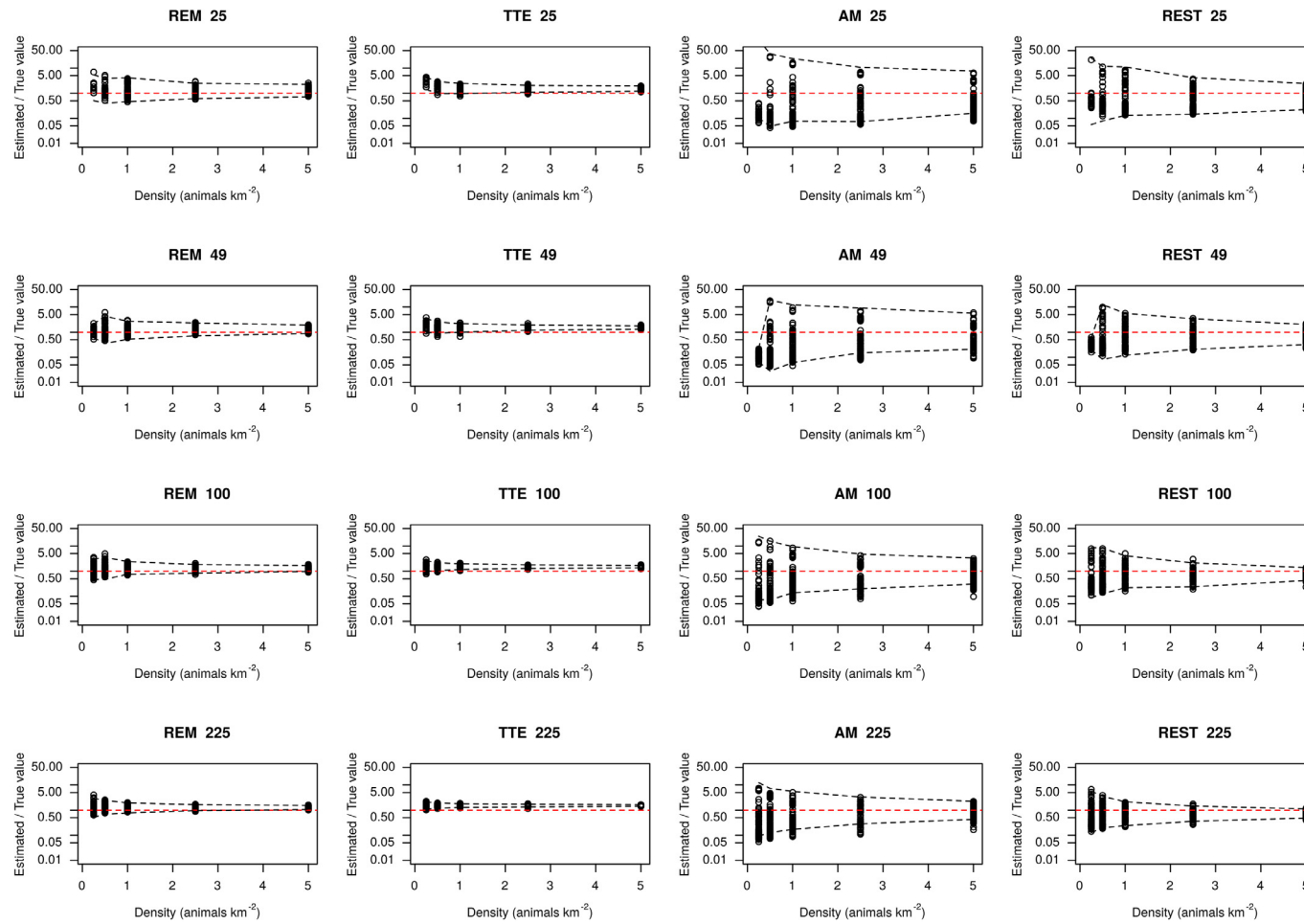
The performance of the four methods with more realistic simulations including three different behaviours is shown in Fig. 3, with the numerical values of confidence intervals reported in Table S2. In these scenarios, AM and REST performed worse than REM and TTE. Indeed, REM and TTE confirmed the pattern observed for the simplest scenario (Fig. 2). The results of these models showed a tendency to overestimate the density, but they attained a good precision when high density and large effort were considered. TTE appeared to be almost two times more precise than REM, while the precision of REST and AM was very poor. At low density and effort levels, the upper limits of the confidence intervals were generally 2–10 times the actual density, with one AM estimate being 135 times larger. At high density and large effort, the confidence intervals were 100% for REST and 300% for AM. Overall, AM remained unbiased while REST tended to be biased low towards underestimated values.



**Fig. 1.** Six examples of simulated animal trajectories. (A) One behaviour (moving,  $p_{move} = 1$ ), correlation parameter = 0.05; (B) One behaviour (moving), correlation parameter = 0.1; (C) Three behaviours, namely resting, moving, and grazing ( $p_{graze} = 0.3$ ,  $p_{move} = 0.1$ ), correlation parameter = 0.05; (D). Three behaviours ( $p_{graze} = 0.3$ ,  $p_{move} = 0.1$ ), correlation parameter = 0.1. In all the examples, average speed was  $V_a = 0.033$  m/s. In panels (E) and (F) the trajectories have the same parameter values as in panels (C) and (D), respectively, but the constant  $K$  is doubled ( $K = 1.414 \cdot 10^{-5} \text{ s}^{-2}$ ). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 2.** The ratio between population estimate and true density is reported as a function of true density (x-axis) for the four considered methods and four levels of effort (25, 49, 100 and 225 camera traps). Model names are as in Table 1. Black dashed lines define the 95% confidence intervals. The red dashed line denotes lack of bias. One behaviour (moving),  $V_a = 0.03$ , 30 days of sampling. For each combination of values we performed 100 simulations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 3.** The ratio between population estimate and true density is reported as a function of the true density (x-axis) for the four considered methods, and four levels of effort (25, 49, 100 and 225 camera traps). Model names are as in Table 1. Black dashed lines define the 95% confidence intervals. The red dashed line denotes lack of bias. Three behaviours (resting, moving, and grazing),  $V_a = 0.03$ , 30 days of sampling. For each combination of values we performed 100 simulations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



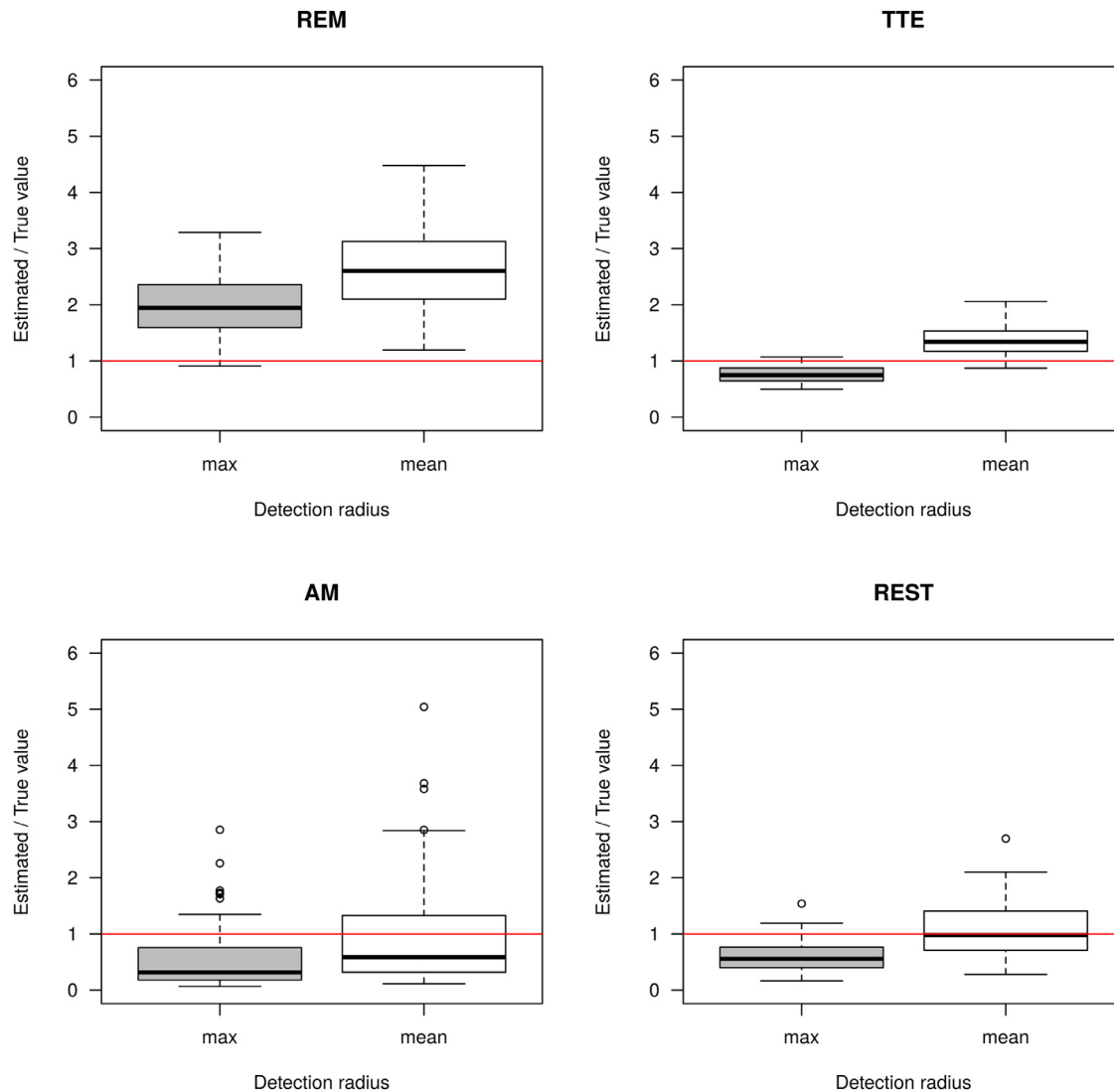
The importance of estimating correctly CT parameters is illustrated in Fig. 4, where we compare the use of the maximum detection distance, with the average effective detection distance (usually lower than the former). The use of the average detection distance instead of the maximum potential value increased the overall variance of density estimates. For REM, REST and TTE the use of the mean instead of the maximal detection distance tends to overestimate abundance. However, in the case of REST, this bias compensates for its tendency to underestimate, thus providing apparently accurate abundances.

Lastly, in Fig. 5 we show the impact of an over- or underestimation of the animal mean speed for REM and TTE models, since the daily range enters directly in the computational formula (REM model, see Eq. (2)) and in the definition of duration of the *period* in TTE. In both methods,

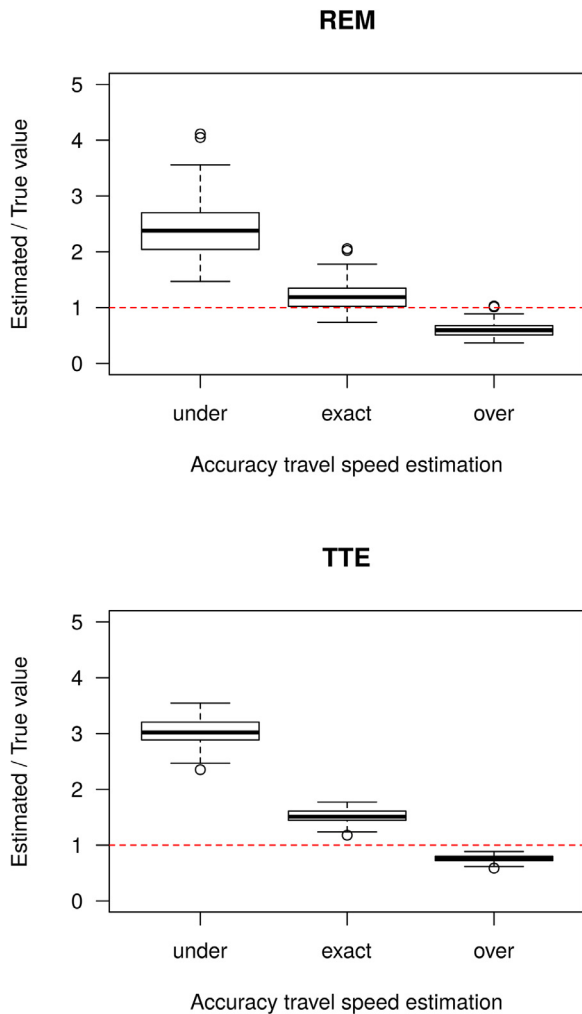
speed overestimation produced a low-biased density value while speed underestimation produced a severe positive bias. Interestingly, in both models the underestimation of the speed decreased the density estimate precision.

## Discussion

This work represents the first attempt to critically evaluate comparatively several recently proposed methods to assess the size of wildlife populations using data simulated from the same realistic model of animal movement. All estimators considered have important limitations in providing robust estimates of population density, with potential consequences if used for conservation and management. Indeed, we showed that despite their good performance under “ideal”



**Fig. 4.** Boxplots showing the accuracy of density estimates when using the maximal (grey) or mean (white) certain detection distance for each of the considered models. Model names are as in Table 1. We use three behaviors, density set at 2.5 animals/km<sup>2</sup> and 100 deployed CTs and 120 simulations per group. The three behaviors were resting, moving, and grazing. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 5.** Boxplots of the distribution of accuracy of density estimation values when mean animal speed is exact, over or under-estimated. Model names are as in Table 1. The dashed red line denotes the reference value. We used three behaviors, density set at 2.5 animals/km<sup>2</sup>, 100 deployed camera traps and 120 simulations per group. The three behaviors were resting, moving, and grazing. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

survey conditions, when we introduced more realistic movement patterns, the robustness of estimates decreased, with decreased accuracy and precision.

It is clearly impossible to obtain good estimates using few CTs when densities of animals are low. Depending on the other parameters, we showed that >100 CTs are usually necessary to get a good trade-off between accuracy and precision. This is more valid for REST than for REM and TTE, as the latter two methods tend to provide more precise estimates even with fewer camera traps. This was recently confirmed by an empirical comparison amongst methods (Palencia et al., 2021a) for camera trap data concerning three species (red deer *Cervus elaphus*, wild boar *Sus scrofa*, and red fox *Vulpes vulpes*).

Our results were obtained with a set of population density values which can be considered medium or low for the species of reference. We expect that all these methods would perform better with higher true density values, especially when using AM and REST. Still, the values we used can approximate the situation of rare species of conservation concern, or recently introduced invasive alien species.

Our results also suggest that the effective estimate of the FOV is critical to obtain valid results, especially in the case of REST. The FOV is determined by different camera parameters: maximal distance of certain detection,  $d_{max}$ , lens angle-of-view and trigger delay. We have focused our study on  $d_{max}$  for which any CT exhibits a certain detection probability. This is an often overlooked problem in field studies but, based on our findings, we recommend to experimentally assess this distance for each camera. Hofmeester et al. (2019) showed that a number of factors, depending on CT technology, animal species and habitat, may influence CT detection probability. A number of methods have been devised to estimate the detection distance from the analysis of CT pictures (Caravaggi et al., 2016; Howe et al., 2017; Johanns, Haucke, & Steinhage, 2022; Rowcliffe et al., 2011). An easy way is to compute  $d_{max}$ , using a laser range finder. We also assumed that the CT was able to detect any animal crossing the FOV between 0 and  $d_{max}$  but, depending on the species size and CT positioning, it is also possible that an animal moving very close to the CT or crossing the FOV very rapidly may go undetected. Howe et al. (2017) proposed to apply mark–recapture distance sampling methods to deal with this problem, whose practical importance is well illustrated by Bessone et al. (2020). In relation to left-truncation of detectability, Rowcliffe et al. (2011) showed that this process influences at a larger extent smaller mammal species.

A useful feature of our model is that synthetic animals perform a continuous random walk with a high temporal resolution, and Abolaffio et al. (2019) showed that the spatial resolution of an animal's path is quite relevant to obtain a correct estimate of detection rates. We have developed our model framework according to Gurarie et al. (2017) and we modelled the movement of animals as a correlated-speed movement model. With respect to discrete movement models (e.g. Signer, Fieberg, & Avgar, 2017 or Neilson et al., 2018), speed attains a value which is independent of the temporal step used in simulations. A clear limitation of our model is that it yields circular home ranges whereas animal home ranges are actually more complex (Börger, Dalziel, & Fryxell, 2008) but a similar assumption is also used in SECR modelling (cf Efford, 2019 for a discussion on this topic). In general, home range shapes more complex than bivariate normal would result in an increased variance of the estimates.

Finally, we believe that the model used here to reproduce animal movements represents an improvement with respect to those previously used to evaluate CT methods. The features we introduced in the movement of synthetic animals

capture essential properties of animal movement such as the alternation of different behavioural states. Despite the simplicity of the implemented mechanism, this complication has important consequences in the performance of the different estimators. The fact that the introduction of multiple behavioural states compromises the results of the studied estimators is probably linked to a specific bias in the sampling process. Indeed, the chance that an animal gets detected by CTs depends positively on its speed. When the animal's speed is not constant it is easier to detect an animal during a relocation phase than while grazing because its speed is higher. Therefore not considering movement variability could bias density estimation.

Our simulations assume that users have a perfect knowledge of parameter values. This is very seldom the case under actual field conditions. We agree with Rowcliffe et al. (2012) that “the underestimation of distance travelled is a serious but underappreciated problem”. Currently, there is no reliable, widely applicable method to obtain approximately unbiased estimates of distance travelled by animals. However, new emerging techniques such as dead-reckoning (Bidder et al., 2015) can be used to improve the estimates of animal speed. As well, interpolation methods can be applied to telemetry data especially when sampling rate is high (e.g. high GPS frequency) so that the estimation of the movement via interpolation is close to the real one (Fleming et al., 2016). Also well Rowcliffe et al. (2016) and Palencia et al. (2021b) had proposed a method to estimate daily range from CT observations. Although these methods are promising they are also expensive and complex, whereas easy-to-use methods to estimate parameter values would strongly support the use of movement models (see Calabrese et al., 2016 and Noonan et al., 2019 for useful examples).

Our simulations showed that REM overestimated population size. This is in agreement with Cusak et al. (2015), who provided a very careful analysis of lioness (*Panthera leo*) density in the Serengeti, finding that REM estimates tended to be higher than those obtained with other reliable methods. Similarly, Rovero and Marshall (2009) showed that REM estimates for a population of Harvey's duiker (*Cephalophus harveyi*) in Tanzania were higher than those obtained through other methods.

REST seems more appropriate than REM for practical management since it appears to be less expensive and simpler to be put in place, although more complex to parameterize. A comparative analysis of the two models (Palencia et al., 2021a) showed that for both red deer and wild boar there were no significant differences between these models and, moreover, that the estimates were similar to the ones obtained via line transect distance sampling, although the authors pointed out that “In general, the REM estimates tended to be higher than those obtained by REST”. Our simulations have shown that with a high sampling effort or large animal densities one can obtain estimates with a level of bias which can be acceptable in most

situations. Thus, in case a REM or a TTE survey is outside the possibility of implementation, one should resort to REST modelling, which is less time-consuming than REM when the daily range has to be estimated from camera trap data (Palencia et al., 2019; 2021b).

It is necessary to stress that respecting methods' assumptions is essential to lead to reliable results. Broadley, Burton, Avgar, and Boutin (2019) have made clear that an animal's speed depends on density and on home range size which in turn depends on habitat characteristics (Efford et al., 2016), and that these relationships vary with the studied taxon and site. In most other studies where the methods here evaluated were applied, though, authors were forced to use speed estimates from studies carried out elsewhere. As we have shown, the use of animal daily range obtained in a different context will lead to biased population estimates. This approach has been used in several studies, for instance Schaus et al. (2020) attempted to use REMs to estimate hedgehog (*Erinaceus europaeus*) density in an urban area, Manzo et al. (2012) estimated the density of pine martens (*Martes martes*) in central Italy, Anile et al. (2014) used REM to estimate the density of a small wildcat (*Felis silvestris*) population in Sicily, Caravaggi et al. (2016) investigated the threat posed by the invasive European hare (*Lepus europaeus*) on the endemic Irish hare (*Lepus timidus hibernicus*) and Carbajal-Borges, Godínez-Gómez, and Mendoza (2014) used REMs to investigate the status of the endangered tapir, *Tapirus bairdii* in Mexico.

The methods tested here are not the only ones which can be used for surveying populations of non-individually recognisable animals by CTs. Howe et al. (2017) have proposed to apply distance sampling to CT detections and such a promising methodology has been validated with a chimpanzee population of known size (Cappelle et al., 2019) and used for a multi-species assessment (Bessone et al., 2020). Note that this method is similar to the AM but, more realistically, it relaxes the assumption of certain animal detection in the FOV. To apply distance sampling technique to CT data, one has to evaluate the distance between the animal and the CTs while crossing the FOV. Moeller et al. (2018) proposed a space-to-event model (STE), and used it to assess the population of elk (*Cervus canadensis*). *N-mixture* models (Royle, 2004) have also been evaluated for their performance. Some authors (Knape et al., 2018; Linket et al., 2018; Nakashima, 2020) found a lack of robustness to departures from assumptions relative to different aspects of *N-mixture* models such as double counting, variation in the population size and in the detection probability over time (Link et al., 2018). Also Barker et al. (2018) found that it may be difficult to identify both the population size and the detection probability. On the other hand, Kéry (2018) detected no problem of parameter identification.

Our results show that the estimation of population density of wild mammals using CTs without individual recognition can be questionable and warn against its uncritical application and acceptance, even though some of the tested

methods performed quite well in specific situations. In our view, it is very important that population estimation methods are subject to careful assessment to evaluate their strengths and weaknesses before being used for conservation and management. Indeed, robustness to violations of assumption is a key element for judging the quality of statistical estimators and the reliability of results returned. A better understanding of the properties of the studied models could derive from comparison of estimated values with simulated data with known properties, or populations of wild animals of known density.

Despite such limitation, however, we still feel that CT-based density estimations could be a promising tool in animal ecology, representing an appealingly cheap alternative to more traditional approaches. Our tests, however, compared the methods in their very basic form and we did not suggest possible improvements. Some of the methods described here, for example, may, at least in theory, be used to estimate densities at the scale of a single camera/grid-cell and/or over periods significantly shorter than the survey duration. This type of analysis offers the appealing option of being able to relate density estimates to spatial and/or temporal covariates, and hence improve estimates and facilitate extrapolation of results.

## Author contributions

GS, MA, and SF designed the study. GS and SF analysed the data and wrote a first draft of the manuscript. MA coded the simulation. FO, BF, and FC improved the manuscript and provided suggestions for the analyses.

## Declaration of competing 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.

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## Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:[10.1016/j.baae.2022.03.007](https://doi.org/10.1016/j.baae.2022.03.007).

## References

- Abolaffio, M., Focardi, S., & Santini, G. (2019). Avoiding misleading messages: Population assessment using camera trapping is not a simple task. *Journal of Animal Ecology*, 88, 2011–2016. doi:[10.1111/1365-2656.13085](https://doi.org/10.1111/1365-2656.13085).
- Allen, A. M., Månsson, J., Sand, H., Malmsten, J., Ericsson, G., & Singh, N. J. (2016). Scaling up movements: From individual space use to population patterns. *Ecosphere (Washington, D.C.)*, 7, e01524. doi:[10.1002/ecs2.1524](https://doi.org/10.1002/ecs2.1524) Article.
- Anile, S., Ragni, B., Randi, E., Mattucci, F., & Rovero, F. (2014). Wildcat population density on the Etna volcano, Italy: A comparison of density estimation methods. *Journal of Zoology*, 293, 252–261. doi:[10.1080/11250000903419731](https://doi.org/10.1080/11250000903419731).
- Barker, R. J., Schofield, M. R., Link, W. A., & Sauer, J. R. (2018). On the reliability of N-mixture models for count data. *Biometrics*, 74, 369–377. doi:[10.1111/biom.12734](https://doi.org/10.1111/biom.12734).
- Bessone, M., Köhl, H. S., Hohmann, G., Herbinger, I., N'Goran, K. P., Asanzi, P., et al. (2020). Drawn out of the shadows: Surveying secretive forest species with camera trap distance sampling. *Journal of Applied Ecology*, 57, 963–974. doi:[10.1111/1365-2664.13602](https://doi.org/10.1111/1365-2664.13602).
- Bidder, O. R., Walker, J. S., Jones, M. W., Holton, M. D., Urge, P., & Scantlebury, D. M. (2015). Step by step: Reconstruction of terrestrial animal movement paths by dead-reckoning. *Movement ecology*, 3, 1–16. doi:[10.1186/s40462-015-0055-4](https://doi.org/10.1186/s40462-015-0055-4).
- Borchers, D. L., & Efford, M. G. (2008). Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics*, 64, 377–385.
- Börger, L., Dalziel, B. D., & Fryxell, J. M. (2008). Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters*, 11, 637–650. doi:[10.1111/j.1461-0248.2008.01182.x](https://doi.org/10.1111/j.1461-0248.2008.01182.x).
- Broadley, K., Burton, A. C., Avgar, T., & Boutin, S. (2019). Density-dependent space use affects interpretation of camera trap detection rates. *Ecology and Evolution*, 9, 14031–14041. doi:[10.1002/ece3.5840](https://doi.org/10.1002/ece3.5840).
- Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., & Fisher, J. T. (2015). Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, 52, 675–685. doi:[10.1111/1365-2664.12432](https://doi.org/10.1111/1365-2664.12432).
- Calabrese, J. M., Fleming, C. H., & Gurarie, E. (2016). Ctm: An R Package for analyzing animal relocation data as a continuous-time stochastic process. *Methods in Ecology and Evolution*, 7, 1124–1132. doi:[10.1111/2041-210X.12559](https://doi.org/10.1111/2041-210X.12559).
- Campos-Candela, A., Palmer, M., Balle, S., & Alós, J. (2018). A camera based method for estimating absolute density in animals displaying home range behaviour. *Journal of Animal Ecology*, 87, 825–837. doi:[10.1111/1365-2656.12787](https://doi.org/10.1111/1365-2656.12787).
- Campos-Candela, A., Palmer, M., Balle, S., & Alós, J. (2019). Response to Abolaffio et al. (2019): Avoiding misleading

- messages. *Journal of Animal Ecology*, 88, 2017–2021. doi:10.1111/1365-2656.13084.
- Cappelle, N., Després-Einspenner, M. L., Howe, E. J., Boesch, C., & Kühl, H. S. (2019). Validating camera trap distance sampling for chimpanzees. *American Journal of Primatology*, 81, e22962. doi:10.1002/ajp.22962 Article.
- Caravaggi, A., Zaccaroni, M., Riga, F., Schai-Braun, S. C., Dick, J. T., & Montgomery, W. I. (2016). An invasive-native mammalian species replacement process captured by camera trap survey random encounter models. *Remote Sensing in Ecology and Conservation*, 2, 45–58. doi:10.1002/rse2.11.
- Carbajal-Borges, J. P., Godínez-Gómez, O., & Mendoza, E. (2014). Density, abundance and activity patterns of the endangered *Tapirus bairdii* in one of its last strongholds in southern Mexico. *Tropical Conservation Science*, 7, 100–114. doi:10.1177/194008291400700102.
- Chauvenet, A. L., Gill, R. M., Smith, G. C., Ward, A. I., & Massei, G. (2017). Quantifying the bias in density estimated from distance sampling and camera trapping of unmarked individuals. *Ecological Modelling*, 350, 79–86. doi:10.1016/j.ecolmodel.2017.02.007.
- Cusack, J. J., Swanson, A., Coulson, T., Packer, C., Carbone, C., Dickman, A. J., et al. (2015). Applying a random encounter model to estimate lion density from camera traps in Serengeti National Park, Tanzania. *The Journal of Wildlife Management*, 79, 1014–1021. doi:10.1002/jwmg.902.
- Durbach, I., Borchers, D., Sutherland, C., & Sharma, K. (2020). Fast, flexible alternatives to regular grid designs for spatial capture-recapture. *Methods in Ecology and Evolution*, 12, 298–310. doi:10.1111/2041-210X.13517.
- Efford, M. G. (2019). Non-circular home ranges and the estimation of population density. *Ecology*, 100, e02580. doi:10.1002/ecy.2580 Article.
- Efford, M. G., Dawson, D. K., Jhala, Y. V., & Qureshi, Q. (2016). Density-dependent home-range size revealed by spatially explicit capture–recapture. *Ecography*, 39, 676–688 <https://doi.org/10.1111/ecog.01511>.
- Engeman, R. M. (2005). Indexing principles and a widely applicable paradigm for indexing animal populations. *Wildlife Research*, 32, 203–210. doi:10.1071/WR03120.
- Fleming, C. H., Calabrese, J. M., Mueller, T., Olson, K. A., Leimgruber, P., & Fagan, W. F. (2014). From fine-scale foraging to home ranges: A semivariance approach to identifying movement modes across spatiotemporal scales. *American Naturalist*, 183, E154–E167. doi:10.1086/675504.
- Fleming, C. H., Fagan, W. F., Mueller, T., Olson, K. A., Leimgruber, P., & Calabrese, J. M. (2016). Estimating where and how animals travel: An optimal framework for path reconstruction from autocorrelated tracking data. *Ecology*, 97, 576–582. doi:10.1890/15-1607.1.
- Focardi, S., La Morgia, V., Montanaro, P., Riga, F., Calabrese, A., Ronchi, F., et al. (2020). Reliable estimates of wild boar populations by nocturnal distance sampling. *Wildlife Biology*, 2020(4), 00694. doi:10.2981/wlb.00694 Article wlb.
- Garrote, G., Pérez de Ayala, R., Álvarez, A., Martín, J., Ruiz, M., De Lillo, S., et al. (2021). Improving the random encounter model method to estimate carnivore densities using data generated by conventional camera-trap design. *Oryx: The Journal of the Fauna Preservation Society*, 55, 99–104. doi:10.1017/S0030605318001618.
- Gilbert, N. A., Clare, J. D., Stenglein, J. L., & Zuckerman, B. (2021). Abundance estimation of unmarked animals based on camera-trap data. *Conservation Biology*, 35, 88–100 <https://doi.org/10.1111/cobi.1351>.
- Gurarie, E., Fleming, C. H., Fagan, W. F., Laidre, K. L., Hernández-Pliego, J., & Ovaskainen, O. (2017). Correlated velocity models as a fundamental unit of animal movement: Synthesis and applications. *Movement Ecology*, 5, 1–18. doi:10.1186/s40462-017-0103-3.
- Hofmeester, T. R., Crowsigt, J. P., Odden, J., Andrén, H., Kindberg, J., & Linnell, J. D. (2019). Framing pictures: A conceptual framework to identify and correct for biases in detection probability of camera traps enabling multi-species comparison. *Ecology and Evolution*, 9, 2320–2336. doi:10.1002/ece3.4878.
- Howe, E. J., Buckland, S. T., Després-Einspenner, M. L., & Kühl, H. S. (2017). Distance sampling with camera traps. *Methods in Ecology and Evolution*, 8, 1558–1565. doi:10.1111/2041-210X.12790.
- Hutchinson, J. M., & Waser, P. M. (2007). Use, misuse and extensions of “ideal gas” models of animal encounter. *Biological Reviews*, 82, 335–359. doi:10.1111/1365-2664.13913.
- Johanns, P., Haucke, T., & Steinhage, V. (2022). Distance estimation and animal tracking for wildlife camera trapping. *arXiv preprint. arXiv:2202.04613*.
- Jourdain, N. O. A. S., Cole, D. J., Ridout, M. S., & Rowcliffe, J. M. (2020). Statistical development of animal density estimation using random encounter modelling. *Journal of Agricultural, Biological, and Environmental Statistics*, 25, 148–167. doi:10.1007/s13253-020-00385-4.
- Kéry, M. (2018). Identifiability in *N*-mixture models: A large-scale screening test with bird data. *Ecology*, 99, 281–288. doi:10.1002/ecy.2093.
- Knape, J., Arlt, D., Barraquand, F., Berg, Å., Chevalier, M., Pärt, T., et al. (2018). Sensitivity of binomial *N*-mixture models to overdispersion: The importance of assessing model fit. *Methods in Ecology and Evolution*, 9, 2102–2114. doi:10.1111/2041-210X.13062.
- Link, W. A., Schofield, M. R., Barker, R. J., & Sauer, J. R. (2018). On the robustness of *N*-mixture models. *Ecology*, 99, 1547–1551. doi:10.1002/ecy.2362.
- Loonam, K. E., Ausband, D. E., Lukacs, P. M., Mitchell, M. S., & Robinson, H. S. (2020). Estimating abundance of an unmarked, low-density species using cameras. *Journal of Wildlife Management*, 85, 87–96. doi:10.1002/jwmg.21950.
- Loonam, K. E., Ausband, D. E., Lukacs, P. M., Mitchell, M. S., & Robinson, H. S. (2021). Estimating abundance of an unmarked, low-density species using cameras. *The Journal of Wildlife Management*, 85, 87–96 <https://doi.org/10.1002/jwmg.21950>.
- Manzo, E., Bartolommei, P., Rowcliffe, J. M., & Cozzolino, R. (2012). Estimation of population density of European pine marten in central Italy using camera trapping. *Acta Theriologica*, 57, 165–172. doi:10.1007/s13364-011-0055-8.
- Moeller, A. K., Lukacs, P. M., & Horne, J. S. (2018). Three novel methods to estimate abundance of unmarked animals using remote cameras. *Ecosphere (Washington, D.C.)*, 9, e02331. doi:10.1002/ecs2.2331 Article.
- Nakashima, Y. (2020). Potentiality and limitations of *N*-mixture and Royle-Nichols models to estimate animal abundance based on noninstantaneous point surveys. *Population Ecology*, 62, 151–157. doi:10.1002/1438-390X.12028.

- Nakashima, Y., Fukasawa, K., & Samejima, H. (2018). Estimating animal density without individual recognition using information derivable exclusively from camera traps. *Journal of Applied Ecology*, 55, 735–744. doi:10.1111/1365-2664.13059.
- Neilson, E. W., Avgar, T., Burton, A. C., Broadley, K., & Boutin, S. (2018). Animal movement affects interpretation of occupancy models from camera-trap surveys of unmarked animals. *Ecosphere (Washington, D.C.)*, 9, e02092. doi:10.1002/ecs2.2092 Article.
- Noonan, M. J., Fleming, C. H., Akre, T. S., Drescher-lehman, J., Gurarie, E., Kays, R., et al. (2019). The fast and the spurious: Scale-free estimation of speed and distance traveled from animal tracking data. *Movement Ecology*, 7, 1–15. doi:10.1186/s40462-019-0177-1.
- Okubo, A. (1980). *Diffusion and ecological problems: Mathematical models*. Springer-Verlag.
- Palencia, P., Fernández-López, J., Vicente, J., & Acevedo, P. (2021). Innovations in movement and behavioural ecology from camera traps: Day range as model parameter. *Methods in Ecology and Evolution*. doi:10.1111/2041-210X.13609.
- Palencia, P., Rowcliffe, J. M., Vicente, J., & Acevedo, P. (2021). Assessing the camera trap methodologies used to estimate density of unmarked populations. *Journal of Applied Ecology*, 58, 1583–1592. doi:10.1111/1365-2664.13913.
- Palencia, P., Vicente, J., Barroso, P., Barasona, J.Á., Soriguer, R. C., & Acevedo, P. (2019). Estimating day range from camera-trap data: The animals' behaviour as a key parameter. *Journal of Zoology*, 309, 182–190. doi:10.1111/jzo.12710.
- Plummer, M. (2003). JAGS: A program for analysis of bayesian graphical models using gibbs sampling. In *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*.
- Preisler, H. K., Ager, A. A., Johnson, B. K., & Kie, J. G. (2004). Modeling animal movements using stochastic differential equations. *Environmetrics*, 15, 643–657. doi:10.1002/env.636.
- Rovero, F., & Marshall, A. R. (2009). Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology*, 46(5), 1011–1017. doi:10.1111/j.1365-2664.2009.01705.x.
- Rovero, F., Zimmermann, F., Berzi, D., & Meek, P. (2013). "Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix (Online)*, 24, 148–156. doi:10.4404/hystrix-24.2-8789.
- Rowcliffe, J. M., Field, J., Turvey, S. T., & Carbone, C. (2008). Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, 45, 1228–1236. doi:10.1111/j.1365-2664.2008.01473.x.
- Rowcliffe, J. M., Jansen, P. A., Kays, R., Kranstauber, B., & Carbone, C. (2016). Wildlife speed cameras: Measuring animal travel speed and day range using camera traps. *Remote Sensing in Ecology and Conservation*, 2, 84–94. doi:10.1002/rse2.17.
- Rowcliffe, J. M., Carbone, C., Kays, R., Kranstauber, B., & Jansen, P. A. (2012). Bias in estimating animal travel distance: The effect of sampling frequency. *Methods in Ecology and Evolution*, 3(4), 653–662. doi:10.1111/j.2041-210X.2012.00197.x.
- Rowcliffe, J. M., Carbone, C., Jansen, P. A., Kays, R., & Kranstauber, B. (2011). Quantifying the sensitivity of camera traps: An adapted distance sampling approach. *Methods in Ecology and Evolution*, 2, 464–476.
- Royle, J. A. (2004). N-mixture models for estimating population size from spatially replicated counts. *Biometrics*, 60, 108–115. doi:10.1111/j.0006-341X.2004.00142.x.
- Royle, J. A., & Young, K. V. (2008). A hierarchical model for spatial capture–recapture data. *Ecology*, 89, 2281–2289. doi:10.1890/07-0601.1.
- Schaus, J., Uzal, A., Gentle, L. K., Baker, P. J., Bearman-Brown, L., Bullion, S., et al. (2020). Application of the Random Encounter Model in citizen science projects to monitor animal densities. *Remote Sensing in Ecology and Conservation*, 6, 514–528. doi:10.1002/rse2.153.
- Signer, J., Fieberg, J., & Avgar, T. (2017). Estimating utilization distributions from fitted step-selection functions. *Ecosphere (Washington, D.C.)*, 8, e01771. doi:10.1002/ecs2.1771 Article.
- Skalski, J. R., Ryding, K. F., & Millsbaugh, J. J. (2005). *Wildlife demography*. Elsevier.
- Spiegelhalter, D., Best, N., Carlin, B., & van der Linde, A. (2002). Bayesian measures of model complexity and fit (with discussion). *Journal of the Royal Statistical Society Series B*, 64, 583–639. doi:10.1111/1467-9868.00353.
- Trolliet, F., Vermeulen, C., Huynen, M. C., & Hambuckers, A. (2014). Use of camera traps for wildlife studies: A review. *Biotechnologie, Agronomie, Société et Environnement*, 18, 446–454.
- Turchin, P. (1998). *Quantitative analysis of movement*. Cambridge University Press.
- Van Ballenberghe, V., & Miquelle, D. G. (1990). Activity of moose during spring and summer in interior Alaska. *The Journal of Wildlife Management*, 54, 391–396. doi:10.2307/3809645.
- Vander Vennen, L. M., Patterson, B. R., Rodgers, A. R., Moffatt, S., Anderson, M. L., & Fryxell, J. M. (2016). Diel movement patterns influence daily variation in wolf kill rates on moose. *Functional Ecology*, 30, 1568–1573. doi:10.1111/1365-2435.12642.
- Williams, B. K., Nichols, J. D., & Conroy, M. J. (2002). *Analysis and management of animal populations. modeling, estimation and decision making*. Academic Press.