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Assessing the camera trap methodologies used to estimate density of unmarked populations

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Abstract

1. Population density estimations are essential for wildlife management and conservation. Camera traps have become a promising cost-effective tool, for which several methods have been described to estimate population density when individuals are unrecognizable (i.e. unmarked populations). However, comparative tests of their applicability and performance are scarce.
2. Here, we have compared three methods based on camera traps to estimate population density without individual recognition: Random Encounter Model (REM), Random Encounter and Staying Time (REST) and Distance Sampling with camera traps (CT-DS). Comparisons were carried out in terms of consistency with one another, precision and cost-effectiveness. We considered six natural populations with a wide range of densities, and three species with different behavioural traits (red deer *Cervus elaphus*, wild boar *Sus scrofa* and red fox *Vulpes vulpes*). In three of these populations, we obtained independent density estimates as a reference.
3. The densities estimated ranged from 0.23 individuals/km^2 (fox) to 34.87 individuals/km^2 (red deer). We did not find significant differences in terms of density values estimated by the three methods in five out of six populations, but REM has a tendency to generate higher average density values than REST and CT-DS. Regarding the independents' densities, REM results were not significantly different in any population, and REST and CT-DS were significantly different in one population. The precision obtained was not significantly different between methods, with average coefficients of variation of 0.28 (REST), 0.36 (REM) and 0.42 (CT-DS). The REST method required the lowest human effort.
4. *Synthesis and applications*. Our results show that all of the methods examined can work well, with each having particular strengths and weaknesses. Broadly, Random Encounter and Staying Time (REST) could be recommended in scenarios of high abundance, Distance Sampling with camera traps (CT-DS) in those of low abundance while Random Encounter Model (REM) can be recommended when camera trap performance is not optimal, as it can be applied with less risk of bias. This broadens the applicability of camera trapping for estimating densities of unmarked populations using information exclusively obtained from camera

traps. This strengthens the case for scientifically based camera trapping as a cost-effective method to provide reference estimates for wildlife managers, including within multi-species monitoring programmes.

KEYWORDS

abundance, carnivores, Distance Sampling, Random Encounter and Staying Time, Random Encounter Model, remote sensing, ungulates, wildlife monitoring

1 | INTRODUCTION

Obtaining accurate estimates of population density (i.e. the number of individuals per area) continues to be a constant challenge for wildlife management and conservation (Nichols & Williams, 2006). It is widely recognized that estimating population size is costly, and that results are often not sufficiently precise for well-informed management purposes (Morellet et al., 2007). Feasible methods with which to attain precise and accurate estimates of population density are, therefore, in great demand. The use of remotely triggered cameras (camera traps) for this purpose has substantially increased over the last few years (Rovero & Zimmermann, 2016). Camera trapping is relatively low cost (except the initial inversion), generates information on multiple species, is minimally invasive and makes it possible to obtain information on highly cryptic species inhabiting a wide range of habitats (Steenweg et al., 2017). As a result, camera trapping methods are increasingly core tools for wildlife population monitoring (e.g. for wild boar at the European level, ENETWILD-consortium et al., 2019).

When population densities are the target parameter, camera trapping is frequently used to obtain data for spatially explicit capture–recapture models that require individually identifiable animals (Royle et al., 2013). However, many wildlife species have no natural markings to allow individual identification, so require physical capture and marking to apply this family of models to camera trap data. In this case, the application of such capture–recapture models (in a broad sense) can be expensive, invasive and logistically challenging. Validating methods for estimating population density using camera traps in the absence of identifiable individuals can broaden their applicability for wildlife monitoring. In this context, there are different methods to estimate population size (number of animals) without individual recognition: Time to Event Model (Moeller et al., 2018), Random Encounter Model (REM; Rowcliffe et al., 2008), Spatial Counts (Chandler & Royle, 2013; Evans & Rittenhouse, 2018), Distance Sampling based on camera traps (CT-DS; Howe et al., 2017), Random Encounter and Staying Time (REST; Nakashima et al., 2018) and, more recently, a model that considers the species' use of space (Luo et al., 2020). Most of these methods are based on modelling the encounter rate, and the main divergence point between them is the procedure to address the effective sampling frame (i.e. the broader study area about which one wishes to make inference). While some of them estimate abundance within an area explicitly defined in the model by accounting when and where animals are detected (Chandler & Royle, 2013), others estimate density within the collective field of view (FOV) of the cameras which are representative of the sampling frame (Rowcliffe et al., 2008). A more in-depth theoretical comparison between unmarked methods was described by Gilbert et al. (2020). However, an empirical comparison of these methods under field conditions is lacked and highly demanded.

We have compared the performance of three methods to estimate population density with compatible sampling design: REM, REST and CT-DS. The CT-DS is based on Distance Sampling, a framework that is considered as a core method for wildlife monitoring (Buckland et al., 2001; Thomas et al., 2010). Considering the robust theoretical framework, specific software and advice for study design, testing CT-DS could considerably increase the applicability of camera traps for the monitoring of unmarked populations. To date, CT-DS has been applied in a chimpanzee population (Cappelle et al., 2019), a community of species of the rainforest (Bessone et al., 2020, Cappelle et al., 2021), a bighorn sheep population (Harris et al., 2020) and a marmot population (Corlatti et al., 2020). The REM is, without a doubt, the most applied method (Gilbert et al., 2020). Over the last few years, it has been used for a wide range of species (Cusack et al., 2015; ENETWILD-consortium et al., 2019; Pfeffer et al., 2018; Zero et al., 2013), and it is constantly developing (Caravaggi, 2017; Lucas et al., 2015). Its application was originally limited by the need to estimate day range (i.e. distance travelled by an individual during a day). However, approaches for estimating day range exclusively from camera trap data were described (Palencia et al., 2021; Rowcliffe et al., 2016), which has significantly increased its applicability. Nakashima et al. (2018) described the REST model as an extension of REM, but we would like to highlight the mathematical equivalence between REST and CT-DS (Appendix S1). The REST model considers the staying time (i.e. the amount of time detected animals remain within a specific area within the FOV of a camera trap) instead of day range. This could enhance applicability relative to REM, as day range is the most time-consuming parameter to be obtained for REM. To date, the REST model has been applied to estimate the density of forest ungulates (Nakashima et al., 2020) and has been tested with human volunteers (Garland et al., 2020). We have summarized the assumptions of these methods in Table 1. A common feature of these methods is that they do not require spatial autocorrelation in the captures as mark–recapture and related methods do (i.e. one animal does not need to have probability of been captured in more than one camera trap). This allows sampling

TABLE 1 Assumptions for the three methods to estimate density of unmarked species tested on this study: Random Encounter Model (REM), Random Encounter and Staying Time (REST) and Distance Sampling based on camera traps (CT-DS)

Assumption	REM	REST	CT-DS
Camera trap placed randomly with respect to animal movement	X	X	X
Certain detection at 0 distance	X		X
Certain detection at focal area		X	
Closed population	X	X	X
Animal movement and behaviour not affected by camera trap	X	X	X
Objects are detected at their initial locations	X		X
Measurements are exact	X	X	X
Observations are independent events	X	X	X
Snapshot moments selected independently of animal locations			X

designs to use any spacing of camera traps, and therefore larger areas and a wide range of species can be sampled with single surveys. Moreover, these methods share most of the assumptions, and analyses are based on rescaling encounter rate accounting for that on movement parameters (REM and REST) or detectability process (CT-DS). In this respect, we would like to clarify key points. Regarding the closure assumptions, it should be noted that if abundance does change during the survey, these methods will provide an average density across the sampling period. This is a key difference in relation to capture–recapture methods, in which violations of closure can result in detection probability estimates that are too low or the effective sampled area being considered too small, generating positively biased densities (Obbard et al., 2010). Regarding the certain detection at distance 0, estimates of density are negatively biased in proportion to $p(0)$. For instance, if $p(0) = 0.30$, estimates will on average be only 30% of the true density (Borchers et al., 2002). Similarly, if detection is not certain in REST focal area, density will be underestimated. To minimize violations of these assumptions, camera trap should be set at an appropriate height, and activated as faster as possible. Second, in spite of all the methods assumed that animal movement behaviour is not affected by camera traps, each method deals with violations of that assumption in a different way. For REM, those sequences in which animals react to the camera trap are considered for encounter rate but not for speed (Rowcliffe et al., 2016). However, there is not a clear procedure for this violation in REST and CT-DS. Those animals which react by leaving the detection zone will suppose an underestimation of staying time in REST, and encounter rate in CT-DS, and in consequence, underestimation of density. For animals that stand in the detection zone, staying time (REST) and encounter rate (CT-DS) will be inflated. Also, a severe violation of the independence between events is expected because multiple detections of the same individual are considered, but this assumption can be avoided by estimating density variances using a nonparametric bootstrap, resampling points with replacements; and in CT-DS, by applying specific selection criteria to choose the best models (Howe et al., 2019).

In this work, we compared the consistency, precision and cost-effectiveness of the REM, REST and CT-DS methods for population density estimation in a Mediterranean environment, monitoring six wildlife populations of three species (red deer *Cervus elaphus*, wild boar *Sus scrofa* and red fox *Vulpes vulpes*), spanning different behavioural traits and a wide range of densities. Additionally, in three of these populations, we obtained independent estimates by applying distance sampling on line transects and drive counts.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was carried out in two natural areas of Spain with distinct environmental conditions. One of them (site-A), the Doñana Biological Reserve, is a territory of approximately 6,800 ha located in Doñana National Park (37°0′N, 6°30′W). It is located on the Atlantic coast of south-west Spain, dominated by Mediterranean shrubland and 300 ha of marshland. The climate is thermomediterranean, with marked seasons. The average altitude is 15 m a.s.l. The second study area (site-B) is a territory of approximately 6,800 ha that is located in Montes de Toledo (39°23′N, 4°4′W), a mountain chain located in central Spain. Vegetation is dominated by woodland habitats (*Quercus* spp.) and 'dehesas' (savannah-like habitats composed of pastures that mainly include oak trees). The climate is mesomediterranean, and the average altitude is 900 m a.s.l.

2.2 | Camera trap survey

In all, 25 camera traps Bushnell Aggressor Trophy Cams were used in site-A (from September till November 2018), and 20 in site-B (from November 2018 till April 2019) covering the central zone of each study area. We used a systematic design with a random origin. Camera traps were deployed facing north at the intersection of a grid with 2 km (site-A) or 1.5 km (site-B) spacing, 40–50 cm above the ground and angled to be parallel to the slope of the ground. Camera traps were not baited. Realized sampling locations deviated from the design by as much as 80 m in order to mount camera traps on trees and avoid very unfavourable conditions (e.g. dense shrubland). Only one camera trap in site-B had to be deployed outside the 80 m buffer. During the installation of each camera trap, natural marks (rocks, branches, etc.) were placed in the FOV at 2.5 m intervals from the camera trap (Figure 1). These marks were later used to locate the position of the individuals captured with the camera trap.

The camera traps were set to be operative all day, to record a burst of three consecutive photos (rapid fire) at each activation, and with the minimum triggering interval between activations (0.6 s). The date and time of capture were automatically stamped onto each

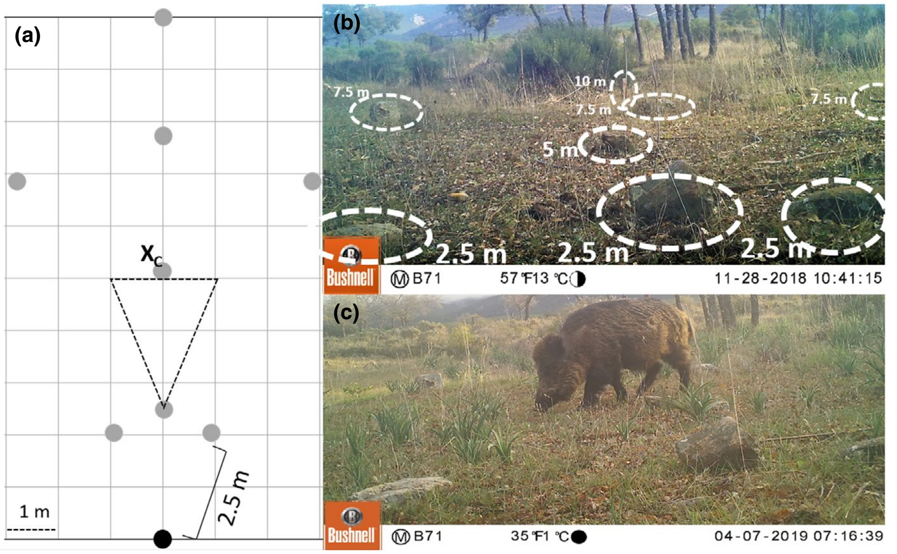

FIGURE 1 (a) Scheme of the position markers (grey dots) used to reference the animal captured by the camera trap (black dot). The central triangle represents the detection zone considered for REST. X_C indicates the position of the wild boar captured in the image c. (b) Marks (stones) were used as references to locate individual positions. Numbers indicate the distance between the stones and the camera trap. (c) A wild boar photo-capture

image. Camera traps were checked every 3 weeks to change their batteries and memory cards.

2.3 | Camera trapping analysis

We exclusively consider the information obtained from camera traps to apply REM, REST and CT-DS.

2.3.1 | Shared features between methods

Some parameters and practical considerations are shared between methods:

1. Animal location: it is necessary to identify the position of each photo-captured animal in the detection zone for the three methods. The natural marks that we deployed in the cameras' FOV during the deployment of the camera traps were used for that purpose (Appendix S2).
2. Regarding group size: because accurate group size estimations are not easily obtained from camera traps, individuals were considered as the unit of observation in the three methods (see also Cusack et al., 2015; Thomas et al., 2010).
3. Movement behaviour: consistent with the approach for estimating day range described by Rowcliffe et al. (2016), those sequences in which animals react to the camera trap were considered for the estimation of the encounter rate, but not for the estimation of either staying time or day range.
4. Activity level: the activity level (i.e. the proportion of time that animals spend active) is a key parameter in the three approaches. Camera traps record animals only when they move outside refuges (Rowcliffe et al., 2014). In the case of REM, the activity level is required to estimate the day range (Rowcliffe et al., 2016). In the case of REST and CT-DS, the activity level is necessary to estimate the proportion of animals that are available for detection (i.e. active). The final density value is corrected by multiplying the density estimated (through REST or CT-DS) by the inverse value of activity (Howe et al., 2017; Nakashima et al., 2018). Activity level was estimated following Rowcliffe et al. (2014) and using the R package `activity` R package (Rowcliffe, 2019).

2.3.2 | REM parameterization

REM is based on modelling the process of random encounters between animals and cameras and accounting for all the variables that affect the encounter rate (Rowcliffe et al., 2008). The equation for estimating density from camera trap encounter rate is:

$$D = \frac{Y}{H} \cdot \frac{\pi}{v \cdot r \cdot (2 + \theta)}, \tag{1}$$

in which Y is the number of encounters (i.e. number of independent photographic sequences), H is the total camera survey effort, v is the average distance travelled by an individual during a day (day range), and r and θ are the radius and angle of the camera traps detection zone, respectively. We considered an individual of the target species entering and exiting the FOV of the camera trap as independent contact. Day range was estimated as the product of speed and activity. First, speed was measured on each sequence by dividing the distance travelled by the duration of the sequence. Second, we estimated activity level. Finally, we estimated day range by following the procedure described by Palencia et al. (2021). Briefly, using `trappingmotion` R package (Palencia, 2020), we identified different movement behaviours on the basis of the speeds measured for the sequences. For each behaviour, we estimated the average speed and we weighted the activity level considering the proportion of the time that the population spent on each behaviour. Day range was finally estimated as the sum of the product of the mean speed and the proportion of the activity level associated with each behaviour. We recorded the position (radial distance and angle) of an animal when it first triggered the camera trap and we 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 resampling camera locations with replacement. We also considered standard errors of day range, radius and angle of detection. We computed the overall variance of density estimates using the delta method (Seber, 1982) and R package 'emdbook' (Bolker, 2019). All the analyses were carried out using 'camtools' R functions (https://github.com/MarcusRowcliffe/camtools).

2.3.3 | REST parameterization

The REST model describes the relationship among population density, encounter rate and staying time of animals in a predetermined detection zone (Nakashima et al., 2018):

$$D = Y \cdot T / (s \cdot H), \tag{2}$$

where T is the staying time per encounter and s is the area of the detection zone (Y and H previously defined). The REST model assumes that camera traps detect animals entering the detection zone (focal area) with certainty. To define the focal area, we fitted distance sampling functions to each species detected (Hofmeester et al., 2017), and selected the area in which the detection was certain for the three species sampled in this study. It was an isosceles triangle that covers the central area of the FOV of the camera trap, from 2.5 to 5 m (Figure 1). The outer corners of this triangle were defined during image processing as the central half of the FOV. The initial description of REST estimates T from information recorded from camera traps in video mode. Since video processing is more time-consuming than photos, we here generalized REST to be applied with information from photo mode obtaining consistent results (Appendix S3). Thus, staying time in the focal area was measured as follows: considering the references located in the FOV of the camera (Figure 1), we recorded the difference of time between the last and the first photo in which an individual was inside the focal area (see also Appendix S2). As in the REM parametrization, we considered an individual of the target species entering and exiting the focal area of the camera trap as an independent contact. Model fitting used maximum likelihood estimation as in Nakashima et al. (2018), using an exponential distribution for expected staying time, and a negative binomial distribution for the expected number of encounters. The variance of the population density was estimated by the delta method combining model and activity level variances.

2.3.4 | CT-DS parameterization

This method is an adaptation of point transect distance sampling considering camera traps instead of humans as observers. In traditional point transect surveys, the observer samples each location at one or a few instants in time; however, camera traps remain at the point for prolonged periods. Considering that, it is necessary to discretize the number of times that the camera trap can potentially record an animal (T_k/t see below). The main equation is (Howe et al., 2017):

$$D = \frac{Y}{\pi \cdot w^2 \cdot e \cdot p}, \tag{3}$$

where $e = \theta \cdot H/2 \cdot \pi \cdot t$ is the sampling effort, t is the length of the time step between snapshot moments (fixed value of 2 s in this case), Θ is the angle of the FOV of the camera trap, w is the truncation distance and p is the estimated probability that an animal within distance w is detected by the camera trap, estimated from a detection function model fitted to animal distances from camera (Buckland et al., 2001). Parameters Y and H were previously defined.

We recorded observation distances between camera traps and animals at 2 s intervals (i.e. at 0, 2, 4, …). Following the exploratory analyses, we left-truncated the data when fewer than expected detection near the camera traps were recorded (Buckland et al., 2001). We right-truncated the data when the probability of detection was lower than 0.1. As multiple detections of the same animal during a single pass through the detection zone are considered, we estimated variances using a nonparametric bootstrap, resampling points with replacement and we followed Howe et al. (2019) to select the best models.

To evaluate the cost-effectiveness of each method, we recorded the time taken to process the images (i.e. parameter estimation) and carry out the analysis for each method. Finally, the density values were statistically compared using the Wald test, with a test statistic W assessed on the chi-squared distribution with one degree of freedom (Wald & Wolfowitz, 1940).

2.4 | Independent density estimates

2.4.1 | Red deer populations (A and B)

In the red deer populations, we obtained independent estimates by applying line-transect distance sampling, which is considered a gold standard method for reed deer in Mediterranean habitats (Acevedo et al., 2008). Surveys were carried out during the rutting season (September), began 2 hr before the sunset and were carried out from a four-wheel-drive vehicle with an average speed of 10 km/hr in population A, and carried out on foot in population B. The total distance surveyed considering all the transects were 71 and 51 km in populations A and B, respectively. Each transect was repeated twice. When a group of deer was detected, we recorded distance between the observer and the animals with a telemeter, as well as group composition considering different sex and age classes when it was possible.

We applied stratified convectional distance sampling. We considered two strata in both populations, one of them characterized by high encounter rate and good visibility (open habitats), and the other one by low encounter rate and poor visibility (woody habitats).

Data were right-truncated to eliminate the 10%–15% (approx.) of the furthest observations (Buckland et al., 2001). Half-normal, hazard rate and uniform models using cosine, hermite polynomial and simple polynomial were fitted for detection function. The selection of the best model and adjustment term was based on AIC (Buckland et al., 2001).

2.4.2 | Wild boar population B

In this population, we applied drive counts to estimate the density of wild boar (ENETWILD-consortium et al., 2019). Concretely, we applied three independent drive counts between November and January in three different scrubland zones of the study area, and overlapping with hunting activities. Each day we surveyed an average of 697.21 ha ± 74.42 (*SE*), with an average of 37.33 observers ± 5.37 (*SE*). Observers were placed in fixed locations with a relatively open field of view (e.g. firebreaks). The drive count duration was 4 hr (from 11:00 to 15:00), and while the observers were in their locations, 44 beaters ± 5.29 (*SE*) with 440 dogs ± 52.92 (*SE*) were moving across the area; and assuming that all the animals were detected. Finally, a coordinator collected all the information and minimize the likelihood of double counting. Density was estimated by dividing the number of observed animals between the survey area, and by assuming that at the moment of drive counts (midday), all the wild boar were in the scrubland and woodlands areas, and density in grassland zones (dehesas) was 0. This assumption was supported by telemetry data of animals tagged on this population (E. Laguna, unpubl. data).

3 | RESULTS

3.1 | Camera trapping methods

The densities estimated from camera trapping methods ranged from 0.23 individuals/km^2 (red fox—CT-DS—site-B) to 34.87 individuals/km^2 (red deer—REM—site-B; Figure 2). The estimated parameter values are shown in Table 2. We found a significant positive correlation between the density values (per species and site, $n = 6$) estimated by each method (Pearson correlation: REM-REST: $R = 0.87$, $p = 0.025$, $n = 6$; REM-CTDS: $R = 0.93$, $p = 0.0063$, $n = 6$; REST-CTDS: $R = 0.88$, $p = 0.02$, $n = 6$). We only found significant differences between the estimates obtained with the three methods in wild boar population, site-B (Wald test: CT-DS vs. REM: $W = 5.63$, $p = 0.02$; REM vs. REST: $W = 4.90$, $p = 0.03$). Significant differences among methods were not found in the other populations. In general, the REM estimates tend to be higher than those obtained by REST and CT-DS (Figure 2).

In relation to the precision of the estimates, we did not find significant differences in coefficients of variation (CV) between methods (ANOVA repeated measurements, p: 0.698). The average CV for REST was 0.28, for REM was 0.36 and 0.42 for CT-DS.

In relation to the effort required (Table 2), REST was the least time-consuming method both in terms of image processing and carrying out the analysis. REM required more time for image processing, and CT-DS required more time for the analysis.

3.2 | Independent density estimates

During the surveys, 51 groups (site-A) and 259 (site-B) of red deer were observed. Best detection models were half normal cosine (site-A) and hazard-rate cosine (site-B). The average densities estimated in red deer populations surveyed with line transects were 10.68 individuals/km^2 ± 2.31 (*SE*) and 22.94 individuals/km^2 ± 2.98 (*SE*) in sites A and B, respectively.

Regarding the drive counts, the average number of wild boar detected per day was 66.33 ± 22.81. After discarding open areas, average population density was 8.24 individuals/km^2 ± 2.18 (*SE*).

In the red deer populations, we did not find significant differences in estimates from line transects and camera trapping methods. In wild boar site-B, drive counts results were not significantly

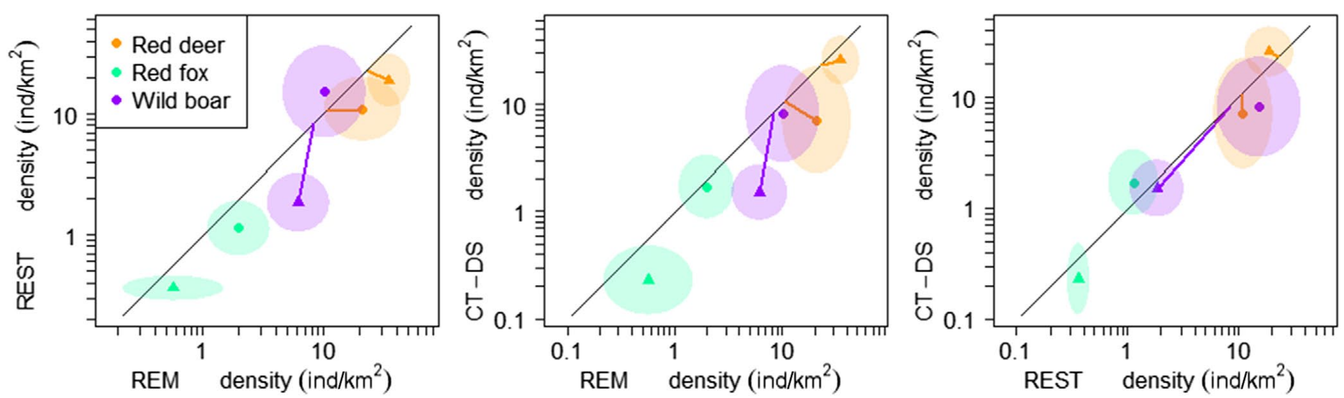

FIGURE 2 Estimated densities plotted in pairwise comparisons between methods. Solid points represent density values (circles and triangles, respectively, populations a and b), and translucent ellipses represent 95% confidence intervals. The diagonal is the equality line. Lines joining points to the equality line indicate independent estimates (line-transect distance sampling and drive counts)

TABLE 2 Estimated parameter values for each method (see main text for details) including those related to effort, namely the time required for image processing and for data analysis

		Site-A			Site-B		
Method	**Parameter**	**Red deer**	**Wild boar**	**Red fox**	**Red deer**	**Wild boar**	**Red fox**
REM	*Y/H* (individuals·cam/day)	0.74	0.93	0.22	0.7	0.15	0.05
	v (km/day)	4.85	13.10	26.74	3.83	5.03	16.71
	r (km)	0.0084	0.008	0.0049	0.006	0.0057	0.0064
	Θ (radians)	0.733	0.733	0.705	0.733	0.733	0.733
	Image processing (min)	610	900	288	1,269	505	140
	Analysis (min)	40	45	32	39	41	35
REST	*T* (s)	9.00	3.05	1.14	7.14	2.58	1.16
	Y (individuals)	72.71	153.98	116.71	317.75	167.34	63.64
	s (km^2)	2.5×10^{-6}	2.5×10^{-6}	2.5×10^{-6}	2.5×10^{-6}	2.5×10^{-6}	2.5×10^{-6}
	H (s)	3.85×10^{7}	3.85×10^{7}	9.84×10^{7}	1.02×10^{8}	2.09×10^{8}	2.09×10^{8}
	Image processing (min)	220	250	61	340	113	55
	Analysis (min)	10	15	8	12	11	7
CT-DS	*Y* (individuals)	751	821	305	2,567	958	116
	w (m)	10	11.5	10	9.5	10.5	7
	P	0.23	0.44	0.22	0.12	0.34	0.71
	Image processing (min)	577	490	188	11,035	370	110
	Analysis (min)	110	100	85	123	97	81
	Activity level	0.62	0.32	0.48	0.47	0.45	0.39

different from the REM estimate (Wald test, $W = 0.50$, $p = 0.48$), but it was significantly different from the REST (Wald test, $W = 8.33$, $p = 0.004$) and CT-DS estimates ($W = 9.13$, $p = 0.003$).

4 | DISCUSSION

The possibility of using camera traps to estimate densities of unmarked populations substantially increases the range of species and situations for which density estimates can be obtained. In this study, we have compared three methodologies (REM, REST and CT-DS) to estimate population density from camera trap data without the need for either individual identification or spatial autocorrelation in the captures. Two of them, REST and CT-DS, have so far been very little tested on natural populations (but see Bessone et al., 2020; Cappelle et al., 2019; Nakashima et al., 2020).

Our results show a high correlation, and no significant differences in the density values estimated through each method in five of the six populations monitored. Additionally, comparing the camera trapping results with the independent estimates available for red deer populations and wild boar site-B population, REM estimates were not significantly different in any comparison while REST and CT-DS were only significantly different from the independent estimate in the wild boar population. This suggests a consistency of camera trapping methods to estimate density of unmarked populations, especially REM. Regarding the wild boar site-B population, the results suggest that REST and CT-DS may be underestimating density in this population, but we do not currently have a clear hypothesis about why this is.

Our results highlight a general tendency for REM to generate higher density values than REST and CT-DS, which generated equivalent results. We found this pattern in five of the six sampled populations. Previous study described a tendency of CT-DS to underestimate density (Corlatti et al., 2020). The equivalence obtained between REST and CT-DS estimates (Figure 2) reinforces the mathematical equivalence of both methods (Appendix S1). The higher values obtained by REM can be partially explained as a consequence of a malfunction problem of the camera traps. Despite being set to record bursts of three consecutive photos, we noted that in around 12% activations the camera traps only took one or two photos, and in a further 9% of activations, time between photos within a burst was longer than 2 s (Appendix S4). Furthermore, other evaluations of this camera trap model have concluded that the recovery time is higher than the manufacturer's rating (0.6 s) and it is not consistent between activations (https://www.trailcampro.com/products/bushnell-trophy-cam-hd-low-glow?_pos=40&_sid=6a15c66a4&_ss=r). These problems could suggest an underestimation of density in the case of CT-DS and REST because, in some sequences, we did not effectively record complete trajectories of animals within the field of view. In the case of CT-DS, this could underestimate the number of observations (*Y*, Equation 3). In the case of REST, this could underestimate both the staying time (if precise times of entry to and exit from the focal zone were not recorded) and the encounter rate (if the animal entered and left the focal zone without being photographed). The influence of these problems on REM estimates is lower because (a) one photo is enough to consider the sequence for encounter rate and (b) those sequences with high time-lapse between consecutive photos were not considered for travel speed estimation. In these methods, it is recommended to use camera traps with reliably fast trigger and photo burst rates to generate more accurate registration of animal trajectories inside the FOV, and in consequence, more accurate density results. Any poor performance of the camera traps will compromise population density estimates (McIntyre et al., 2020).

In relation to precision, previous studies did not consider the uncertainty associated with all the parameters (e.g. Cappelle et al., 2019; Howe et al., 2017; Nakashima et al., 2018), but we have considered the variance in all the parameters of each method, including the activity level. We found no significant differences between methods, with an average CVs ranging from 0.28 (REST) to 0.42 (CT-DS). Most of the variance in these methods was attributable to the variation in encounter rate between camera traps (Buckland et al., 2001; Howe et al., 2017). This variation could be reduced using a stratified sampling design (Buckland et al., 2001; Rowcliffe et al., 2008), but this may be challenging in camera trapping studies because of the small sampling area covered by each camera; this means that encounter rate is more strongly influenced by microsite conditions than by larger-scale habitat characteristics that can be defined across wide areas and therefore used for pre-stratification. Additionally, to consider covariates accounting of microsite conditions could also improve estimates precision. The variance can also be reduced by increasing the sampling effort, by means of increasing the number of camera placement (Schaus et al., 2020). Eventually, a protocol equivalent to adaptive distance sampling surveys can be applied. It consists of conducting an additional survey effort in those sampling points where more animals are recorded, which is especially useful in populations distributed patchily and sparsely (Buckland, 2004). Simulations have shown that a situation of high variance in encounter rate with around 20–25 camera traps is expected to yield a coefficient of variation around 0.40 (figure 4, Rowcliffe et al., 2008), which is consistent with the results of our study (mean CV of 0.36 in REM estimates). Accordingly, to obtain a CV lower than 0.20, required for effective wildlife management (Williams et al., 2002), the effort with REM will be around 100 camera traps. Regarding CT-DS, Bessone et al. (2020) obtained an average CV of 0.37 in spite of sampling 750 locations. In this respect, Cappelle et al. (2021) concluded that a wide variety of survey designs can be applied to achieve CV between 0.10 and 0.20 with CT-DS, for instance, with at least 100 sampling days at as few 50 camera trap placements. Future field studies are needed to evaluate the improvement in precision regarding the number of sampled locations. For instance, a moving survey (i.e. place camera traps in one place and then move them to a new location) will increase the sampled locations, and in consequence precision. This is a relatively cost-effective approach as it reduces the required number of devices.

Our application of the three methods explored here was free-standing, in that it derived all the necessary parameters exclusively from the camera trap survey, without references to auxiliary data that is a habitual practice in previous studies (Caravaggi et al., 2016; Cusack et al., 2015; Manzo et al., 2012). In this respect, it should be noted that more accurate day range values are estimated from camera trap data, because telemetry usually underestimates this parameter (Palencia et al., 2021; Rowcliffe et al., 2012). Derive all the parameters from the camera trap data required additional effort in the field to identify reference objects at known distances from camera traps (Figure 1), and these time costs were similar across methods. However, time costs for image processing were distinctly different across methods (Table 1). The REST method was the least-time consuming, mainly because not all the animals captured by the camera traps were considered in the analysis, only those that crossed the focal triangle of detection defined within the wider camera field of view. Although this can be considered as a strong point for REST, we should highlight that this can limit the applicability of the method when low-density species are monitored, with low sampling efforts, in which the expected encounter rate can be not enough to obtain precise estimates. On the other hand, the image processing effort for CT-DS was relatively high in this study (Corlatti et al., 2020), but it could be substantially reduced using a snapshot interval longer than 2 s, or by analysing only the data collected in the peak of the activity pattern, assuming that all individuals in the population are active at this time (Howe et al., 2017). In this respect, CT-DS could be proposed as a useful method to monitor low-density species because the number of records is increased when the same individual spends more than one snapshot moment in front of the camera trap. In terms of the effort needed to analyse the data, CT-DS is the most time-consuming method, mainly because the exploratory analyses, goodness-of-fit testing and model selection are critical (Howe et al., 2019).

Finally, we would like to discuss how to deal with those animals that react to the camera traps, since these reactions influence time spent in front of the camera, and can therefore result in bias. While REM and REST can adjust for this by discarding records with evident reactions for the purposes of speed and staying time estimations, respectively (see ‘Shared features between methods’ section in Materials and methods), there is no consensus on how to deal with this problem in CT-DS. It is well described that attraction or avoidance of observers is expected to induce bias in distance sampling (Buckland et al., 2001). Because of this, some authors proposed to discard the first period of the survey to allow animals to become accustomed to the camera traps (Howe et al., 2017); other authors discarded all the observations where animal behaviour indicated a reaction to the camera traps (Bessone et al., 2020) while others discarded some data to obtain a reasonable detection function fitting (Cappelle et al., 2019). In our opinion, none of these approaches totally solves the bias induced by reactive animals, and further research is needed to solve this problem in CT-DS.

In conclusion, this is the first study in which REM, REST and CT-DS have been compared. The results showed no significant differences in terms of density estimates (in five of the six populations sampled), or in precision; which clearly enhances the applicability of any of these methods. However, a high priority for future development is to improve the precision of estimates (e.g. as function of the number of camera traps placements) which would notably increase the utility of these methods. Considering the human effort and the optimization of the camera trap records, REST could be recommended in scenarios of highly abundant species, CT-DS could be recommended for low-density species, while if the camera traps used do not have a reliably rapid response time, REM may be preferable because it can be applied with less risk of bias in this case. But it should be noted that camera traps with fast response and recovery times are highly recommended for the three methods.

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AUTHORS' CONTRIBUTIONS

P.P., J.M.R., J.V. and P.A. conceived the study and designed the methodology; P.P. conducted the field survey; P.P., J.M.R. and P.A. analysed the data; P.P. and P.A. managed the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via Zenodo https://zenodo.org/record/4745594#.YJkJ1j_tbIU (Palencia, 2021). Camera trap images used are available on a case-by-case basis request to the corresponding author.

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REFERENCES

Acevedo, P., Ruiz-Fons, F., Vicente, J., Reyes-García, A. R., Alzaga, V., & Gortázar, C. (2008). Estimating red deer abundance in a wide range of management situations in Mediterranean habitats. *Journal of Zoology*, *276*(1), 37–47. https://doi.org/10.1111/j.1469-7998.2008.00464.x

Bessone, M., Kühl, H. S., Hohmann, G., Herbinger, I., N'Goran, K. P., Asanzi, P., Da Costa, P. B., Dérozier, V., Fotsing, E. D. B., Beka, B. I., Iyomi, M. D., Iyatshi, I. B., Kafando, P., Kambere, M. A., Moundzoho, D. B., Wanzalire, M. L. K., & Fruth, B. (2020). Drawn out of the shadows: Surveying secretive forest species with camera trap distance sampling. *Journal of Applied Ecology*, https://doi.org/10.1111/1365-2664.13602

Bolker, B. (2019). *emdbook: Ecological models and data in R*, R package version 1.3.11. https://CRAN.R-project.org/package=emdbook

Borchers, D. L., Buckland, S. T., Stephens, W. E., & Zucchini, W. (2002). *Estimating animal abundance: Closed populations* (Vol. 13). Springer Science & Business Media.

Buckland, S. T. (2004). *Advanced distance sampling*. Oxford University Press.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2001). *Introduction to distance sampling: Estimating abundance of biological populations* (1st ed.). Oxford University Press.

Cappelle, N., Després-Einspenner, M., Howe, E. J., Boesch, C., & Kühl, H. S. (2019). Validating camera trap distance sampling for chimpanzees. *American Journal of Primatology*, *81*(3), e22962. https://doi.org/10.1002/ajp.22962

Cappelle, N., Howe, E. J., Boesch, C., & Kühl, H. S. (2021). Estimating animal abundance and effort–precision relationship with camera trap distance sampling. *Ecosphere*, *12*(1), e03299. https://doi.org/10.1002/ecs2.3299

Caravaggi, A. (2017). remBoot: An R package for random encounter modelling. *The Journal of Open Source Software*, *2*(10), 176. https://doi.org/10.21105/joss.00176

Caravaggi, A., Zaccaroni, M., Riga, F., Schai-Braun, S. C., Dick, J. T. A., Montgomery, W. I., & Reid, N. (2016). An invasive-native mammalian species replacement process captured by camera trap survey random encounter models. *Remote Sensing in Ecology and Conservation*, *2*(1), 45–58. https://doi.org/10.1002/rse2.11

Chandler, R. B., & Royle, J. A. (2013). Spatially explicit models for inference about density in unmarked or partially marked populations. *Annals of Applied Statistics*, *7*(2), 936–954. https://doi.org/10.1214/12-AOAS610

Corlatti, L., Sivieri, S., Sudolska, B., Giacomelli, S., & Pedrotti, L. (2020). A field test of unconventional camera trap distance sampling to estimate abundance of marmot populations. *Wildlife Biology*, *2020*(4). https://doi.org/10.2981/wlb.00652

Cusack, J. J., Swanson, A., Coulson, T., Packer, C., Carbone, C., Dickman, A. J., Kosmala, M., Lintott, C., & Rowcliffe, J. M. (2015). Applying a random encounter model to estimate lion density from camera traps in Serengeti National Park, Tanzania. *The Journal of Wildlife Management*, *79*(6), 1014–1021. https://doi.org/10.1002/jwmg.902

ENETWILD-consortium, Vicente, J., Palencia, P., Plhal, R., Blanco-Aguiar, J. A., Laguna, E., Soriguer, R., López, J. F., Podgórski, T., Petrović, K., Apollonio, M., Scandura, M., Ferroglio, E., Zanet, S., Brivio, F., Keuling, O., Smith, G. C., Guibert, M., Villanúa, D., Rosell, C., … Acevedo, P. (2019). Harmonization of the use of hunting statistics for wild boar density estimation in different study areas. *EFSA Supporting Publications*, *16*(9), https://doi.org/10.2903/sp.efsa.2019.EN-1706

Evans, M. J., & Rittenhouse, T. A. G. (2018). Evaluating spatially explicit density estimates of unmarked wildlife detected by remote cameras. *Journal of Applied Ecology*. https://doi.org/10.1111/1365-2664.13194

Garland, L., Neilson, E., Avgar, T., Bayne, E., & Boutin, S. (2020). Random encounter and staying time model testing with human volunteers. *The Journal of Wildlife Management*, *84*(6), 1179–1184. https://doi.org/10.1002/jwmg.21879

Gilbert, N. A., Clare, J. D. J., Stenglein, J. L., & Zuckerberg, B. (2020). Abundance estimation of unmarked animals based on camera-trap data. *Conservation Biology*, *35*(1), 88–100. https://doi.org/10.1111/cobi.13517

Harris, G. M., Butler, M. J., Stewart, D. R., Rominger, E. M., & Ruhl, C. Q. (2020). Accurate population estimation of Caprinae using camera traps and distance sampling. *Scientific Reports*, *10*(1), 17729. https://doi.org/10.1038/s41598-020-73893-5

Hofmeester, T. R., Rowcliffe, J. M., & Jansen, P. A. (2017). A simple method for estimating the effective detection distance of camera traps. *Remote Sensing in Ecology and Conservation*, *3*(2), 81–89. https://doi.org/10.1002/rse2.25

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*(11), 1558–1565. https://doi.org/10.1111/2041-210X.12790

Howe, E. J., Buckland, S. T., Després-Einspenner, M., & Kühl, H. S. (2019). Model selection with overdispersed distance sampling data. *Methods in Ecology and Evolution*, *10*(1), 38–47. https://doi.org/10.1111/2041-210X.13082

Lucas, T. C. D., Moorcroft, E. A., Freeman, R., Rowcliffe, J. M., & Jones, K. E. (2015). A generalised random encounter model for estimating animal density with remote sensor data. *Methods in Ecology and Evolution*, *6*(5), 500–509. https://doi.org/10.1111/2041-210x.12346

Luo, G., Wei, W., Dai, Q., & Ran, J. (2020). Density estimation of unmarked populations using camera traps in heterogeneous space. *Wildlife Society Bulletin*, *44*(1), 173–181. https://doi.org/10.1002/wsb.1060

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*(2), 165–172. https://doi.org/10.1007/s13364-011-0055-8

McIntyre, T., Majelantle, T. L., Slip, D. J., & Harcourt, R. G. (2020). Quantifying imperfect camera-trap detection probabilities: Implications for density modelling. *Wildlife Research*, *47*(2), 177–185.

Moeller, A. K., Lukacs, P. M., & Horne, J. S. (2018). Three novel methods to estimate abundance of unmarked animals using remote cameras. *Ecosphere*, *9*(8), e02331. https://doi.org/10.1002/ecs2.2331

Morellet, N., Gaillard, J.-M., Hewison, A. J. M., Ballon, P., Boscardin, Y., Duncan, P., Klein, F., & Maillard, D. (2007). Indicators of ecological change: New tools for managing populations of large herbivores. *Journal of Applied Ecology*, *44*(3), 634–643. https://doi.org/10.1111/j.1365-2664.2007.01307.x

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*(2), 735–744. https://doi.org/10.1111/1365-2664.13059

Nakashima, Y., Hongo, S., & Akomo-Okoue, E. F. (2020). Landscape-scale estimation of forest ungulate density and biomass using camera traps: Applying the REST model. *Biological Conservation*, *241*. https://doi.org/10.1016/j.biocon.2019.108381

Nichols, J., & Williams, B. (2006). Monitoring for conservation. *Trends in Ecology & Evolution*, *21*(12), 668–673. https://doi.org/10.1016/j.tree.2006.08.007

Obbard, M. E., Howe, E. J., & Kyle, C. J. (2010). Empirical comparison of density estimators for large carnivores. *Journal of Applied Ecology*, *47*(1), 76–84.

Palencia, P. (2020). *trappingmotion: Integrate camera-trapping in movement and behavioural studies*. R package version 0.1.1. https://github.com/PabloPalencia/trappingmotion

Palencia, P. (2021). Data availability: Assessing the camera trap methodologies used to estimate density of unmarked populations (version 1.0). *Journal of Applied Ecology*. https://doi.org/10.5281/zenodo.4745594

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*. https://doi.org/10.1111/2041-210X.13609

Pfeffer, S. E., Spitzer, R., Allen, A. M., Hofmeester, T. R., Ericsson, G., Widemo, F., Singh, N. J., & Cromsigt, J. P. G. M. (2018). Pictures or pellets? Comparing camera trapping and dung counts as methods for estimating population densities of ungulates. *Remote Sensing in Ecology and Conservation*, *4*(2), 173–183. https://doi.org/10.1002/rse2.67

Rovero, F., & Zimmermann, F. (2016). *Camera trapping for wildlife research*. Pelagic Publishing Ltd.

Rowcliffe, J. M. (2019). *activity: Animal activity statistics*. R package version 1.3. https://CRAN.R-project.org/package=activity

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*(5), 464–476. https://doi.org/10.1111/j.2041-210X.2011.00094.x

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. https://doi.org/10.1111/j.2041-210X.2012.00197.x

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*(4), 1228–1236. https://doi.org/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*(2), 84–94. https://doi.org/10.1002/rse2.17

Rowcliffe, J. M., Kays, R., Kranstauber, B., Carbone, C., & Jansen, P. A. (2014). Quantifying levels of animal activity using camera trap data. *Methods in Ecology and Evolution*, *5*(11), 1170–1179. https://doi.org/10.1111/2041-210x.12278

Royle, J. A., Chandler, R. B., Sollmann, R., & Gardner, B. (2013). *Spatial capture-recapture*. Academic Press.

Schaus, J., Uzal, A., Gentle, L. K., Baker, P. J., Bearman-Brown, L., Bullion, S., Gazzard, A., Lockwood, H., North, A., Reader, T., Scott, D. M., Sutherland, C. S., & Yarnell, R. W. (2020). Application of the Random Encounter Model in citizen science projects to monitor animal densities. *Remote Sensing in Ecology and Conservation*. https://doi.org/10.1002/rse2.153

Seber, G. A. F. (1982). *The estimation of animal abundance and related parameters*. *Griffin, London 1973, 1. Aufl. XII, 506 S., 34 Abb., 116 Tab., £ 12* (Vol. 16). Macmillan. https://doi.org/10.1002/bimj.19740160115

Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J., Fisher, J. T., Burton, C., Townsend, S. E., Carbone, C., Rowcliffe, J. M., Whittington, J., Brodie, J., Royle, J. A., Switalski, A., Clevenger, A. P., Heim, N., & Rich, L. N. (2017). Scaling-up camera traps: Monitoring the planet's biodiversity with networks of remote sensors. *Frontiers in Ecology and the Environment*, *15*(1), 26–34. https://doi.org/10.1002/fee.1448

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B., Marques, T. A., & Burnham, K. P. (2010). Distance software: Design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, *47*(1), 5–14. https://doi.org/10.1111/j.1365-2664.2009.01737.x

Wald, A., & Wolfowitz, J. (1940). On a test whether two samples are from the same population. *The Annals of Mathematical Statistics*, *11*(2), 147–162. http://www.jstor.org/stable/2235872

Williams, B., Nichols, J., & Conroy, M. (2002). *Analysis and management of animal populations*. Academic Press. https://doi.org/10.2307/3802722

Zero, V. H., Sundaresan, S. R., O'Brien, T. G., & Kinnaird, M. F. (2013). Monitoring an Endangered savannah ungulate, Grevy's zebra *Equus grevyi*: Choosing a method for estimating population densities. *Oryx*, *47*(03), 410–419. https://doi.org/10.1017/S0030605312000324

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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