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RESEARCH ARTICLE

Evaluating camera-based methods for estimating badger (*Meles meles*) density: Implications for wildlife management

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Abstract

1. Accurate and precise assessment of population density plays a critical role in effective wildlife management, but reliable estimates are often difficult to obtain. Camera traps have emerged as valuable noninvasive tools for studying elusive species, offering cost-effective solutions for both marked and unmarked populations.
2. We evaluated the consistency of badger (*Meles meles*) density estimates obtained from the random encounter model (REM) and camera trap distance sampling (CT-DS) with independent estimates from spatial mark-resight (SMR) models and quantified the bias in CT-DS arising from animals reacting to camera traps. Six camera trap surveys were conducted in Cornwall, UK, in 2019 and 2021, and data were used to estimate badger density using the REM and CT-DS. Four sites were included in a badger vaccination research project, providing an opportunity to mark badgers with uniquely identifiable fur clips to facilitate resighting within a SMR framework.
3. We found consistency in the density estimates across all methods, but results had wide confidence intervals. Density estimates derived from CT-DS tended to be higher than those from the REM and were sensitive to the exclusion of reactive sequences, resulting in a twofold decrease in the estimated density in one case. The REM tended to be the most precise method; however, where badger density was low, precision was low using all methods.
4. Practical implication: our findings suggest animal density can be assessed from camera traps in the absence of individual identification; however, it is important to account for reactive behaviours, especially where such behaviour is prevalent. In these circumstances, we recommend utilising the REM which offers a clear methodology for addressing bias arising from reactive sequences. In addition, we

emphasise the need for improved precision to ensure the effectiveness of these methods in the context of wildlife management. We offer practical considerations to facilitate the broader application of these methods, drawing upon the example of disease control through badger vaccination.

KEYWORDS
badger, camera trap, density, distance sampling, random encounter model, spatial mark-resight

1 | INTRODUCTION

Reliable population estimates are essential for ecological assessment, conservation biology, and wildlife management. Quantifying badger (*Meles meles*) populations, for example, is relevant in the context of disease control, because badgers can transmit *Mycobacterium bovis*, the causative agent of bovine tuberculosis (bTB), to cattle. In the British Isles, bTB is a chronic infectious disease that greatly impacts the farming industry, leading to substantial economic losses and affecting livestock health. Badger management aimed at bTB control currently involves large-scale badger culling in England. Badger density estimates have contributed to the understanding of the species' role in *M. bovis* transmission (Delahay et al., 2013; Rogers et al., 1998; Woodroffe et al., 2006), informed disease management plans (Scott et al., 2018; Smith et al., 2012), helped establish culling targets (DEFRA, 2022), and facilitated policy evaluation (Donnelly & Woodroffe, 2015). In England, the government is currently scaling back badger culling, and encouraging badger vaccination (DEFRA, 2020); however, lack of accurate badger density data means, at present, there is no framework in place for establishing vaccination targets, evaluating the effectiveness of post-cull vaccination or tracking the recovery of post-cull badger populations.

Badgers are nocturnal and fossorial, making direct population counts challenging, particularly on large scales. Counts of badger dens ('setts') are used as indices of density (Judge et al., 2014; Wilson et al., 1997), assuming a typical group size and pattern of sett use. However, such metrics can change with habitat (Judge et al., 2017), geology (Neal, 1986), resource availability (Kruuk & Parish, 1982), and human intervention (Rogers et al., 1997). Other measures of relative abundance, such as faecal counts (Buesching et al., 2015) and road casualties (Woodroffe et al., 2008), are similarly prone to bias (Hutchings et al., 2002). Conventional minimum number alive analysis is not recommended where accuracy is important because it underestimates density to an unpredictable degree (Byrne & Do Linh San, 2016).

Mark-recapture is generally regarded as a reliable method of estimating population density (Borchers & Efford, 2008; Efford, 2004; Royle et al., 2013) but trapping and marking badgers is logistically challenging and both are licensed activities (Natural England, 2015). DNA-based capture–recapture, using noninvasive samples such as hair or faeces, has alleviated some of these challenges (Judge et al., 2017; Wilson et al., 2003), although laboratory procedures can be costly (Davis et al., 2020) and some data are inevitably lost due to incomplete DNA amplification (Woodruff et al., 2015). Camera traps offer a relatively inexpensive alternative (Davis et al., 2020; Twining et al., 2022). Deployed as a tool for resighting, camera traps allow density estimation using spatial mark-resight or -recapture (SMR) frameworks (Efford, 2023a). Individual identification is central to SMR, and the method is popular for species with unique pelage markings (Alonso et al., 2015; Karanth & Nichols, 1998; Teton et al., 2020). SMR can also be used for species with uniform pelage, by artificially marking some individuals (Carter et al., 2019; Jimenez et al., 2019; Jordan et al., 2011).

Marking individual animals may be challenging and risks harming study subjects. Consequently, spatial count models have been developed to enable noninvasive density estimation for animals without distinctive markings, by using spatial correlation in counts across sensors as information about the density of animal activity centres (Chandler & Royle, 2013). Alternatives use modelled detection rates to minimise bias in density estimates. Among these, the most popular approaches are the random encounter model (REM; Rowcliffe et al., 2008), camera trap distance sampling (CT-DS; Howe et al., 2017), the time-to-event and related models (Moeller et al., 2018), and the random encounter and staying time model (Nakashima et al., 2018). These methods are promising, but testing them against independent estimates to validate their accuracy and reliability is recommended (Rowcliffe et al., 2008).

The REM and CT-DS share similar methods for data collection, enabling simultaneous estimation of density. Both models require information on the position of animals relative to the camera; for the REM, distance data allow the estimation of the focal species' speed and the dimensions of the camera detection zone, which affect the encounter rate (the number of photographs per unit of time) from which density is estimated. In CT-DS, a detection function is fitted to distance observations and density is estimated by modelling the probability of detecting an animal within the detection zone at a given time. However, the methods differ in how they address 'reactive' sequences, where animals' attraction to (or avoidance of) cameras may bias density estimates (Howe et al., 2017; Palencia et al., 2021). Using the REM, this bias can be controlled by removing reactive sequences from speed estimation but including them in total encounter rate (Palencia et al., 2021; Rowcliffe et al., 2008). Approaches within CT-DS studies vary, with some discarding data collected immediately after camera deployment to allow animals to become accustomed to camera traps (Howe et al., 2017), others removing potential investigative behaviour by left-truncating the detection distance data (Cappelle et al., 2019), and some identifying and removing all reactive sequences (Bessone et al., 2020). Defining a smaller sample of data for density estimation may be appropriate if reactive behaviour varies predictably in time (Mason et al., 2022). However, the impact of these differing methods on the accuracy and precision of density estimates is not well understood (Palencia et al., 2019).

In this study, we aimed to evaluate the performance of the REM and CT-DS at estimating badger density in a badger vaccination context. We compared the REM and CT-DS density estimates with independent estimates derived from SMR using marked badgers. We also compared different methods of processing reactive sequences and examined the practical implications of using camera-based density estimation methods.

2 | MATERIALS AND METHODS

2.1 | Study area

Data were collected from six camera trap surveys at five sites in Cornwall, UK, in 2019 and 2021 (Table 1; Figure 1). Each site comprised at least two farms (Table 1). Sites included several habitats and farming practices, including arable fields, livestock pasture, woodland, and moorland. All data were collected with landowner consent.

2.2 | Data collection

2.2.1 | Camera surveys

All surveys were planned to coincide with the open season for badger vaccination, which runs annually from the 1 May–30 November (Natural England, 2023). We determined the number and duration of camera deployments at each site (Table 1) using recommendations from Rowcliffe et al. (2008). Specifically, we estimated that a minimum of 1000 camera nights were required at each site, based on a badger day range of 1.2 km (estimated using data from Global Positioning System-collared badgers recorded by Woodroffe et al. (2017)) and a local minimum number alive density estimate of 4.2 badgers per km^2 (Woodroffe et al., 2017). We planned to deploy enough cameras to ensure we would have data from ≥40 cameras per site (recommended by Rowcliffe et al., 2008), allowing for anticipated camera failures or theft.

To meet the assumptions of the REM and CT-DS, we used a systematic grid with a random origin to plan the location of cameras at each site, with a spacing of 155–250 m between predetermined locations (Table 1). In the field, we attached cameras (Browning StrikeForce HD Pro X) to suitable objects as near as possible to predetermined locations. If deployment was not possible at the exact coordinates, we aimed to keep within ≤20% of the distance between predetermined locations, ensuring the habitat remained unchanged and orientating the camera towards the planned location. This method was chosen over trying for a fixed aspect (e.g. north) due to the anticipated difficulty of finding suitable attachment sites for cameras in the farming landscape. We positioned cameras 30–40 cm high, parallel to the ground and did not use bait. Cameras took photographs 24 h/day with no time lapse and a 1-s passive infra-red trigger interval.

At each camera location, we took calibration images of a 1 m pole marked at 20 cm intervals, at a range of distances and angles from the camera (Figure 2). Similar calibration images were taken ex situ at a range of angles and known distances, to enable accurate calibration and estimation of distances and angles in images.

2.2.2 | Badger vaccination and marking

Sites B to E (Table 1; Figure 1) were included in an existing research project. Badgers were trapped and handled under licence from the UK Home Office (project licence PB32E4DFC) and Natural England (research licence 2021-53121-SCI-SCI). Cage traps were placed near badger setts, latrines and runs, and pre-baited with peanuts for 7–10 days prior to trapping. On capture, badgers were anaesthetised with an intramuscular injection of medetomidine and ketamine (de Leeuw et al., 2004), and individually identified using microchips (FriendChip, Avid PLC, Lewes, UK). We recorded age class (cub or adult), sex, tooth wear, and reproductive status.

Cage trapping provided the opportunity for SMR analysis, which requires an initial marking phase followed by re-sightings in which previously captured animals must be individually recognisable. Each badger was assigned a unique mark which was clipped onto both sides of the animal, by carefully trimming the dark tips of the guard hairs, revealing the pale undercoat (Stewart & Macdonald, 1997; Figure 3). We recorded a photograph of each mark and the badger's identity (Figure 3).

2.3 | Data analysis

2.3.1 | Image processing

Badger images from surveys 1, 2, and 4 were isolated manually. During data analysis, the image processing tool Sherlock (Penn et al., 2024) became available and was used to isolate badger images from the remaining sites. Images were tagged using XnView MP (version 0.99.6; Gougelet (2020)).

Some cameras were displaced by livestock. Where this substantially changed or obscured the field of view (FOV), we truncated that camera's deployment period at the point the camera was moved, discarding any subsequent badger encounters and removing the affected hours from effort calculations.

Except for the first night of cage trapping at site B in 2019, badgers were trapped and marked during the camera deployment periods. We therefore limited resighting data for SMR to images

TABLE 1 Details of six camera surveys at five sites used to estimate badger density.

	Camera survey					
	1	2	3	4	5	6
Site	A	B	B	C	D	E
Number of farms	2	2	2	2	3	4
Total area	2.3 km^2	2.4 km^2	2.4 km^2	1.8 km^2	2.0 km^2	4.6 km^2
Badger bTB management	Culled	Vaccinated (surrounding land culled)	Vaccinated (surrounding land culled)	Vaccinated	Vaccinated	Vaccinated
Year studied	2019	2019	2021	2021	2021	2021
Date of badger vaccination and marking	NA	22nd May 27th May	15th June 16th June 24th June 1st July	25th May 27th May	8th June 9th June	6th October 7th October
Number of badgers individually marked	0	0	23	19	12	4
Camera deployment period	5th Jun–11th Jul	23rd May–17th Jul	1st June–29th July	17th May–21st Jun	26th May–23rd Jul	27th Sep–4th Nov
Number of camera deployments (number of usable deployments)	87 (85)	64 (63)	59 (56)	50 (45)	50 (48)	78 (75)
Predetermined camera spacing (m)	155	155	200	200	195	250
Number of usable camera nights	1145	1217	1464	1052	917	2277

Note: Usable deployments are lower than the total set because some cameras failed. Usable camera nights exclude time from deployments after cameras were moved by cattle.

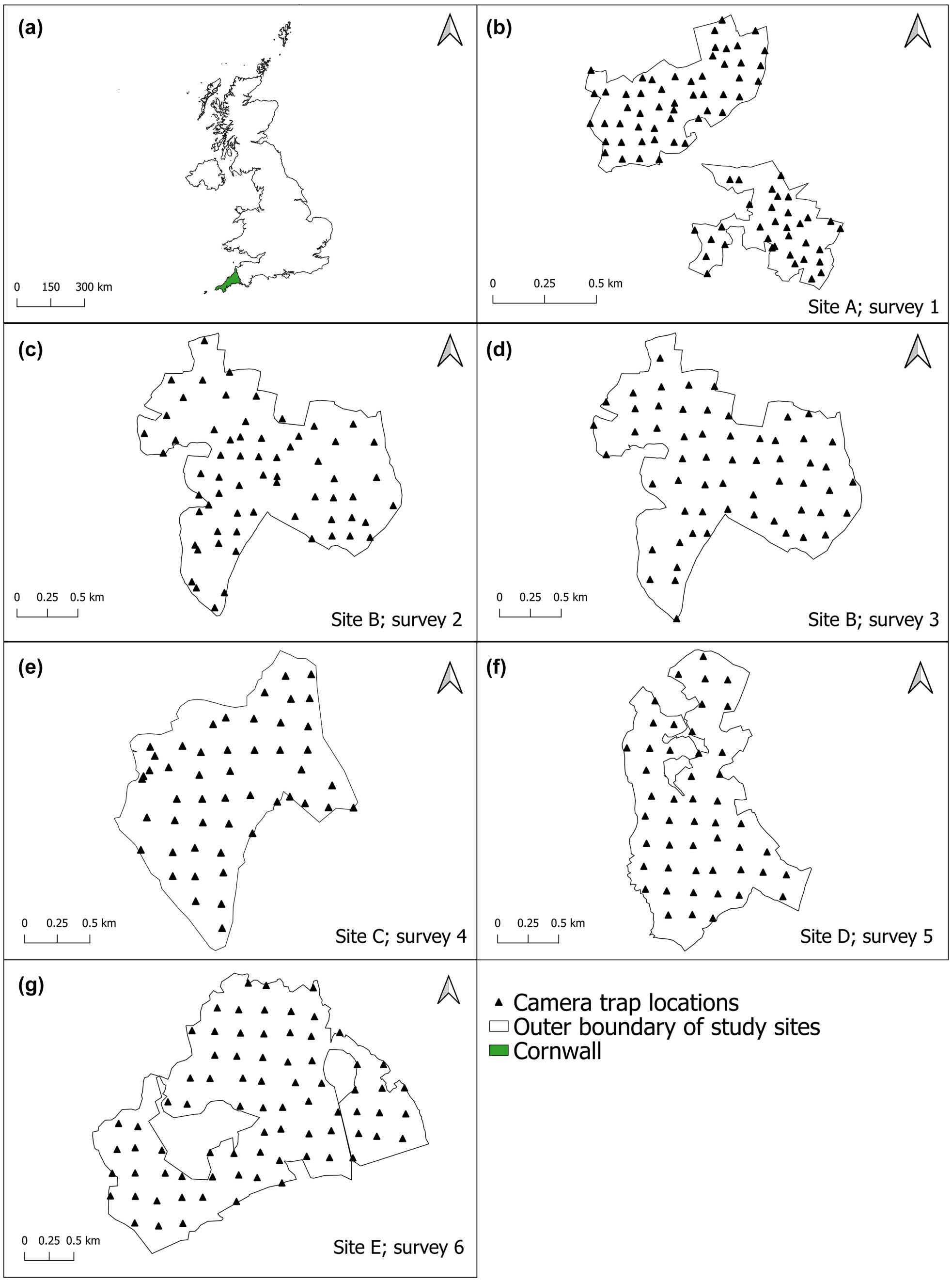

FIGURE 1 (a) Location of the five sites in Cornwall, UK and (b–g) layout of the camera grids deployed for each survey.

obtained after marking was completed. For the REM and CT-DS, we excluded data from cage trapping nights (18:00 until 08:00) to avoid bias in encounter rate due to part of the population being caught in cage traps.

2.3.2 | Outlier analysis

Our survey design, which entailed random camera placement across a total area larger than the typical home range of badgers, was carefully considered to minimise sampling bias. This strategy, coupled with the sparse distribution of badger setts across the landscape, ensured a broad representation of badger activity, minimising the potential for biased sampling. However, if areas of high badger activity (e.g. setts) were by chance included in the sample, they might inflate encounter rates and bias density estimates. To identify potential outliers, we fitted a negative binomial distribution to the per-deployment photographic encounter rate data (Anscombe, 1949) using maximum likelihood. We simulated 1000 datasets from this distribution and considered the maximum observed photographic encounter rate to be an outlier if it fell above the 95th percentile of the simulated distribution. If an outlier was identified, the process was repeated with the outlier removed. We excluded outliers from density estimation using the REM and CT-DS but not SMR, which is not sensitive to encounter rate outliers.

FIGURE 2 Example of a deployment calibration image taken at each camera location. The camera was triggered to capture images of a calibration pole at a range of angles and distances from the camera. Similar images were taken ex situ at a range of angles and known distances, enabling accurate camera calibration.

2.3.3 | REM density estimation

Although badgers are a social species, outside of the sett they do not form cohesive groups (Kruuk, 1989), so we considered individuals as the unit of observation for all models (Rowcliffe et al., 2008; Thomas et al., 2010).

Density estimates were obtained from encounter rates using Equation 1 from Rowcliffe et al. (2008)

$$D = \frac{y}{t}\frac{\pi}{vr(2+\theta)} \tag{1}$$

where y is the number of independent badger encounters (defined as a badger entering and exiting the FOV), t is the temporal survey effort (the total number of camera nights during the survey period, excluding nights affected by cage trapping, camera movement, and camera failure), v is the long-term average distance travelled by a badger per night (the product of average speed while active and the proportion of time spent active; hereafter referred to as activity level; Rowcliffe et al., 2014), and r and θ are the dimensions of the camera detection zone (radius and angle, respectively).

All model parameters were estimated from the camera images. Calibration images and badger sequences were digitised using AnimalTracker (Vargas Zarco, 2019) and processed to produce

FIGURE 3 Representative images of three individually marked badgers during the marking (a–c) and resighting (d–f) stages of spatial mark-resight (SMR) analysis.

badger position data (defined in polar coordinates as radial distance from the camera and angular distance from the camera view centre) using the '*CTtracking*' package (Rowcliffe, 2021b). Speed was measured for each badger sequence by dividing the distance travelled summed across all positions in the sequence by the duration of the sequence, using the time stamp on the images. Overall average speed while active was estimated as the harmonic mean of these speed observations after removing reactive sequences (Rowcliffe et al., 2016), defined as a badger observing the camera followed by a change in directional movement with respect to the camera. Activity level was estimated by fitting a circular kernel model to radian time of day distributions of camera trap records of badgers using the '*activity*' package (Rowcliffe et al., 2014). The effective detection radius and angle were estimated by fitting distance sampling detection functions to the radial and angular distance observations at the beginning of each badger sequence (Rowcliffe et al., 2011). The '*camtools*' package (Rowcliffe, 2021a) was used to estimate density, including bootstrapping of trap rate errors and incorporating variance using the delta method (Rowcliffe et al., 2008).

2.3.4 | CT-DS density estimation

We used point transect distance sampling methods (Howe et al., 2017) adapted for use with still images. A key distinction between CT-DS and traditional point transect surveys is the calculation of effort, because camera traps (active 24h/day in our study), replace human observers surveying at intervals. We therefore discretized the number of times animals could potentially be photographed ('snapshot moments'), given a certain interval time between camera images (Howe et al., 2017). We calculated the mean interval between sequential badger images within captures to define the length of the time between snapshot moments, *T*. Temporal effort for each camera was calculated as the number of snapshot moments within the time that the camera was operational, *H*, given in Equation 2:

$$H = t / T \tag{2}$$

where *t* is as defined for the REM.

The effort of the camera is given by the proportion of a circle covered by its estimated FOV. The angle of the detection zone, θ, was estimated using digitised badger images, as described above for the REM. The overall sampling effort, *e*, is a product of temporal effort and spatial effort, given in Equation 3:

$$e = \frac{\theta H}{2\pi T} \tag{3}$$

Density was estimated using Equation 4 (Howe et al., 2017)

$$D = \frac{y}{\pi w^2 epa} \tag{4}$$

where *y* is the number of badger observations, *w* is the truncation distance (beyond which badger detections were disregarded to avoid heavy-tailed detection functions), *p* is the probability that a badger within a camera's FOV is detected, and *a* is the activity level, estimated as described for the REM.

We performed exploratory analysis for each camera survey to determine left- and right-truncation distances, below and beyond which badger detections were excluded, respectively. The purpose of left-truncation is to control bias arising from animals passing under the camera undetected which could violate a key assumption of distance sampling models, that animals are detected with certainty at the point where the observer is situated (Buckland et al., 2001). We chose to left-truncate the data at distances below which there were fewer than the expected number of badger detections. Right-truncation distances were decided by fitting an exploratory model and choosing to truncate the data at distances beyond which the detection probability was lower than 0.15. We estimated density under two scenarios, in which reactive sequences were included or excluded from analyses.

We fitted detection function models, and estimated density and the variance in density estimates, using the '*Distance*' package in R (Miller et al., 2019). We considered models of the detection function with the uniform key function with 1, 2, or 3 cosine adjustments, the half-normal key function with 0, 1, or 2 cosine adjustments, and the hazard rate key function with 0 or 1 simple polynomial adjustments. We discarded models where the detection function did not decline monotonically in relation to the detection distance. Models were adjusted for overdispersion and final model selection was based on $\hat{c}$ scores, following Howe et al. (2019).

2.3.5 | SMR density estimation

Individual badgers were identified by comparing marks in camera images with those taken during handling (Figure 3). Identifiable badgers were distinguished from unmarked, marked-unidentifiable, and indeterminable badgers (Efford, 2023a). Retrospective capture histories of identifiable badgers were constructed using the cage trap and camera locations. SMR models were fitted to the data using the '*secr*' package in R (Efford, 2023b).

Spatial mark-resight analysis requires estimating the effective sampled area, a buffer around the camera traps where detection probability declines towards the outer limit (Efford, 2022a). The size of the buffer is not critical but must be large enough to account for all detected individuals, while individuals with home range centres at the outer limit should have zero probability of being detected (Efford, 2022a).

We used a buffer width of 4σ (Efford, 2022a), where σ is a function of the distance between capture and resighting locations, assuming that detection probability declines as the distance between the two locations increases. Where sites bordered the sea, we fitted a shape file habitat mask to restrict the buffer to terrestrial habitat. A retrospective buffer sensitivity analysis was also performed to confirm that wider buffers did not influence estimated density.

Since the marking and resighting processes are fundamentally different, we used a variable detection probability between marking and sighting occasions. Exploratory analysis considered models with exponential, hazard rate, and half-normal detection functions. Models were compared using QAIC values (Borchers & Efford, 2008) and their performance in the retrospective buffer sensitivity analysis (Efford, 2022b). Models and standard errors were adjusted for overdispersion by simulating an overdispersion factor (Efford, 2023a).

In SMR models, incomplete identification of marked individuals can introduce bias, particularly if there is individual heterogeneity in resighting probability (McClintock et al., 2014). To account for this, our models included data from both identified and unidentifiable marked individuals, estimating a corrective factor, *pID*, which quantifies the proportion of marked animals identified upon resighting. We also conducted retrospective simulations across a range of *pID* values under similar detection conditions to assess the impact of incomplete identification on the precision and accuracy of density estimates. Capture histories were simulated using the 'secr' package, with a spatial grid comprising 49 detectors and specifying detection probabilities for two marking occasions and 36 resighting occasions. The spatial scale parameter σ and detection probabilities were based on mean values derived from observed data. We fixed the population density at 10 individuals per km^2 and systematically varied the *pID* value. For each scenario, we simulated capture data and subsequently fitted mark-resight models using the same detection function applied to the observed data, assessing the impact of varying *pID* on the accuracy and precision of density estimates.

All calculations were performed in R (R Core Team, 2021).

3 | RESULTS

3.1 | Camera survey

We obtained 5,049,759 images from 388 camera placements over 8467 camera nights. Badgers were identified in 9784 (0.2%) images, totalling 1739 independent encounters. The majority of badger detections involved solitary badgers, with only 19 (1.1%) encounters featuring groups of two or three animals. The mean group size was 1.024 (95% confidence interval [CI] 1.018–1.029), supporting the use of individuals as the unit of observation.

Interference from livestock meant that 31 (8%) camera deployments were truncated early, amounting to a loss of 396 (5%) camera nights and 218 independent badger encounters. Lack of suitable attachment sites meant that cameras were often situated at field boundaries. On average, cameras deviated by 35.8 m (median 28.0 m) from the planned deployment location or 17.4% of the distance between predetermined locations. Accurate deployment locations were not recorded for 21 cameras and were not included in the analysis of camera deviation. Cameras missing accurate location data were from surveys 1 and 2, where SMR analysis was not performed, thus not compromising the method. Following outlier analysis and removal of data due to livestock interference and trapping (detailed below) 7023 badger images and 1252 independent badger encounters were considered for the REM and CT-DS analyses.

3.2 | Outlier analysis

We identified one observed photographic encounter rate as an outlier (Figure 4, survey 3) and excluded this camera deployment from the REM and CT-DS analyses. After removing this outlier there were 1543 independent badger encounters captured over 8071 camera nights, giving 0.2 encounters per camera-night.

3.3 | Marking badgers

Of the 63 badgers trapped in 2021, 58 were given unique marks (Table 2) to facilitate SMR analysis, while five could not be marked due to insufficient anaesthesia.

3.4 | Reactive sequences

We identified 138 independent encounters in which badgers displayed reactive behaviour, which represented 10% of the encounters considered for the REM and CT-DS analyses. Of these, 100 (72%) involved investigative behaviour, 18 (13%) avoidance behaviour, and 20 (14%) involved a mixture of these behaviours.

3.5 | Density estimation

Spatial mark-resight analyses, which were limited to data collected following individual marking, included 579 independent badger encounters. The presence or absence of a mark was confirmed in 374 (65%) encounters, with badger identity confirmed in 33 (6%) encounters (Table 2). During survey 6, we obtained only two re-sightings of one marked badger, so we excluded this survey from further SMR analysis.

Estimated badger densities ranged from 1.4 (95% CI 0.6–3.0) badgers per km^2 (REM at site E, survey 6) to 20.2 (95% CI 11.8–34.4) badgers per km^2 (REM at site B, survey 2; Table 3 and Figure 5). Density estimates using CT-DS tended to be higher than those using the REM (Table 3; Figure 5). When reactive sequences were excluded from CT-DS analysis, density estimates were on average 22%

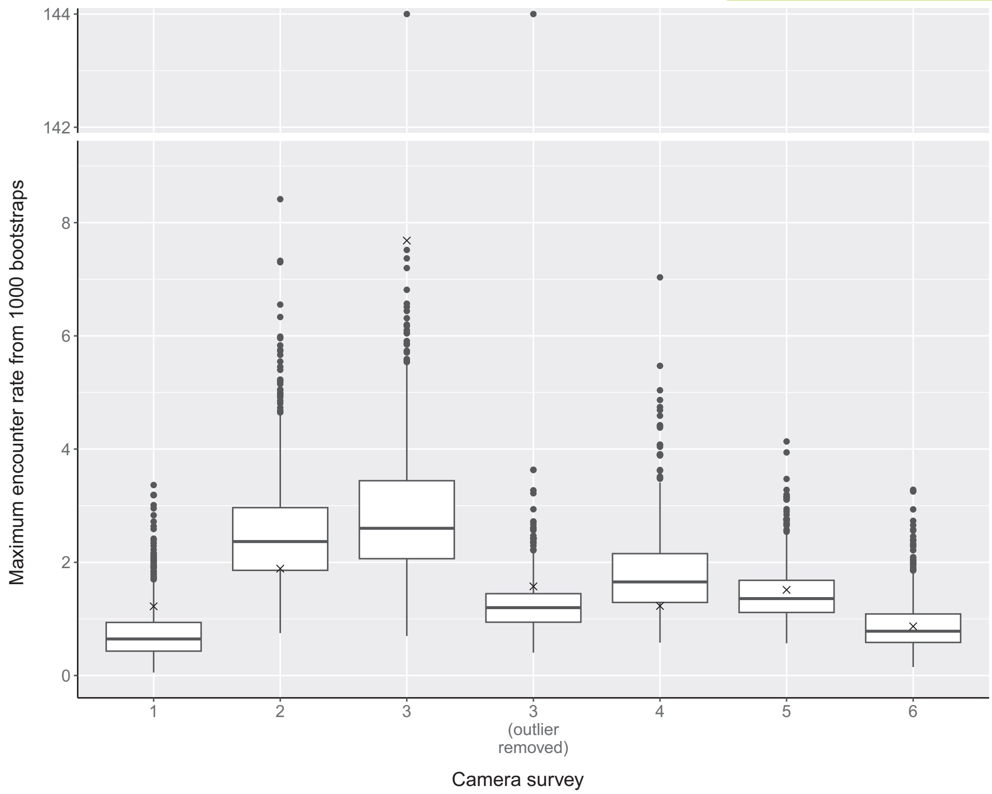

FIGURE 4 Boxplot showing the median (thick horizontal lines), interquartile range (boxes) and 2.5th and 97.5th centiles (vertical lines) of maximum encounter rates from seven data sets using 1000 samples from a negative binomial distribution fitted to the data, with sample sizes equal to the number of deployments in the data set. Black crosses show the maximum encounter rate from the observed data at each site, with an outlier identified in camera survey 3 (site B). The analysis for survey 3 was repeated with the outlier removed.

TABLE 2 Badger encounters considered for SMR analysis.

	Site			
	B	C	D	E
Survey	3	4	5	6
Number of badgers individually marked	23	19	12	4
Resighting	Number of independent encounters			
Identifiable (number of individuals resighted)	11 (5)	15 (7)	5 (4)	2 (1)
Marked, unidentifiable	31	45	2	0
Unmarked	37	82	72	72
Indeterminable	60	56	64	22
Total independent encounters	139	198	143	99

Note: Site E was excluded from analysis due to the small number of marked and resighted individuals.

(range 3%–51%) lower than when those sequences were included (Table 3; Figure 5).

The REM estimates tended to be the most precise (Table 3). The average coefficient of variation (CV) for the REM was 0.36, for CT-DS (reactive sequences included) it was 0.41, for CT-DS (reactive sequences excluded) it was 0.42 and for SMR it was 0.35.

3.6 | SMR simulations

On average, 56% (range 25%–100%) of marked badger sightings were identifiable (Table 2), prompting simulations with *pID* values of 1, 0.75, 0.50 and 0.25. Models fitted to the simulated data demonstrated a direct correlation between *pID* values and the accuracy and precision of the estimated densities. When *pID* was 100%, the model yielded density estimates closest to the actual population density used in simulations (10 individuals per km^2), with an estimated density of 9.8 individuals per km^2 and a CV of 0.22. This scenario illustrated minimal bias and lower variability, suggesting optimal model performance under full identification conditions. As *pID* decreased, estimated density was less accurate and variability increased (Table 4).

4 | DISCUSSION

Our study suggests that the REM and CT-DS are reliable methods of estimating the density of unmarked animal populations. The density estimates obtained using the REM and CT-DS were similar to each other and to the estimates obtained independently using SMR. The 95% confidence intervals of all methods overlapped substantially. In contrast with previous studies (Henrich et al., 2022; Palencia

TABLE 3 Badger density per km^2 and associated 95% confidence intervals and coefficient of variation (CV) estimated from six camera surveys at five sites, using three camera trap-based methods. SMR analysis was only possible for three of the surveys.

Site	Survey	Density estimation method	Density (badgers per km^2)	SE	95% CI	CV
A	1	REM	4.9	3.3	1.5–16.1	0.67
		CT-DS (reactive included)	6.2	5.4	1.4–27.3	0.86
		CT-DS (reactive excluded)	6.0	5.2	1.4–26.4	0.86
B	2	REM	20.2	5.6	11.8–34.4	0.28
		CT-DS (reactive included)	19.8	5.5	11.4–34.1	0.28
		CT-DS (reactive excluded)	13.8	4.2	7.6–25.1	0.31
B	3	REM	11.7	3.9	6.3–22.0	0.33
		CT-DS (reactive included)	14.5	3.2	9.4–22.4	0.22
		CT-DS (reactive excluded)	13.1	2.8	8.7–19.8	0.21
		SMR	16.8	4.2	10.4–27.1	0.25
C	4	REM	12.1	2.8	7.7–18.9	0.23
		CT-DS (reactive included)	14.0	3.2	8.9–22.0	0.23
		CT-DS (reactive excluded)	12.5	3.0	7.8–20.0	0.24
		SMR	11.8	3.5	6.6–21.0	0.30
D	5	REM	14.5	3.5	9.1–23.1	0.24
		CT-DS (reactive included)	18.1	6.4	9.1–36.2	0.36
		CT-DS (reactive excluded)	8.9	3.0	4.6–17.2	0.34
		SMR	17.6	9.0	6.8–45.3	0.51
E	6	REM	1.4	0.6	0.6–3.0	0.42
		CT-DS (reactive included)	2.3	1.1	0.9–5.7	0.49
		CT-DS (reactive excluded)	1.6	0.9	0.6–4.5	0.54

et al., 2021; Twining et al., 2022), density estimates derived from CT-DS tended to be higher than those using the REM, although not consistently so. As the REM and CT-DS are mathematically similar, their consistency with SMR is encouraging and supports their use for estimating the density of terrestrial mammals without needing to mark individuals.

Challenges with determining the identity of marked individuals, arising from incomplete visual captures or indistinct markings, are well documented in mark-resight studies (Jimenez et al., 2019; McClintock et al., 2014). On average, we were able to identify 56% of the encounters with marked individuals (Table 2) consistent with rates reported in other studies employing camera traps for resighting (Greenspan et al., 2020; Jimenez et al., 2019). Our simulations with varying *pID* values suggested that with comprehensive capture histories for all marked badgers, we may have seen more accurate and precise results. When 100% of the marked individuals were identifiable, the model had minimal bias. However, reducing *pID* to 50% resulted in a density estimate that was 13% lower than the fixed simulated density, with an increase in CV from 0.22 to 0.28 (Table 4). At a *pID* of 25%, density was underestimated by 15% and the CV increased to 0.29. Our SMR results may therefore represent an underestimate of badger density, although comparisons with our REM and CT-DS estimates do not consistently reflect this. Alternative methods to address imprecision arising from marked unidentifiable individuals have been proposed. For example, spatial partial identity models (SPIMs) specifically address the challenge of imperfect identification by adding partially known information about identity, such as sex, to probabilistically determine identities obtained from camera traps, thereby improving density estimate precision (Augustine et al., 2019). Such models may outperform other spatial models (Sun et al., 2022), particularly where the resighting rate is low (Greenspan et al., 2020), so it is possible that we could have obtained more accurate and precise estimates with the use of SPIMs.

The REM and CT-DS methods negate the need for individual identification, thereby maximising data usage and circumventing challenges such as incomplete identification. However, our survey design, which used a randomised grid to meet the assumptions of the REM and CT-DS, was not optimised to maximise encounter rates for SMR. The precision of SMR estimates is sensitive to the resighting rate of identifiable individuals (Carter et al., 2019) and, while SMR models necessitate coverage across the target species' density distribution, they do not require random camera placement and can support strategic camera placements in areas likely to detect the target species, as well as the use of bait to increase re-sightings (Jimenez et al., 2019). In this study, we utilised the existing camera grid and the opportunity to individually mark badgers as part of ongoing research to provide independent density estimates, but insufficient recaptures meant SMR analysis could not be conducted for

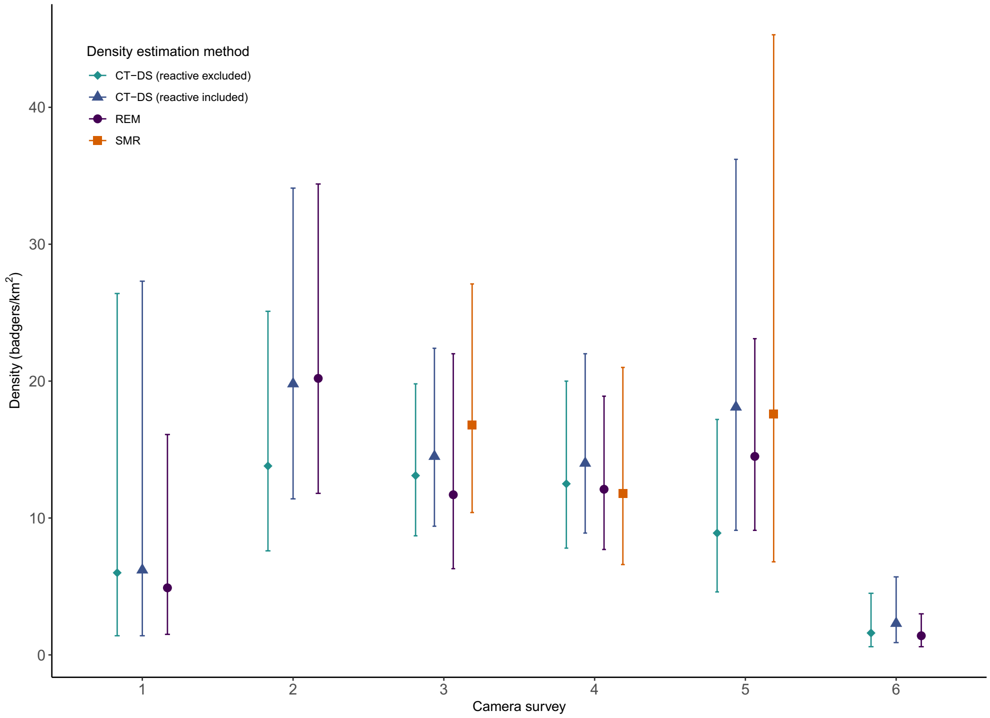

FIGURE 5 Badger densities per km^2 and associated 95% confidence intervals estimated from six camera surveys at five sites, using three camera trap-based methods (SMR analysis was only possible for three of the surveys).

TABLE 4 Estimated animal density per km^2, with associated 95% confidence intervals and coefficient of variation (CV), derived from simulated mark-resight models.

pID	Estimated density (individuals per km^2)	SE	95% CI	CV
1	9.8	2.2	6.3–15.1	0.22
0.75	9.3	2.3	5.8–15.1	0.25
0.50	8.7	2.4	5.1–14.9	0.28
0.25	8.5	2.5	4.9–14.9	0.29

Note: Data were simulated with fixed model parameters reflecting observed data from badgers: A density of 10 individuals per km^2, detection probabilities for marking and sighting occasions of 0.09 and 0.04, respectively, and a spatial scale parameter (σ) of 219.3.

survey 6 and all SMR density estimates were imprecise. More precise reference estimates could have been obtained with additional cameras for SMR targeting areas with higher badger activity.

Our density estimates generally exceeded those from the most recent badger census in England and Wales (e.g. 5.65 [95% CI 3.15–8.15] in Land Class 1 and 5.98 [95% CI 4.57–7.39] in Land Class 4; Judge et al., 2017). However, the census assumed one main badger sett per km^2, whereas sett densities were higher than this in our survey areas. Conversely, at sites affected by culling (site A) or characterised by moorland with low badger activity and few setts (site E), our estimates were lower than the census average (Judge et al., 2017). Notably, the REM estimate at site B, survey 2 (20.2 badgers per km^2, 95% CI 11.8–34.4) indicates high badger density, comparable to that of Woodchester Park, Gloucestershire, where at its peak, density was estimated at 47 badgers per km^2 (Delahay et al., 2013). A subsequent survey at site B two years later (survey 3) yielded a markedly lower REM estimate (Table 3; Figure 5), which is consistent with badger culling that took place on nearby land. However, the confidence intervals of the results overlap, and the consistency of CT-DS estimates across the two surveys does not reflect this pattern. Successive annual surveys would be necessary to ascertain if the observed variations indicate a persistent trend detectable by the REM.

The precision of our estimates was similar to results reported elsewhere (Bengsen et al., 2022; Cappelle et al., 2021; Palencia et al., 2021) but falls short of the recommended variance of CV <0.20 suggested for wildlife management (Cappelle et al., 2021; Pollock et al., 1990). Although previous studies have highlighted the suitability of the REM and CT-DS for studying populations at low densities given sufficient survey effort (Palencia et al., 2021; Rowcliffe et al., 2008), our results had high variance at sites E and A, which were characterised by low density, with CV values ranging from 0.42 to 0.86. This imprecision, which was unexpected for the REM as we surpassed the suggested survey effort (Rowcliffe et al., 2008), suggests the need to re-evaluate current guidelines. In our study, variability in trap rate was the biggest component of overall variance for the REM, but uncertainty in the speed parameter also had a substantial influence on overall precision. Aggregating data from surveys with analogous conditions could potentially mitigate this, if conditions influencing parameters can be assumed invariant between sites, but the influence of external factors, such as badger culling, on animal behaviour

(Ham et al., 2019) made this approach unsuitable for our study. Enhancing precision of the REM and CT-DS through denser camera grids, either by adding cameras or redeploying them, is most effective (Rowcliffe et al., 2008), though as few as 50 cameras could suffice for precise CT-DS estimates if deployment times exceed 100 days (Cappelle et al., 2021). Considering our findings, we recommend further investigation into the impact of camera number and deployment duration on the precision of estimates in low-density populations under real survey conditions.

Density estimates obtained using CT-DS were sensitive to the exclusion of reactive sequences. In the least-affected survey (survey 1), excluding reactive sequences reduced estimated density by 3.4% without altering precision, but in the worst-affected survey (survey 5), excluding these sequences reduced estimated density by 51.0%, although variance was slightly improved. This result is consistent with previous studies which have found reactive sequences to be the biggest source of bias in CT-DS (Bessone et al., 2020). Our results highlight the importance of quantifying and addressing the influence of reactive sequences on density estimates to ensure accuracy and precision. Left-truncation is proposed as an approach to control bias caused by investigative behaviour towards cameras (Cappelle et al., 2019), which can result in spikes at zero distance (Howe et al., 2017). In this study, we observed both investigative and avoidance behaviour, sometimes within the same sequence. As a result, we rarely detected spikes at zero distance, making left-truncation an unsuitable approach for our data. An alternative approach is to minimise the occurrence of reactive behaviour, for example by deploying cameras for a pre-survey acclimation period, allowing animals to become accustomed to their presence (Bessone et al., 2020). However, this strategy would require increased field effort to maintain camera performance over an extended period, which may be infeasible for small-scale projects. Furthermore, if avoidance of cameras is elicited by human scent or disturbance, an acclimation period would be necessary each time the cameras were checked. In contrast, by allowing reactive sequences to be removed from speed and detection zone parameter estimation but not the overall trap rate, the REM offers a clear and effective way of handling bias from reactive sequences without additional effort, making it a more suitable choice for this application.

In terms of practical considerations, the biggest challenge we encountered was interference from livestock. Where interference is likely, we suggest checking and recalibrating cameras regularly, and increasing survey effort with more deployments as a buffer for potential losses. In the farming landscapes, pre-planned coordinates for camera placement often fell in open fields, where there were few existing structures on which to mount cameras. As prior work had shown that cattle almost invariably disturb posts deployed specifically to mount cameras, we placed cameras preferentially at field boundaries. Though true random placement is difficult to achieve (Foster & Harmsen, 2012), the potential impact on density estimates may only be substantial if coupled with species-specific over- or underuse of the area (Cusack et al., 2015). For many species, linear landscape features, such as hedgerows, can act as corridors for movement or are an essential refuge in an intensively farmed landscape (Fitzgibbon, 1997; Hof & Bright, 2010), potentially leading to overestimation in this case. The fact that the REM and CT-DS estimates were not higher than SMR estimates (which are robust to non-random placement relative to animal movement) suggests that this may not have been a major issue. However, incorporating understanding of spatial habitat utilisation by the target species is highly recommended when using camera traps to estimate density, particularly in scenarios where camera placement may introduce bias. Failure to account for these spatial biases could lead to biased density estimates.

To conclude, our results show that badger density can be estimated non-invasively with camera traps, without the need for individual recognition. This approach could offer a promising tool for badger management in the context of current bTB policies, for example, to estimate the coverage achieved by badger vaccination efforts. Additionally, since the REM and CT-DS are capable of simultaneously estimating multiple species' densities, these methods offer a means to analyse the broader impacts of badger management strategies on ecosystems. However, given that precision was poor using all methods, particularly in areas of low badger density, these methods may be unable to detect population trends over time unless survey designs are refined to improve the precision of the results.

More generally, our study provides valuable insights into the use of camera-based methods for estimating the density of unmarked animal populations. We found that both the REM and CT-DS can yield reliable density estimates but recommend prioritising the REM for species showing reactive behaviour. We also recommend taking precautions to limit interference from other species, to ensure accurate estimation of model parameters, minimise data loss and improve precision. Combining the REM and CT-DS with alternative methods, such as SMR, may help validate density estimates but requires careful survey design. In future studies, the accuracy of density estimates could be improved by incorporating spatial movement patterns into analyses, to account for the bias that may arise from factors such as habitat preferences, resource availability, and human disturbances, thus increasing the applicability of these methods. Finally, we have illustrated how the REM and CT-DS can be used to inform wildlife management policy but recommend practical considerations to improve the accuracy and precision of density estimates.

AUTHOR CONTRIBUTIONS

Verity Miles, Rosie Woodroffe, Marcus Rowcliffe, and Christl A. Donnelly conceived the ideas and designed the methods; Verity Miles, Marcus Rowcliffe, Joana Aurélio, Rosie Woodroffe, Cally Ham and Kelly Astley collected the data; Verity Miles, Marcus Rowcliffe, and Joana Aurélio analysed the data; Verity Miles led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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DATA AVAILABILITY STATEMENT

Code used for this research is available at the Zenodo repository: https://doi.org/10.5281/zenodo.8431621 (Miles, 2024a) and data are available at the Dryad repository: https://doi.org/10.5061/dryad.gb5mkkwwk (Miles, 2024b).

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