

**From pictures to policy: camera-based estimation of animal density
to inform disease control**

Verity Miles

Imperial College London, Department of Infectious Disease Epidemiology

Institute of Zoology, Zoological Society of London

Thesis submitted for PhD examination
2024

16

Statement of Originality

17 I confirm that all work in this thesis is my own, produced under the supervision of Prof. Christl
18 Donnelly, Prof. Marcus Rowcliffe, Prof. Rosie Woodroffe, and Dr Peter Brotherton. All other work is
19 appropriately referenced and contributions from others are outlined in the Contributions Statement.

20

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Acknowledgements

36 I couldn't have completed this research without the incredible support of my supervisory team.
37 Christl, Marcus, and Rosie, thank you so much. Your encouragement made me believe I could do it,
38 and I'm so grateful for the time and knowledge you've shared with me. It's been a fascinating
39 journey, and I've learnt so much from you. I'd also like to thank Pete for your support and giving me
40 the opportunity to collaborate with Natural England. Your insights into the policy aspects of this work
41 have been so valuable.

42

43 A huge thanks to the team at Woodchester Park, especially Amy and Ruth, for your time, energy, and
44 enthusiasm in running such a big camera survey. I really enjoyed working at Woodchester and I have
45 learnt a lot from collaborating with you on two of these chapters.

46

47 I also owe a huge thanks to all the volunteers and MSc students who have given their time to work
48 on this project, particularly Sarah, Sophie, Tania, and Joana. PhD life can be isolating at times, but
49 having a team made all the difference; I'm so glad I got to know you during this process.

50

51 Cally and Kelly, thank you so much for hosting me in Cornwall, for the swims, games nights, amazing
52 food, and cuddles with Willow! I'm beyond grateful for your friendship and for making me feel so
53 welcome. It was a joy learning from friends who have walked this path before.

54

55 To my family: Mum, thank you for inspiring my love and curiosity of the natural world. Your interest
56 in this research has been a huge motivation for me to keep going, and I will always cherish our
57 shared passion for wildlife. And to my nieces and nephew, for keeping life filled with games, laughter,
58 and a good dose of silliness.

59

60 Finally, to Sam. I can't thank you enough for sticking by me over these past few years. You've kept me
61 grounded and reminded me to not let life go by when you're busy working. I can't wait for all the
62 adventures that lie ahead with you and Moose when this chapter is complete!

Abstract

Reliable density estimates are essential for effective wildlife management, yet difficult to obtain. Camera traps have revolutionised density estimation for elusive species where individuals are recognisable, but until recently could not be used for other species. The random encounter model (REM) and camera trap distance sampling (CT-DS) are novel approaches which fill this methodological gap.

The management of European badgers (*Meles meles*) for the control of bovine tuberculosis (bTB) offers an ideal system for testing these methods because counting badgers is difficult, and abundance data are crucial for informing policy decisions. This thesis aimed to assess the REM and CT-DS for estimating animal density to inform disease management, focusing on badger vaccination for the control of bTB.

Density estimates aligned well between methods (Chapters 2, 4, and 5), and with independent reference estimates (Chapters 2 and 4). The REM was the more precise method, but both approaches were imprecise where density was low (Chapters 2 and 4). Precision improved with the use of more cameras, with both methods achieving adequate precision with ≥ 100 cameras (Chapter 4).

Where badgers were not culled, mean vaccination coverage ranged from 50.6% to 74.2%, surpassing the 30% threshold likely to be necessary for bTB elimination in badgers (Chapter 3). At two post-cull sites, point estimates of coverage also exceeded 30%, although confidence intervals were wide (Chapter 5), likely due to the small geographical scale of the study.

These findings show the utility of the REM and CT-DS for estimating the density of individually unidentifiable species. Additionally, the results suggest that badger vaccination can attain high levels of coverage, highlighting this as a feasible strategy for bTB management. However, the imprecision of estimates immediately post-cull calls for larger-scale evaluations. These findings are highly relevant to current bTB policy in England which is prioritising post-cull badger vaccination.

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List of Publications

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264 Miles, V., Woodroffe, R., Donnelly, C. A., Brotherton, P. N. M., Ham, C., Astley, K., Aurélio, J., &
265 Rowcliffe, M. (2024). **Evaluating camera-based methods for estimating badger (*Meles meles*)**
266 **density: Implications for wildlife management.** *Ecological Solutions and Evidence*, 5, e12378.
267 <https://doi.org/10.1002/2688-8319.12378> (Chapter 2; detailed in Appendix 4)

268

269

270 Penn, M. J., Miles, V., Astley, K. L., Ham, C., Woodroffe, R., Rowcliffe, M., & Donnelly, C.
271 A. (2024). **Sherlock—A flexible, low-resource tool for processing camera-trapping images.** *Methods*
272 *in Ecology and Evolution*, 15, 91–102. <https://doi.org/10.1111/2041-210X.14254> (used data from
273 Chapter 2; detailed in Appendix 4)

274

275

276 Woodroffe, R., Astley, K., Barnecut, R., Brotherton, P. N. M., Donnelly, C. A., Grub, H. M.
277 J., Ham, C., Howe, C., Jones, C., Marriott, C., Miles, V., Rowcliffe, M., Shelley, T.,
278 & Truscott, K. (2024). **Farmer-led badger vaccination in Cornwall: Epidemiological patterns and**
279 **social perspectives.** *People and Nature*, 6, 1960–1973. <https://doi.org/10.1002/pan3.10691> (used
280 data from Chapters 2 and 3; detailed in Appendix 4)

281 **List of Acronyms**

282	AI	Artificial intelligence
283	APHA	Animal Plant and Health Agency
284	BCG	Bacille Calmette-Guérin
285	bTb	Bovine tuberculosis
286	CI	Confidence interval
287	CT-DS	Camera trap distance sampling
288	CV	Coefficient of variation
289	DAERA	Department of Agriculture, Environment and Rural Affairs
290	DEFRA	Department for Environment, Food and Rural Affairs
291	DNA	Deoxyribonucleic acid
292	FOV	Field of view
293	HRA	High risk area
294	LRA	Low risk area
295	MNA	Minimum number alive
296	OTF	Officially TB Free
297	PPE	Personal protective equipment
298	QAIC	Quasi Akaike information criterion
299	RBCT	Randomised Badger Culling Trial
300	REM	Random encounter model
301	SD	Standard deviation
302	SD card	Secure digital card
303	SE	Standard error
304	SMR	Spatial mark-resight
305	STE	Space-to-event
306	TB	Tuberculosis
307	TTE	Time-to-event
308	UK	United Kingdom
309	VESBA	Vaccinating East Sussex Badgers
310	WHO	World Health Organisation

Contributions Statement

Verity Miles, Christl Donnelly, Marcus Rowcliffe, and Rosie Woodroffe conceived the ideas of this research and designed the methods.

Camera data for Chapters 2 and 3 were collected by Verity Miles, Cally Ham, Kelly Astley, Marcus Rowcliffe, and Rosie Woodroffe. Several volunteers helped with camera surveys in Cornwall: Anisha Tennant, Joana Aurélio, Natalie Durrant, Nicholas Steyn, Ruth McCabe, Sarah Ferry, and Sarah Hayes. Badger vaccination at sites in Cornwall was carried out by Cally Ham, Kelly Astley, and Rosie Woodroffe, with support from volunteers from the Cornwall Badger Project and the Cornwall Wildlife Trust. Verity Miles tagged all of the images used in Chapters 2 and 3, with help from Joana Aurélio, who tagged all of the images from site four. All data analysis for these chapters was carried out by Verity Miles with support from Christl Donnelly, Marcus Rowcliffe, and Rosie Woodroffe.

The camera survey at Woodchester Park in Chapter 4 was led by Verity Miles with help from Amy Griffiths, Ruth Cox, Delaney Eng, and staff at the Animal and Plant Health Agency (APHA). All badger trapping and sampling was carried out by APHA staff. Image tagging was led by Verity Miles with help from Sarah Lo, Sophie Ryan, Tania Trugman, and APHA staff. Data analysis for four was carried out by Verity Miles with support from Christl Donnelly, Marcus Rowcliffe, Rosie Woodroffe, Sarah Lo, and Sophie Ryan, with feedback on drafts provided by Ruth Cox and Graham Smith.

Camera surveys detailed in Chapter 5 were designed by Ruth Cox with support from Verity Miles. Verity Miles trained APHA staff to run the camera surveys. All badger trapping and vaccination was carried out by APHA staff. Image tagging was led by Verity Miles with help from APHA staff. Data analysis for Chapter 5 was carried out by Verity Miles with support from Christl Donnelly, Marcus Rowcliffe, and Rosie Woodroffe, with feedback on drafts provided by Ruth Cox and Graham Smith.

Verity Miles wrote this thesis, with feedback from Christl Donnelly, Marcus Rowcliffe, Rosie Woodroffe, Peter Brotherton, Ruth Cox, and Graham Smith.

A version of Chapter 2 was published in *Ecological Solutions and Evidence* in September 2024 and benefitted from feedback from Joanna Burgar and an anonymous reviewer. This publication is included in Appendix 4. Data from Chapter 2 were also used for a manuscript published in *Methods in Ecology and Evolution*, and data from Chapters 2 and 3 were included in a manuscript published in *People and Nature*. Details of these papers are included in Appendix 4.

Verity Miles was funded by UKRI (NERC); Imperial College London, through the Science and Solutions for a Changing Planet Doctoral Training Partnership, grant number NE/S007415/1; Natural England; and the Zoological Society London. The Cornwall Badger Project was funded by the Department of Environment, Food and Rural Affairs (DEFRA), the National Trust, the Garfield Weston Foundation, the People's Trust for Endangered Species, private donors to Cornwall Wildlife Trust, the Zoological Society of London, and some participating landholders. The Institute of Zoology is supported by Research England. Research carried out by APHA staff, including the Woodchester Park Study, was supported by DEFRA.

354

Ethical Statement

355 Ethical approval for this research was granted by the Zoological Society London. All badger trapping
356 and vaccination formed part of existing research projects and was carried out by trained and licensed
357 individuals. At sites in Cornwall, badgers were trapped and vaccinated by staff of the Cornwall Badger
358 Project within the Zoological Society of London, under licence from the UK Home Office (project
359 licence PB32E4DFC) and Natural England (research licences 2019-40177-SCI-SCI and 2021-53121-SCI-
360 SCI). Badger trapping and handling at Woodchester Park in 2022 was carried out by APHA staff under
361 the licences 2021-51975-SCI-SCI and 2022-63032-SCI-SCI. Badger trapping and vaccination at all
362 other sites in Gloucestershire and Wiltshire was carried out by APHA staff under licences issued by
363 DEFRA and Natural England.

364

365 All landowners consented to taking part in badger vaccination and camera trap surveys. Volunteers
366 and staff contributing to camera surveys consented to having images of themselves stored and used
367 for research purposes. Images of identifiable members of the public were stored temporarily on
368 secure storage systems to retain a complete raw dataset while data analysis was being conducted.
369 These images were deleted after four years, following Imperial College London's data privacy policies.

370 **1. Chapter 1: General introduction**



371 *A red fox (Vulpes vulpes) on a camera trap in Cornwall.*

1.1. The value of monitoring wildlife populations

Amid the global climate and biodiversity crises and escalating human-wildlife conflicts, the need for effective wildlife management has never been more evident. Population monitoring is critical to wildlife management and has a wide range of applications, from conservation and ecology, to game management and disease control. Data from monitoring programmes are crucial for informing policy decisions, guiding resource allocation and assessing the efficacy of management interventions, and contribute to our understanding of animal behaviour, species ecology and ecosystem dynamics.

Reliable estimates of population abundance (the total number of individuals in a given area) or density (the number of individuals per unit area), as well as the ability to detect change in these metrics, are fundamental to population monitoring. Measuring trends (both increasing and declining) is crucial, since conservation objectives are often to maintain or increase population sizes of specific species or overall biodiversity, while in cases of human-wildlife conflict, the goal is typically to reduce the abundance of problematic species (Wilson & Delahay, 2001).

Examining population estimates and abundance trends are powerful tools in conservation, and form the foundation of conservation assessments such as the Living Planet Index and the International Union for Conservation of Nature Red List of Threatened Species, which have been instrumental in guiding global conservation policies and measuring progress towards global biodiversity targets (Betts *et al.*, 2020; Ledger *et al.*, 2023). Integrated population monitoring combines data from a number of sources to identify the causes of species declines and guide conservationists to target actions (e.g. BirdTrends, Massimino *et al.*, 2023). Additionally, monitoring the abundance of indicator species can provide insights into ecosystem health (e.g. the UK Butterfly Monitoring Scheme; Middlebrook *et al.*, 2023), and inform management interventions such as species reintroductions (Stringer & Gaywood, 2016). The need to obtain accurate and precise abundance data for these purposes has driven the development of statistical methods, and refining such models is now a key focus of many ecological studies.

1.2. Methods of population monitoring

1.2.1. Simple counts and abundance indices

Despite the value of abundance estimation and its diverse range of applications, counting wild animals is often challenging and imprecise. In some scenarios, where terrain and visibility allow, it may be feasible to count the entire population, referred to as a 'population census', by direct observation or with the help of methods such as aerial surveys (e.g. Hedges & O'Brien, 2012). Where a population census is challenging, subjects can be counted in samples and scaled up to the total area (Burnham *et al.*, 1980).

The assumption that all animals in a population are observed during a simple count survey is rarely met, and abundance is likely underestimated as a result (Caughley, 1974; Jachmann, 2002; Schlossberg *et al.*, 2016). This is particularly true of rare, cryptic and/or elusive species, or where impenetrable habitats make direct observations virtually impossible (Zwerts *et al.*, 2021). In such instances, indirect measures of abundance may be easier, more cost effective, and/or the only feasible option (Wilson & Delahay, 2001; Bart *et al.*, 2004). Following the assumption that the frequency or quantity of certain field signs is proportional to animal density, these indices can be quantified to give a relative estimate of abundance. The choice of indicator depends on the ecology of the species of interest (Gompper *et al.*, 2006), with the most common being faecal samples (Fernanda *et al.*, 2001; Hedges, 2012; Ferretti *et al.*, 2016), tracks (Bonesi & Macdonald, 2004; Kawaguchi *et al.*, 2015), breeding dens and refugia (Krebs *et al.*, 2012; Lara-Romero *et al.*, 2012), hunting records (Cattadori *et al.*, 2003; Hušek *et al.*, 2021) and photographic trap rate (the number of photographs per unit of time) with the use of remote cameras (Carbone *et al.*, 2001; Rovero & Marshall, 2009). In most cases these indices are quantified to give a simple relative measure of abundance, though it is possible to convert these into true density by calibration with correction factors (e.g. Schwarz & Seber, 1999).

There is much debate about the validity of relative abundance (Anderson, 2001; Carbone *et al.*, 2001; Jennelle *et al.*, 2002; Sollmann *et al.*, 2013b). While in many circumstances indices may be preferable due to resource constraints, criticism arises because bias may be introduced by sampling effort, detectability, and/or animal activity which are unlikely to remain constant in time and space (Pollock *et al.*, 2002). Consequently, indices often do not relate to actual density (Sollmann *et al.*, 2013b) and may not be sensitive to populations trends (Marchandean *et al.*, 2006). For this reason, several authors caution against the use of indices of abundance without methods to correct bias or quantify the degree of uncertainty (Bart *et al.*, 2004) and instead advocate for statistical methods which account for detectability (Yoccoz *et al.*, 2001; Pollock *et al.*, 2002).

1.2.2. Mark-recapture models

Mark-recapture models are some of the most widely used methods and generally considered the gold standard for estimating animal abundance while considering variation in detectability. In their simplest form, mark-recapture models based on the Lincoln-Petersen index (Lincoln, 1930) involve sampling, marking and releasing a number of animals. After allowing sufficient time for the population to mix, a second sample is taken, and the number of marked animals is recorded. The proportion of marked animals in the second sample is used to estimate the total population size (Nichols, 1992). Marks may be permanent (e.g. bird rings) or temporary (e.g. paint, fur-clips or collars), but must remain for the duration of the study. In addition, mark-recapture models assume

that the population is closed, meaning no births, deaths or migrations occur between sampling occasions. However, adaptations can be made for open populations, which are common in reality and are discussed in detail elsewhere (McDonald & Amstrup, 2001). A limitation of the method is that it is prone to bias when capture probability is heterogeneous.

Considerable development of mark-recapture models beyond the Lincoln-Petersen index have allowed for multiple sampling occasions and the use of non-invasive methods, such as genetic mark-recapture using hair or faeces (see Waits & Paetkau, 2005, for a review of such methods) facilitating extension to species which are difficult to trap (e.g. elephants and large carnivores). The use of 'sighting' data, which relies on animals' natural unique pelage markings, also bypasses the need to trap and handle animals and has enabled application to situations where the number of uniquely marked individuals is unknown (Arnason *et al.*, 1991). However, spatial sampling bias is problematic in such models because animals with home-range centres closer to traps or detectors are more likely to be sampled (Chandler & Royle, 2013). Additionally, estimating density requires accurate knowledge of the size of the sampled area, which is challenging in most situations unless the geographic area is well-defined, such as an island.

These challenges have led to the development of spatially explicit capture-recapture models, which incorporate location data in the capture histories of animals (Borchers & Efford, 2008; Royle & Young, 2008). As a result, spatially explicit capture-recapture allows for modelling of the spatial distribution of animals and the detection process to estimate the probability of detection (Royle & Young, 2008; Efford, 2009; Gardner *et al.*, 2009). This approach corrects for capture heterogeneity, providing a more robust estimate of the effective sampling area and, therefore, density (Borchers & Efford, 2008). These methods are now common with remote cameras (Karanth & Nichols, 1998). However, despite their widespread application and reliability, mark-recapture models remain limited to species which are individually identifiable.

1.2.3. Distance sampling

Distance sampling models are an alternative set of widely used tools for abundance estimation that address the problem of imperfect detection and do not require animals to be individually identifiable (Buckland *et al.*, 2001). Conventional distance sampling models involve observers counting animals within a sample of the study area by recording detections as they move along transects or from fixed points. Unlike traditional line transects, distance sampling models recognise that detection probability is related to the distance of the animal from the observer; animals closer to the observer are more likely to be detected than those further away. Detection distances are therefore recorded during surveys and used to model the detection function, representing the probability of detecting

an animal at a given distance (Buckland *et al.*, 2015). Where exact distances are difficult to obtain, for example, when recording bird vocalisations, distance bands are used. Density is estimated by accounting for the proportion of the population encountered during the survey and the study area, defined by the total area covered by the transects or points. Covariates that may affect the detection probability, such as habitat, weather or the sex of the focal species, can also be included in models (Marques *et al.*, 2007).

The fundamental assumptions of distance sampling models are that the distribution of transects (or points) is independent of animal distribution; animals at the line or point are detected with certainty; distances are accurately measured; and animals do not move within the survey (Buckland *et al.*, 2001). In reality, this final assumption may not always hold true. For example, the reactive movement of animals in response to disturbance caused by the presence of an observer is a well-documented problem (Turnock & Quinn, 1991), particularly when transects are surveyed using vehicles, aircraft or ships. Although methods to quantify and control this bias have been developed (Buckland *et al.*, 2005), there remains a need for solutions that have minimal influence on the species being studied.

1.2.4. Camera-based methods

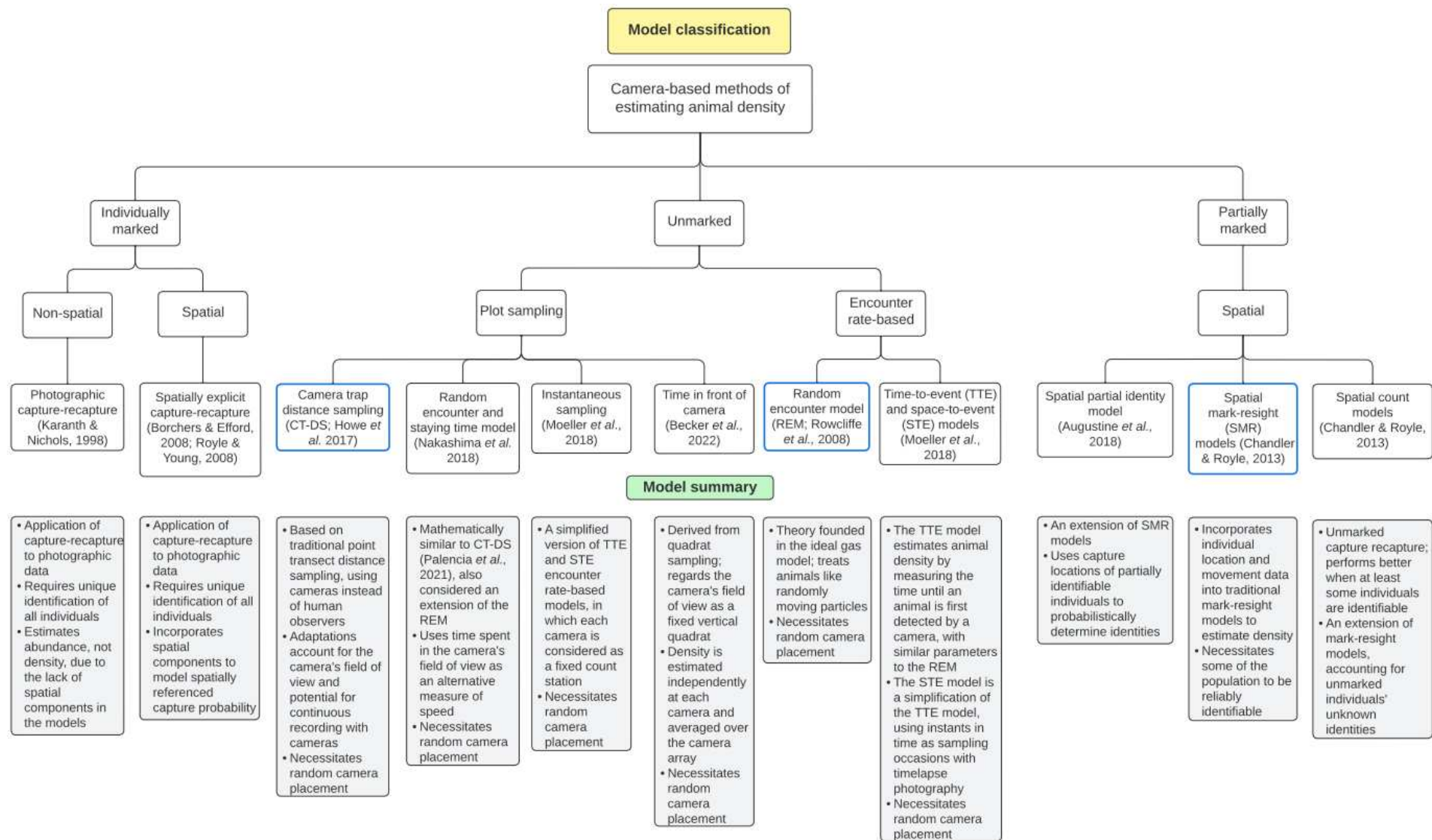
Camera traps – remote cameras that are sensitive to motion and heat and activate upon detecting passing animals – have become invaluable to ecological research and are one of the most popular tools for studying terrestrial species (Burton *et al.*, 2015). Compared with human observers, camera traps cause minimal disturbance and are capable of collecting data for weeks or months without the need for intervention. During a camera trap survey, data can be collected on multiple species simultaneously, providing information on presence, abundance, behaviour and species' ecology (Trolliet *et al.*, 2014). Camera trap studies are relatively easy to implement over large areas and can be more cost effective than traditional approaches of estimating density, particularly with the use of citizen scientists and the integration of artificial intelligence software to optimise camera trap image processing (Schaus *et al.*, 2020; Kissling *et al.*, 2024).

Statistical models for the analysis of camera trapping data have advanced beyond using photographic rate as an index of density, incorporating spatial data and accounting for detectability (Fig. 1.1). The most popular approaches include resighting models adapted for partially identifiable populations, known as spatial mark-resight (SMR) models, and the random encounter model (REM) and camera trap distance sampling (CT-DS), which are applicable to unmarked species. We pay special attention to these three models as the focal methods in this thesis and give a brief overview of alternative camera-based approaches in Figure 1.1.

1.2.4.1. Spatial mark-resight

Mark-resight models are an extension of mark-recapture models in which only a subset of the population is uniquely identifiable. Spatial mark-resight (SMR) models require a proportion of the population to be individually identifiable, through either natural or artificial markings, which are then resighted non-invasively, for example, using camera traps. Location data from detections of marked and unmarked individuals are used to estimate the number and location of animal activity centres (probabilistically determined points that represent the expected central tendency around which animal detections are clustered) (McClintock *et al.*, 2022). This spatial information is used to model detection probabilities as a function of the distance between the known locations of animal detections and the estimated location of activity centres, which enables the calculation of density (Chandler & Royle, 2013; Rich *et al.*, 2014). Such models also allow for the inclusion of individuals with an unknown marking status.

Unlike traditional mark-recapture models, when using artificial marks for resighting in SMR models, no new marks are added after the first occasion (Sollmann *et al.*, 2013a). The main difference between SMR models and spatially explicit capture-recapture models is that SMR models do not require the entire population to be uniquely marked (Fig. 1.1). The requirement of only partial identity information for SMR models is particularly useful for camera trapping studies where marks are often difficult to determine in images. While photographic SMR shares the broad advantages of using camera traps to study wildlife remotely, it is still limited by requiring a proportion of the population to be uniquely recognisable. In addition, density estimates rely on sufficient observations of identifiable individuals, and precision and accuracy are improved with recaptures at multiple sampling locations, necessitating intensive camera spacing relative to animal movement or the use of independent movement data to inform model parameters (Sollmann *et al.*, 2013a). These limitations have encouraged the development of spatial-partial identity models which use the spatial information from resighting data to probabilistically determine the identities of partially identifiable individuals (Augustine *et al.*, 2018), as well as alternative approaches, such as the REM and CT-DS, which do not rely on individual identification.



550 **Figure 1.1** Organisational structure and summary of camera-based methods of estimating animal density. The focal approaches of this thesis are highlighted
 551 in blue.

1.2.4.2. The random encounter model

The random encounter model (REM), first described by Rowcliffe *et al.* (2008), is founded in the theory of the ideal gas model which describes the rate of encounter between gas particles based on the number, speed and size of particles, and the volume in which they are contained. When applied to animal density, encounters are between moving animals and stationary camera traps, and ‘collisions’ occur when animals enter the detection zone and the camera sensor is triggered (Rowcliffe *et al.*, 2008). Density is estimated using the following equation from Rowcliffe *et al.* (2008):

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

where y is the number of independent animal observations per unit time (t) or the ‘encounter rate’, v is the focal species’ average speed of movement (expressed as distance travelled per day), and r and θ are the dimensions of the camera detection zone (radius and angle, respectively; Fig. 1.2). A fundamental assumption is that the placement of cameras is random with respect to animal movement, and density estimates may be biased where this is not achieved (Rowcliffe *et al.*, 2008; Cusack *et al.*, 2015b). It is possible to use cameras targeting areas of high animal activity by applying a correction factor for habitat use (Garrote *et al.*, 2021), although, at present, this is limited to species for which accurate information on habitat selection is available. Less emphasis is placed on population closure as the REM provides an average density for the survey period if the assumption of population closure is not met (Rowcliffe *et al.*, 2008).

Comparison with populations of known size, and with independent estimates of animal density, support the accuracy of the REM (Rowcliffe *et al.*, 2008; Schaus *et al.*, 2020; Palencia *et al.*, 2022; Twining *et al.*, 2022; Wiegers *et al.*, 2024). Early model development focussed on optimising the estimation of model parameters, recognising the importance of using consistent camera models and settings, and estimating the camera parameters within the specific survey conditions (Rowcliffe *et al.*, 2011; Rowcliffe *et al.*, 2012; Rowcliffe *et al.*, 2014). The estimation of animal speed was previously considered the biggest source of model bias due to oversimplification of animal movement when relying on telemetry data (Rowcliffe *et al.*, 2012). However, development in the methodology, specifically calibrating camera deployments using an object of known size to estimate distances in images (Wearn *et al.*, 2022), means these parameters can now be reliably estimated using only data from the images themselves, making the method easier to implement.

Compared with methods such as mark-recapture, the REM is still in its infancy, and further research to test its accuracy across a range of species and habitats, as well as optimising survey designs to improve precision of the results, is recommended (Palencia *et al.*, 2022). Methods to

quantify and mitigate bias arising from failure to meet the model assumptions are also valuable. Reactivity is a common occurrence in camera trap studies and if an animal alters its natural behaviour, parameters of the REM, such as movement speed, can be biased, potentially affecting the accuracy of density estimates (Delisle *et al.*, 2023). This is particularly important as camera traps may not be as unobtrusive as once thought (Meek *et al.*, 2016).

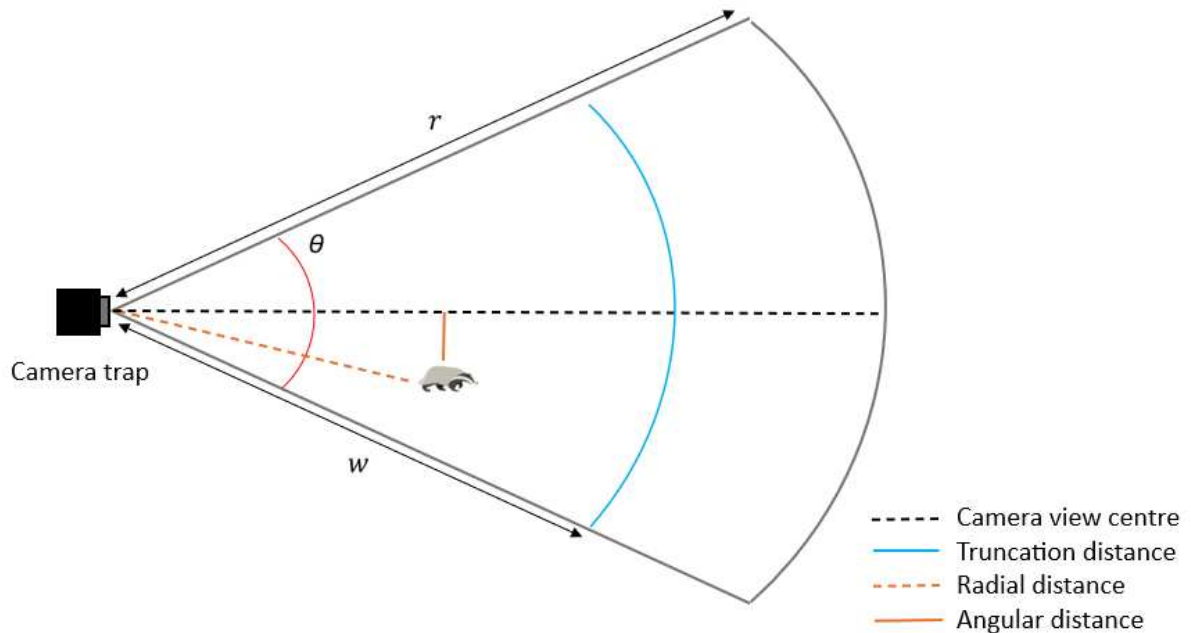


Figure 1.2 Representation of the detection zone of a camera trap, given by the angle θ and radius r , or truncation distance w . Radial and angular distances, demonstrated by the position of the badger, are recorded for each animal during image processing for the random encounter model and camera trap distance sampling.

1.2.4.3. Camera trap distance sampling

The theoretical framework of traditional distance sampling models can be adapted to utilise camera traps instead of human observers. There are two key differences in camera trap distance sampling (CT-DS) concerning spatial and temporal parameters, which affect the calculation of effort. Firstly, while in a traditional point survey an observer would have a 360° view for recording animal observations, camera traps detect animals in a smaller segment-shaped area. As with the REM, spatial effort is given by the dimension of the camera detection zone (Fig. 1.2). Secondly, human observers record the distance of each animal detection at the location it was first observed and may make several repeat visits to each point on separate surveys. In contrast, camera traps remain at fixed locations, may obtain multiple detections of an individual arising from a single sequence, and

can detect animals continuously, either for the entirety of the deployment period or during specific programmed times. For CT-DS models it is therefore necessary to calculate the number of potential opportunities for detecting animals during a survey, referred to as ‘snapshot moments’, H . Temporal effort is estimated using the following equation from Howe *et al.* (2017):

$$H = t/T$$

where t is the amount of time cameras were operational for and T is the mean interval between successive images within sequences. Overall sampling effort, e , is a product of temporal effort and spatial effort, given by the equation:

$$e = \frac{\theta H}{2\pi}$$

where θ is as described for the REM. Density is then estimated using the equation:

$$D = \frac{y}{\pi w^2 e p a}$$

where y is the total number of animal observations, w is the truncation distance (Fig. 1.2), p is the probability that an animal within distance w is detected, and a is the proportion of time for which the focal species is active, referred to as the ‘activity level’ (Howe *et al.*, 2017). Activity level is estimated using records of animals on camera traps by fitting a circular distribution model to time-of-detection data (Rowcliffe *et al.*, 2014).

Fewer studies have been published utilising CT-DS compared to the REM, but research to date suggests consistency with population census data (Harris *et al.*, 2020) and independent density estimates (Cappelle *et al.*, 2019; Twining *et al.*, 2022). However, as with traditional distance sampling models, the influence of camera traps on animal behaviour is a known source of bias (Bessone *et al.*, 2020; Houa *et al.*, 2022; Delisle *et al.*, 2023). Consequently, much of the focus of model development has been on quantifying and mitigating this bias, but, at present, there is no standardised method to address this problem.

1.2.5. Future advances of camera trapping methodologies

While SMR, the REM and CT-DS models have seen considerable development and wide application in recent years, their respective advantages and disadvantages (Table 1.1) suggest that no single model is universally optimal. In addition, ensuring accuracy and precision across a range of environmental conditions, species, and density scenarios is crucial for their broader application in real-world situations. As such, rigorous testing against independent density estimation methods, and evaluation of model performance and potential bias, is critical. Wildlife managers and conservationists face

634 growing demands for accurate and precise density estimates with limited resources, highlighting the
635 need for comparative analyses of camera-based approaches in terms of accuracy, precision, cost, and
636 effort, as well as a need for guidance on optimal survey design to ensure the most reliable results for
637 informed decision-making.

638 **Table 1.1** Summary of the advantages and disadvantages of the three density estimation methods studied in this thesis.

Theme	Density estimation method		
	Spatial mark-resight	Random encounter model	Camera trap distance sampling
Individual identification requirement	A proportion of the population must be uniquely marked	Does not require individual identification	Does not require individual identification
Invasiveness and animal handling	Marking may require capture; resighting process non-invasive	Entirely non-invasive	Entirely non-invasive
Camera placement strategy	Supports strategic deployment to maximise resighting; coverage across species' density distribution is recommended to avoid bias	Cameras must be placed randomly with respect to animal movement; results biased where this is violated	Cameras must be placed randomly with respect to animal movement; results biased where this is violated
Bait dependency	Can use bait to increase resighting rate but may introduce bias	Bait should not be used to avoid biasing animal movement and trap rate	Bait should not be used to avoid biasing animal movement and trap rate
Sensitivity to camera trap influence	Less sensitive to reactive behaviours towards camera traps than REM and CT-DS	Density estimates can be biased by reactivity; method of control standardised	Density estimates can be biased by reactivity; no standardised method to control bias
Requirement for population closure	Assumes population closure; estimates biased if this is violated	Assumes population closure; will estimate average density if this is violated	Assumes population closure; will estimate average density if this is violated
Applicability to multiple species	Possible to study multiple sympatric species if individuals are identifiable	Easy to study multiple sympatric species using the same data	Easy to study multiple sympatric species using the same data
Applicability to rare, cryptic and/or elusive species	Density estimates likely to be imprecise; precision improves as the number of identifiable resighting records increases	Density estimates likely to be imprecise, particularly with high variability in trap rate	Density estimates likely to be imprecise, particularly with high variability in trap rate
Key data challenges	Requires certain identification of individuals and longevity of marks during the study	Necessitates measuring animal speed which is likely the most inaccurate model parameter	Density estimates can be biased by reactivity to camera traps

1.3. Policy relevance of estimating wildlife population density

1.3.1. Human-wildlife conflict

Monitoring wildlife population trends is crucial for informing policy and management decisions, particularly in the context of human-wildlife conflict, which is one of the biggest global challenges for conservationists and policymakers (Dickman, 2010). Such conflict has intensified in many regions in recent decades, exacerbated by human population growth, climate change, resource competition and increasing agricultural demands (Dickman, 2010). For example, the control of wild boar *Sus scrofa* populations across Europe illustrates the value of monitoring animal abundance to mitigate human-wildlife conflict and evaluate management interventions. Wild boar damage crops and pose serious health risks to livestock and humans through road traffic accidents and disease transmission (ENETWILD consortium *et al.*, 2018). Distribution and abundance data are essential for spatial models designed to assess these risks and improve management strategies, with camera trapping highlighted as being particularly effective for this purpose (Acevedo *et al.*, 2022).

The control of zoonotic diseases can cause conflict between humans and wildlife. Host abundance plays a key role in the maintenance and spread of some zoonotic diseases (Cardoso *et al.*, 2022), and therefore accurate estimates of population size, density, and spatial distribution can be crucial for understanding the epidemiology and persistence of these diseases, and informing policy decisions (Ryser-Degiorgis, 2013; Barroso *et al.*, 2023). However, assessment of disease status and prevalence are often hindered by lack of precise host population densities and standardised methods of estimating abundance (Ryser-Degiorgis, 2013). Consequently, wildlife health surveillance programmes frequently lack integration with appropriate population monitoring (Barroso *et al.*, 2024), although efforts to address this issue are underway (e.g. ENETWILD consortium *et al.*, 2018). There is broad recognition of the need to improve methods of estimating animal abundance in this context (Ryser-Degiorgis, 2013).

1.3.2. Bovine tuberculosis

Bovine tuberculosis (bTB) is a chronic respiratory disease of cattle which presents a major global health challenge for cattle farmers. Though considerably less common than tuberculosis (TB) in humans, bTB infections amount to an estimated 140,000 human cases globally each year, leading to over 11,000 deaths (WHO, 2020). The disease is caused by the bacillus *Mycobacterium bovis* (*M. bovis*) which is transmitted mostly by inhalation of infected aerosols. *M. bovis* has a wide host-range, including humans, wildlife, and a number of domesticated mammal species, although cattle are considered to be the primary reservoir of infection (de la Rua-Domenech, 2006).

In the UK, human immunisation, milk pasteurisation, routine cattle testing, and the slaughter of test-positive cattle have largely controlled bTB infections in humans. However, the persistence of the disease in cattle remains “one of the most pressing animal health problems in England” (APHA, 2023). While Scotland has been recognised as Officially TB Free since 2009, in England and Wales, the prevalence in livestock remains relatively high, though there has been some indication of a decline in recent years (DEFRA, 2024f). Around 30,000 cattle are slaughtered annually in the UK in an attempt to control the disease (DEFRA, 2024e), posing a serious threat to the farming industry and an economic challenge for the UK government and taxpayers (DEFRA, 2018). Many of the costs associated with controlling bTB are borne by farmers, affecting the livelihoods and mental health of those involved (Butler *et al.*, 2010; Barnes *et al.*, 2023).

1.3.3. Badgers and bovine tuberculosis control

Though several mammal species are susceptible to *M. bovis* infection (Delahay *et al.*, 2007; Gortazar *et al.*, 2012), in the UK, European badgers (*Meles meles*) are considered to be the most important wild hosts for the persistence of the disease in cattle (Krebs, 1997). As a result, policy to control bTB has included badger management by culling, which began in 1973, and vaccination, which was first licensed in 2010 (DEFRA, 2011).

Badger culling aims to reduce the incidence of bTB in cattle by reducing the number of infectious and susceptible badgers below the threshold required to sustain transmission from badgers to cattle (Carter *et al.*, 2007). However, the situation is complex: the most likely scenario for bTB transmission is a multi-host system with transmission occurring in both directions between wildlife and cattle, with cattle-to-cattle transmission identified as the most important route for maintaining infection in livestock (Donnelly & Nouvellet, 2013; van Tonder *et al.*, 2021). Under this multi-host scenario, simply culling badgers will not eliminate bTB, a hypothesis supported by both modelling studies (Brooks-Pollock & Wood, 2015; Crispell *et al.*, 2019) and field data (Woodroffe *et al.*, 2006b; Jenkins *et al.*, 2007).

The Randomised Badger Culling Trial (RBCT) was the first major controlled study to investigate the impact of culling badgers on the incidence of bTB in cattle. The trial found that, while (and up to one year after) culling was ongoing, the incidence of confirmed bTB in cattle was 23.2% lower (95% confidence interval (CI) 12.4%—32.7% lower) inside widespread ‘proactively’ culled zones, but 24.5% higher (95% CI 0.6%—56.0% higher) on land ≤ 2 km outside them (Donnelly *et al.*, 2007). Localised ‘reactive’ culling was also associated with detrimental effects: areas subjected to reactive culling saw the incidence of confirmed bTB in cattle increase by 27% (95% CI 4.8% – 53%

increase; Donnelly *et al.*, 2003) and the risk of bTB breakdown¹ in nearby herds doubled (Vial & Donnelly, 2012). These patterns are attributed to a change in the social organisation and movement behaviour of badgers in response to culling. Badgers roam further in culled areas, causing greater overlap of home ranges, and more opportunity for intergroup contact and disease transmission (Tuytens *et al.*, 2000a; Woodroffe *et al.*, 2006a; Ham *et al.*, 2019). Roaming further might also increase badger-cattle contact and aid disease transmission in both directions between badgers and cattle (Ham *et al.*, 2019). Badger culling remains highly controversial and has been met with widespread opposition due to concerns about its effectiveness and the implications for animal welfare (McCulloch & Reiss, 2017), encouraging continued research into alternative strategies.

Vaccinating wild animals can be effective in the control of zoonoses, exemplified by the eradication of rabies in most of Western and Central Europe following targeted vaccination in red foxes (*Vulpes vulpes*) and domestic dogs (Freuling *et al.*, 2013). Vaccination works by increasing immunity in the population to a level which reduces pathogen transmission and the risk of infection to unvaccinated susceptible individuals, a concept known as ‘herd immunity’ (Fine *et al.*, 2011). Trials have found that vaccinating badgers with the Bacille Calmette-Guérin (BCG) vaccine can reduce the risk of infection and prevent the onward transmission of *M. bovis* (Corner *et al.*, 2008; Chambers *et al.*, 2011; Lesellier *et al.*, 2011), as well as providing indirect protection to unvaccinated individuals in the same social group (Carter *et al.*, 2012; Gormley *et al.*, 2017; Gormley *et al.*, 2022). There is also limited evidence to suggest that *M. bovis* prevalence declines in vaccinated badger populations (APHA, 2016a; Gormley *et al.*, 2017; Woodroffe *et al.*, 2024) but further research, such as a randomised trial on the scale of the RBCT, is recommended to fully examine this relationship. It is presumed that badger vaccination would also reduce the risk of herd breakdowns. Limited research in this area means it is not possible to confirm this at present, though evidence suggests that badger vaccination is not inferior to badger culling for reducing bTB incidence in cattle (Martin *et al.*, 2020).

1.3.4. Current bTB eradication policy in the UK

There is large variation in the incidence of bTB in cattle across the UK as a result of different farming practices, cattle numbers and the risk of infection from wildlife. As such, the governments of England, Wales, Scotland and Northern Ireland differ in their approach to bTB eradication, with a clear distinction between policies focusing control measures on cattle or badgers.

The current bTB eradication strategy for England, which strives to achieve Officially TB Free status by 2038, was launched in 2013 (DEFRA, 2014) and updated in 2020 (DEFRA, 2020) following an independent policy review (Godfray *et al.*, 2018). England is divided into three epidemiological areas

¹ When bTB is suspected or confirmed in a herd and the herd loses its officially TB free status.

and bTB measures are determined by the expected risk of cattle infection (Fig. 1.3). The 'high risk area' (HRA), predominantly the West and South West of England (Fig. 1.3), represents regions where the incidence of bTB in cattle is high and both badgers and cattle live at relatively high densities. Cattle herds in the HRA undergo six-monthly testing (DEFRA, 2020). Widespread proactive badger culling, which aims to sustain a 70% reduction in the badger population, has been licensed in much of the HRA since 2013. By 2023, 72.3% of the HRA was subject to badger culls (DEFRA, 2024b). Badger vaccination is also licensed in the HRA but until recently, was not funded by the government. As such, most vaccination projects in the HRA have been relatively small scale compared to badger culling and have been delivered predominantly by volunteers and wildlife groups. However, emerging policy suggests a gradual end to badger culling and greater emphasis on badger vaccination, using a government funded "Badger Vaccinator Field Force" (DEFRA, 2024d). At present, it is not clear where badger vaccination will be targeted or the scale at which it will be delivered.

The 'low risk area' (LRA) of England (Fig. 1.3) has relatively low incidence of cattle TB and fewer cattle and badgers, with cattle testing only required once every four years in most places. Both badger culling and vaccination can be licensed in the LRA but badger vaccination is not funded by the government. The area between the HRA and LRA is termed the 'edge' area (Fig. 1.3) where there is an intermediate risk of bTB infection in cattle. Cattle in these areas must undergo testing either annually or six-monthly, depending on the geographical risk of infection, and badger culling has been licensed. Badger vaccination projects in the edge area were eligible for government support (the 'Badger Edge Vaccination Scheme') until 2023 (DEFRA, 2017). A new large-scale government-funded badger vaccination trial is also underway in East Sussex (VESBA, 2024).

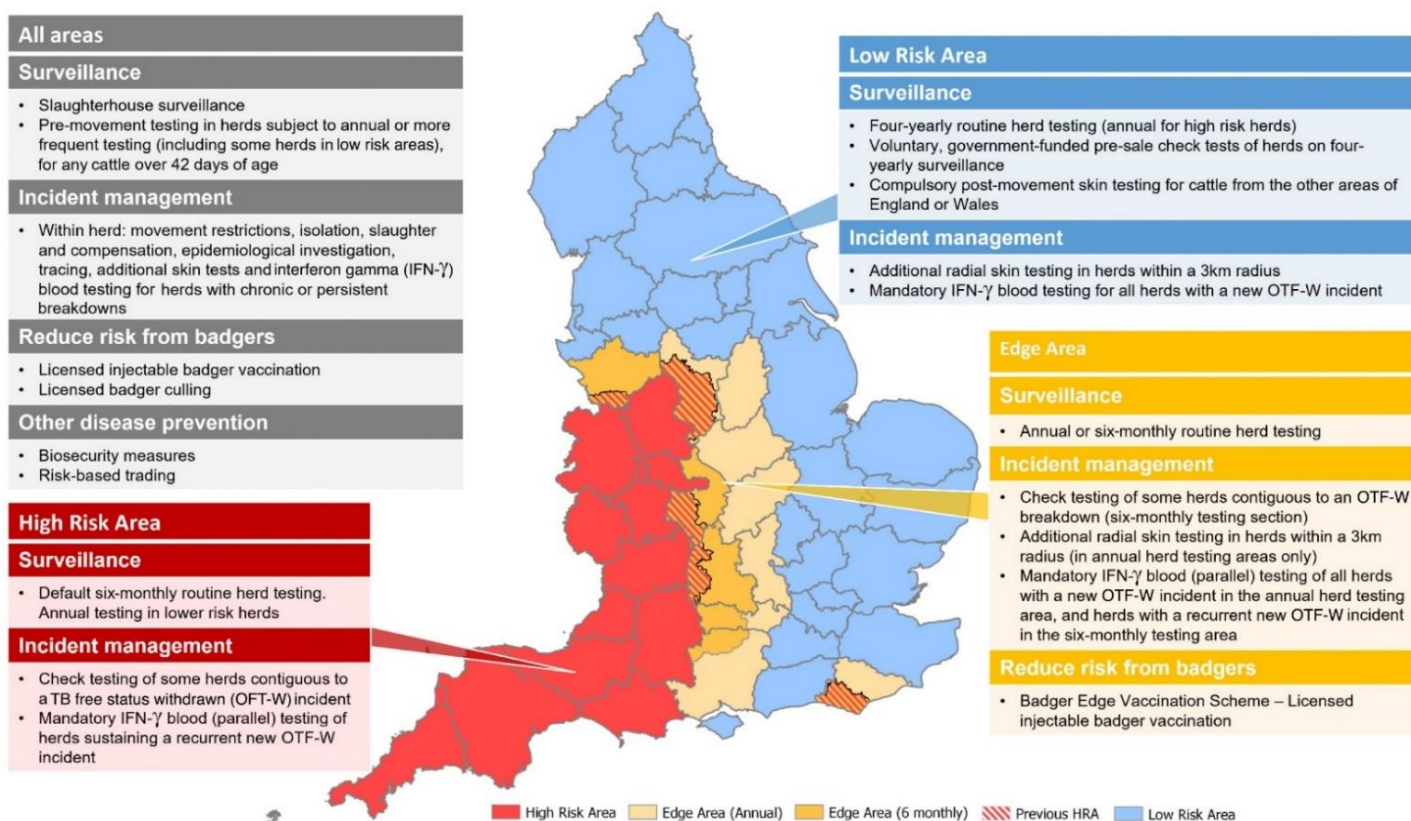


Figure 1.3 Summary graphic of the bovine tuberculosis eradication strategy for England. Figure adapted from APHA (2023).

Wales aims to achieve Officially TB Free status by 2041 with a policy focused on controlling bTB in cattle through disease surveillance, movement restrictions, and biosecurity (Llywodraeth Cymru, 2023). The country is categorised into five regions based on disease risk, with ‘Spatial Units’ within these (Fig. 1.4), each comprising a similar number of herds and incidence of bTB (Llywodraeth Cymru, 2023). Disease outbreaks are monitored within these units and control measures are adapted to manage the risk locally. Testing and slaughtering infected cattle are fundamental to the policy; every herd is tested at least annually, while those in the higher risk areas are tested six-monthly. Badger vaccination is also supported with a 50% contribution from the government, though at present, the scheme is small-scale, covering 46km² (Llywodraeth Cymru, 2023). Disease surveillance is carried out in deceased badgers, but badger culling is no longer licensed, following the end of ‘test, vaccinate or remove’ operations in 2024 (Llywodraeth Cymru, 2023). A limited number of cattle vaccine trials are also currently underway in Wales and England, but cattle vaccination is not yet licensed more generally.

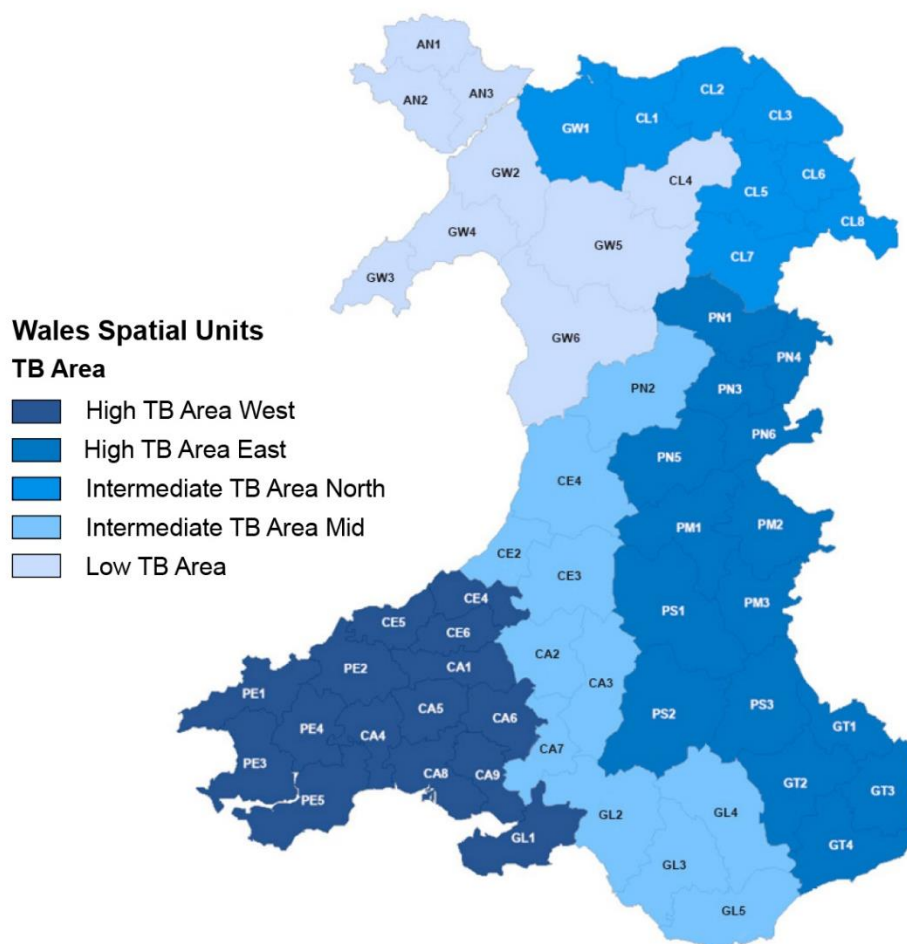


Figure 1.4 Bovine tuberculosis (TB) regionalisation in Wales as of November 2021. Character codes represent Spatial Units within which disease outbreaks are monitored and controlled. Figure adapted from Llywodraeth Cymru (2023).

A new bTB eradication strategy for Northern Ireland was published in 2022 (DAERA, 2022). Similarly to England, the policy prioritises widespread badger culling which is due to be followed by badger vaccination, aiming to reduce transmission between badgers and cattle as the population recovers. A test and vaccinate or remove scheme, which was trialled with badgers in Northern Ireland over five years (Doyle *et al.*, 2023), is not included in the updated bTB management policy. Cattle measures include test and slaughter, restrictions of infected herds, and biosecurity.

Scotland has been Officially TB Free since 2009 and herd prevalence and incidence remain very low (DEFRA, 2024e). Cattle test and slaughter, and restrictions of infected herds still apply, but most herds are tested every four years, with low-risk herds being exempt (Scottish Government,

2023). Though cattle and badger density are relatively low in Scotland, distribution is patchy, and densities are high in some areas, but badger control measures are not licensed.

1.3.5. Why is counting badgers useful to bTB policy?

The inclusion of a national badger survey in England's emerging bTB policy (DEFRA, 2024d) highlights the importance the government places on gaining abundance estimates for policy development. Accurate estimates of badger numbers are useful for effective monitoring, evaluation, and auditing of management strategies. For example, badger culling targets aim to remove 70% of a badger population, making knowledge of the starting population essential to set and evaluate such targets (DEFRA, 2023b). Similarly, population estimates facilitate assessment of vaccination coverage, which is important in the evaluation of the effectiveness of such a strategy (Smith *et al.*, 2020). These estimates also inform the planning of future vaccination delivery by estimating the number of vaccines required per km² (APHA, 2015). Furthermore, such data would facilitate a cost-effort analysis of the government's "Badger Vaccinator Field Force" as proposed in the emerging bTB policy (DEFRA, 2024d).

Setting and evaluating management targets is challenging in the context of bTB control due to the difficulty of estimating badger abundance with certainty (Donnelly & Woodroffe, 2012). Annual badger culling targets use population estimates to specify the minimum and maximum number to be removed, but the uncertainty associated with these population assessments is problematic because culling too few badgers may increase the risk of infection to badgers and cattle (Donnelly *et al.*, 2003; Woodroffe *et al.*, 2009a), while exceeding these targets could risk local extinction (Byrne *et al.*, 2013). Although there is no detrimental epidemiological risk associated with exceeding vaccination targets, such efforts must meet a minimum coverage to reach the threshold required for herd immunity in badgers (Aznar *et al.*, 2018). Application of existing methods of assessing badger abundance for vaccination purposes risks uncertainty in these results, making it difficult to assess the effectiveness of vaccination. Since bTB eradication policy in England is placing growing importance on badger vaccination, there is an urgent need for accurate and precise estimates of badger density for reliable assessment of bTB management interventions.

1.3.6. Applicability of camera-based density models to bTB policy frameworks

Camera-based density estimation methods such as the REM and CT-DS have the distinct advantage of operating without the need for individual identification, inviting application to unmarked species such as badgers. Though the accuracy and precision of these methods for a range of terrestrial mammals is supported by field trials (e.g. Palencia *et al.*, 2021), at present, studies utilising the methods to estimate badger density, or to evaluate bTB management interventions, are lacking.

Furthermore, to recognise the broader value of such methods to policymakers, it would be beneficial to understand the ability of these methods to detect long-term changes in density, as well as the necessary resources and cost-effectiveness of such tools.

1.4. Thesis structure

Against this background, in this thesis I explore the use of camera-based methods for estimating animal density in the context of wildlife management, focusing on badgers and bTB control strategies. I assess two of the most widely used methods for species which are not individually identifiable – the REM and CT-DS – comparing them with SMR to explore their consistency, accuracy, and precision. I also use these models to assess badger vaccination coverage and discuss the implications for current bTB eradication policy.

In Chapter 2 I use data from six camera surveys in Cornwall to assess the reliability of these camera-based approaches. Using an individually marked sample of the badger population, I compare the REM and CT-DS with an independent estimate of badger density using SMR, evaluating the accuracy and precision of the results. I also investigate the bias resulting from badgers' reactivity to camera traps and assess different approaches to controlling this with the REM and CT-DS. I discuss the opportunities and challenges of using these methods in a farmland habitat and suggest refinements to field methodology to ensure maximum data utilisation. A version of this chapter is published in *Ecological Solutions and Evidence* (detailed in Appendix 4).

In Chapter 3 I use the REM and CT-DS to estimate vaccination coverage at four sites in Cornwall and assess the feasibility of badger vaccination in terms of the potential to reach a sufficient proportion of the population, necessary for reducing *M. bovis* transmission in badgers. I also discuss how the precision of estimates could be improved to enable detection of temporal changes in vaccination coverage for disease management purposes.

Recognising the need to improve the precision of density estimates, in Chapter 4 I investigate the impact of increasing the number of camera placements and deployment durations on the precision of badger density estimates. By subsampling the data from an intensive camera survey at Woodchester Park, Gloucestershire, I estimate the minimum survey effort required to achieve adequate precision for the REM and CT-DS and discuss the suitability of the models in a relatively low population density scenario. In addition, by estimating the population densities of four mammal species, I highlight the potential for camera surveys to provide information on a range of species simultaneously, allowing multiple management questions to be addressed.

In Chapter 5, I assess the impact of badger culling on vaccine coverage to explore the likely effectiveness of a post-cull vaccination strategy. I also evaluate the suitability of the REM and CT-DS

853 for long-term monitoring in a post-cull scenario, in terms of the power to detect changes in
854 population size, and the expected financial cost and resource requirements. As vaccine delivery and
855 camera-based population monitoring are scheduled to continue until 2026 at the two sites studied, I
856 provide baseline estimates of density and vaccination coverage from the first year of the study and
857 assess the effectiveness of the current study design for detecting population changes in subsequent
858 years.

859 Finally, in Chapter 6, I bring together the key findings of the research, discuss the
860 implications for bTB control policy, and highlight opportunities for future research.

2. Chapter 2: Evaluating camera-based methods for estimating badger (*Meles meles*) density and the implications for wildlife management

Publication details

Authors: Verity Miles, Rosie Woodroffe, Christl A. Donnelly, Peter N. M. Brotherton, Cally Ham, Kelly Astley, Joana Aurélio, Marcus Rowcliffe

Published in: *Ecological Solutions and Evidence*

Publication date: 2nd September 2024

DOI: <https://doi.org/10.1002/2688-8319.12378>



An anaesthetised badger during vaccination and sampling operations. Anaesthesia, sampling, marking, and vaccination were performed by trained and licensed staff wearing Personal Protective Equipment. Photo by Rosie Woodroffe.

2.1. Abstract

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 non-invasive tools for studying rare, cryptic and/or elusive species, offering cost-effective solutions for both individually marked and unmarked populations. 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. 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 two-fold 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. Our findings suggest that 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.

2.2. 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. 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 (Rogers *et al.*, 1998; Woodroffe *et al.*, 2006a; Delahay *et al.*, 2013), informed disease management plans (Smith *et al.*, 2012; Scott *et al.*, 2018), helped establish culling targets (DEFRA, 2022b), and facilitated policy evaluation (Donnelly & Woodroffe, 2015). In England, the government is currently scaling back badger culling, and

encouraging badger vaccination (DEFRA, 2020, 2024d); 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 (Wilson *et al.*, 1997; Judge *et al.*, 2014), 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 (Efford, 2004; Borchers & Efford, 2008; 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 non-invasive samples such as hair or faeces, has alleviated some of these challenges (Wilson *et al.*, 2003; Judge *et al.*, 2017), 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 tools 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 (Karanth & Nichols, 1998; Alonso *et al.*, 2015; Teton *et al.*, 2020). SMR can also be used for species with uniform pelage, by artificially marking some individuals (Jordan *et al.*, 2011; Carter *et al.*, 2019; Jimenez *et al.*, 2019).

Marking individual animals may be challenging and risks harming study subjects. Consequently, spatial count models have been developed to enable non-invasive 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 minimize 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 (Rowcliffe *et al.*, 2008; Palencia *et al.*, 2021). 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 individually marked badgers. We also compared different methods of processing reactive sequences and examined the practical implications of using camera-based density estimation methods.

2.3. Materials and methods

2.3.1. Study area

Data were collected from six camera trap surveys at five sites in Cornwall, UK, in 2019 and 2021 (Table 2.1; Fig. 2.1). Each site comprised at least two farms (Table 2.1). Sites included several habitats and farming practices, including arable fields, livestock pasture, woodland and moorland. All data were collected with landowner consent.

971 **Table 2.1** Details of six camera trap surveys at five sites used to estimate badger density. The number
972 of usable deployments is lower than the total number set because some cameras failed. Usable
973 camera nights exclude time from deployments after cameras were moved by cattle.

	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	2.3km ²	2.4km ²	2.4km 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	22 nd May 27 th May	15 th June 16 th June 24 th June 1 st July	25 th May 27 th May	8 th June 9 th June	6 th October 7 th October
Number of badgers individually marked	0	0	23	19	12	4
Camera deployment period	5 th Jun – 11 th Jul	23 rd May – 17 th Jul	1 st June – 29 th July	17 th May – 21 st Jun	26 th May – 23 rd Jul	27 th Sep – 4 th Nov
Number of camera deployments (number of usable deployments)	87 (85)	64 (63)	59 (56)	50 (45)	50 (48)	78 (75)
Pre-determined camera spacing (m)	155	155	200	200	195	250
Number of usable camera nights	1145	1217	1464	1052	917	2277

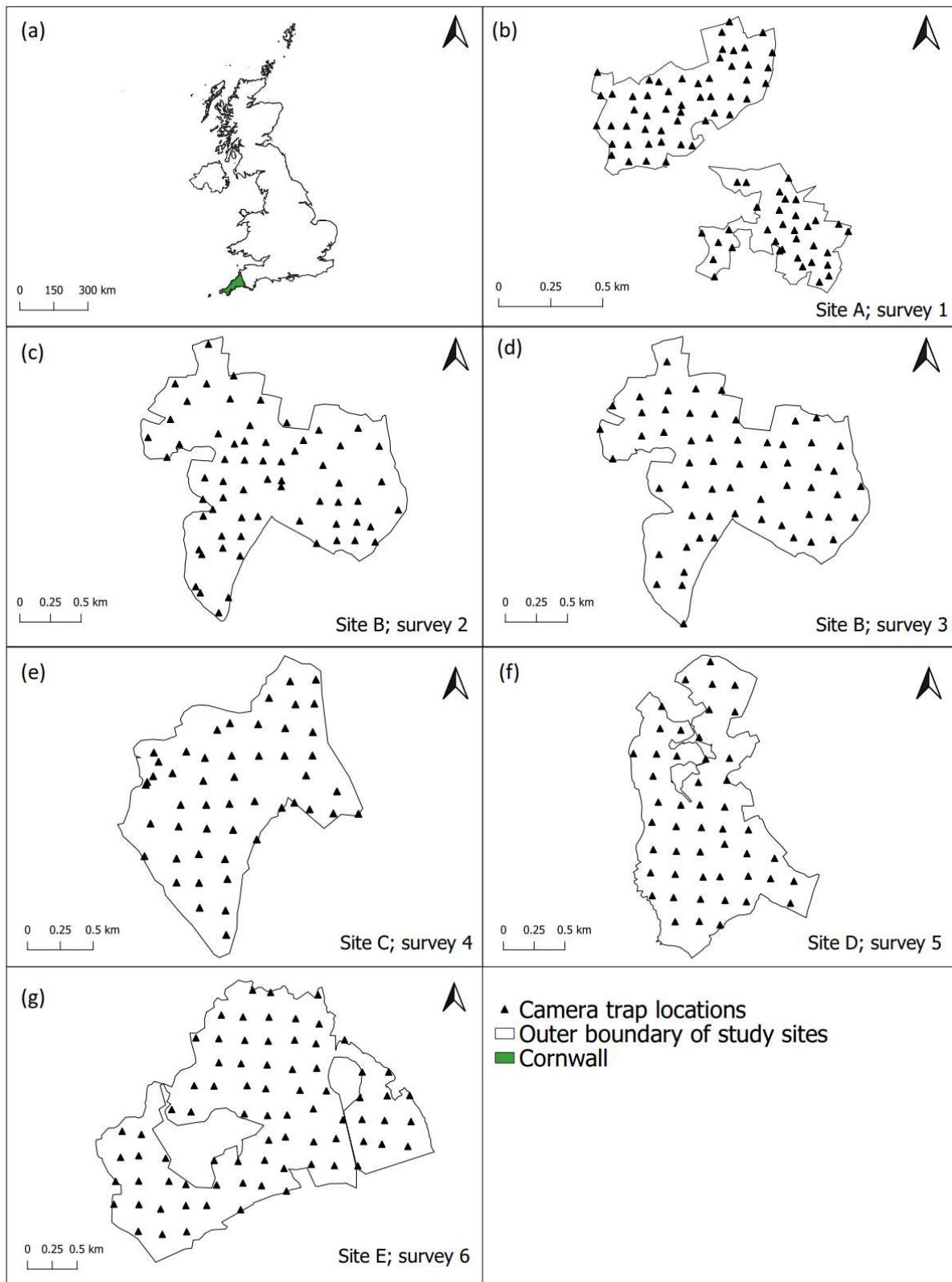


Figure 2.1 (a) Location of the five sites in Cornwall, UK and (b – g) layout of the camera grids deployed for each survey.

2.3.2. Camera trap surveys

All surveys were planned to coincide with the open season for badger vaccination, which runs annually from 1st May – 30th November (DEFRA, 2021a). We determined the number and duration of camera deployments at each site (Table 2.1) using recommendations from Rowcliffe *et al.* (2008). Specifically, we estimated that a minimum of 1,000 camera nights were required at each site, based on a badger day range of 1.2km (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 km² (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 – 250m between predetermined locations (Table 2.1). 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. We positioned cameras 30 – 40cm high, parallel to the ground and did not use bait. Cameras took photographs 24 hours per day with no time lapse and a 1-second passive infrared trigger interval.

At each camera deployment we took calibration images of a 1-metre pole marked at 20cm intervals, at a range of distances and angles from the camera (Fig. 2.2). 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.



Figure 2.2 Example of a calibration image taken at each camera deployment. 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 deployment calibration.

2.3.3. Badger vaccination and marking

Sites B to E 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 licences 2019-40177-SCI-SCI and 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 and anaesthesia provided the opportunity for SMR analysis, which requires an initial marking phase followed by resighting phases 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

1016 undercoat (Stewart & Macdonald, 1997) (Fig. 2.3). We recorded a photograph of each mark and the
1017 badger's identity (Fig. 2.3).



1018 **Figure 2.3** Representative images of three individually marked badgers during the marking (a – c) and
1019 resighting (d – f) stages of spatial mark-resight analysis.

2.3.4. 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 obtained after marking was completed. For the REM and CT-DS, we excluded data from nights when cage traps were set to catch (from 18:00 until 08:00) to avoid bias in encounter rate due to part of the population being caught in cage traps. An alternative would have been to exclude 24-hour periods since there are relatively few badger encounters between 8:00 and 18:00 (Appendix 1, Fig. S1). However, given the large number of usable trap nights (Table 2.1) in each survey, the difference would have been minimal.

2.3.5. 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 1,000 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.

2.3.6. 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 the equation from Rowcliffe *et al.* (2008):

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

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 badger position data (defined in polar co-ordinates 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).

2.3.7. 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 24 hours per day in our study) replace human observers surveying at intervals. We therefore discretized the number of times animals could potentially be photographed (referred to as '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 the equation:

$$H = t/T$$

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 the equation:

$$e = \frac{\theta H}{2\pi}$$

Density was estimated using the equation (Howe *et al.*, 2017):

$$D = \frac{y}{\pi w^2 e p a}$$

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 distance w 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 (Buckland *et al.*, 2001). 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 by computing an overdispersion factor ($\hat{c}$) for each key function group, which was used to compute an adjusted Akaike information criterion (QAIC) score for each model (Howe *et al.*, 2019). QAIC scores were used for model selection within key function groups and final model selection across key function models was based on $\hat{c}$ scores (Howe *et al.*, 2019).

2.3.8. SMR density estimation

Individual badgers were identified by comparing marks in camera images with those taken during handling (Fig. 2.3). 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).

SMR 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 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 (Efford, 2023b), 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 km² 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).

2.4. Results

2.4.1. Camera survey

We obtained 5,049,759 images from 388 camera placements over 8,467 camera-nights. Badgers were identified in 9,784 (0.2%) images, totalling 1,739 independent encounters. The majority of badger detections involved solitary badgers, with only 19 (1.1%) encounters featuring groups of two or three animals. 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 for the REM and CT-DS. Lack of suitable attachment sites meant that cameras were often situated at field boundaries. On average, cameras deviated by 35.8m (median 28.0m) 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 this method. Following outlier analysis and removal of data due to livestock interference and trapping (detailed below) 7,023 badger images and 1,252 independent badger encounters were considered for the REM and CT-DS analyses.

2.4.2. Outlier analysis

We identified one observed photographic encounter rate as an outlier (Fig. 2.4, survey 3) and excluded this camera deployment from the REM and CT-DS analyses. After removing this outlier there were 1,543 independent badger encounters captured over 8,071 camera nights, giving 0.2 encounters per camera-night.

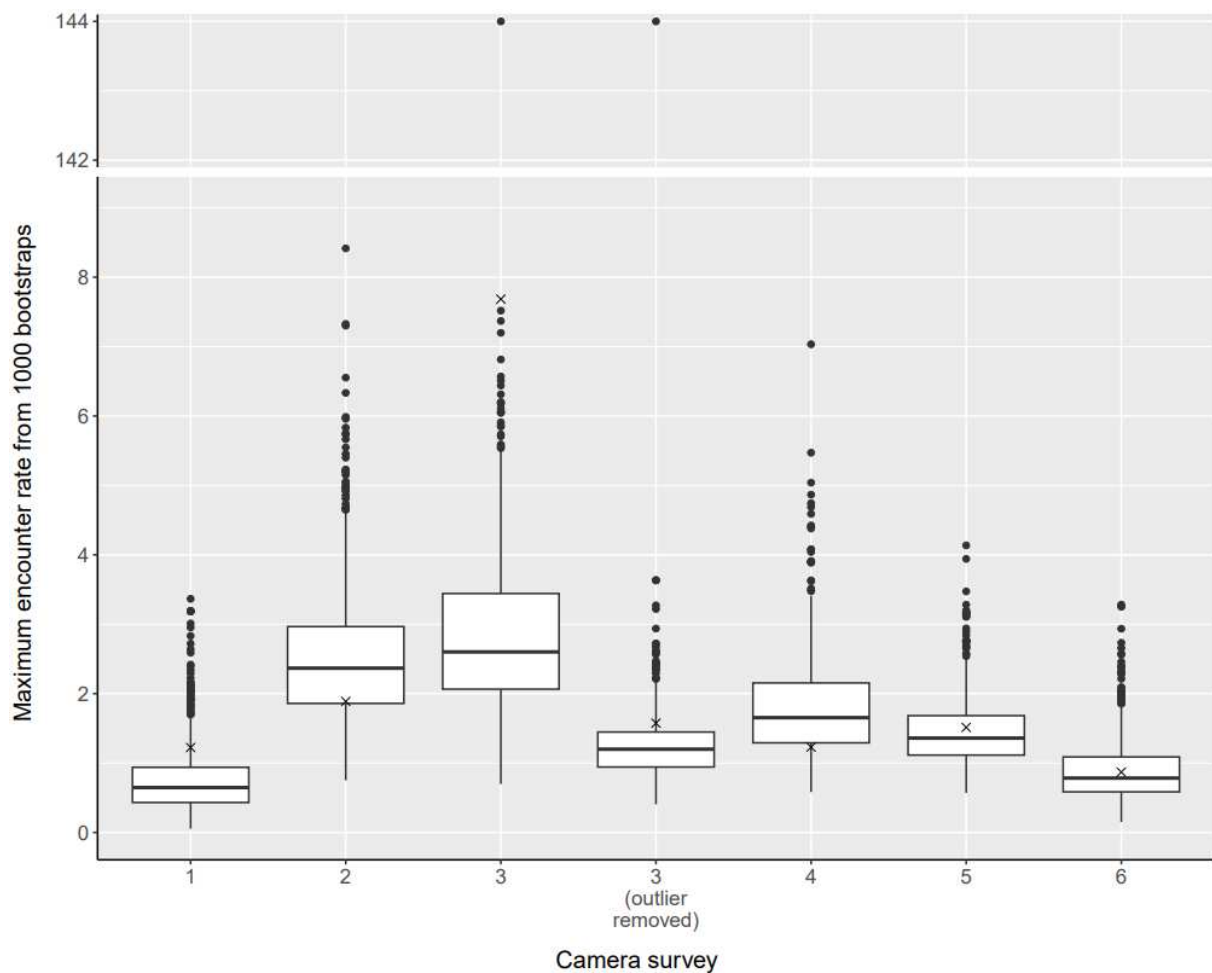


Figure 2.4 Boxplot showing the median (thick horizontal lines), interquartile range (boxes) and 2.5th and 97.5th centiles (vertical lines) of maximum encounter rates from seven data sets using 1000 samples from a negative binomial distribution fitted to the data, with sample sizes equal to the number 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.

2.4.3. Marking badgers

Of the 63 badgers trapped in 2021, 58 were given unique marks (Table 2.2) to facilitate SMR analysis. Five could not be marked due to insufficient anaesthesia.

2.4.4. 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.

Table 2.2 Badger encounters considered for spatial mark-resight analysis. Site E was excluded from analysis due to the small number of marked and resighted individuals.

	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

2.4.5. Density estimation

SMR 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 2.2). 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 badgers per km² (95% CI 0.6 – 3.0 badgers per km²; REM at site E, survey 6) to 20.2 badgers per km² (95% CI 11.8 – 34.4 badgers per km²; REM at site B, survey 2) (Table 2.3 and Fig. 2.5). Density estimates using CT-DS tended to be higher than those using the REM. When reactive sequences were excluded from CT-DS analysis, density estimates were on average 22% (range 3% – 51%) lower than when those sequences were included.

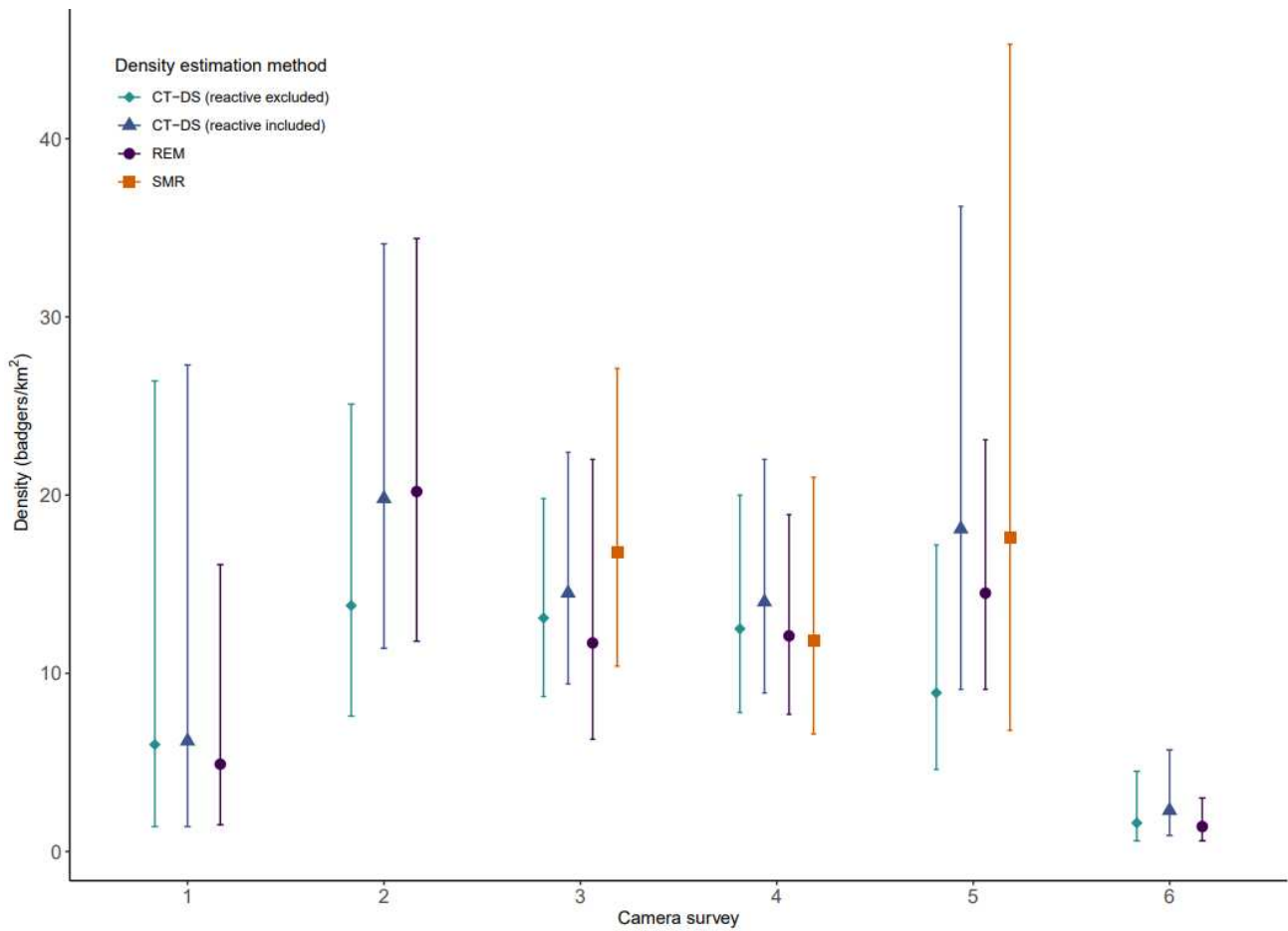
1214 The REM estimates tended to be the most precise (Table 2.3). The average coefficient of
1215 variation (CV) for the REM was 0.36, for CT-DS (reactive sequences included) was 0.41, for CT-DS
1216 (reactive sequences excluded) was 0.42, and for SMR was 0.35.

1217 **2.4.6. SMR simulations**

1218 On average, 56% (range 25% – 100%) of marked badger sightings were identifiable (Table 2.2),
1219 prompting simulations with *pID* values of 1, 0.75, 0.50 and 0.25. Models fitted to the simulated data
1220 demonstrated a direct correlation between *pID* values and the accuracy and precision of the
1221 estimated densities. When *pID* was 100%, the model yielded density estimates closest to the actual
1222 population density used in simulations (10 individuals per km²), with an estimated density of 9.8
1223 individuals per km² and a CV of 0.22. This scenario illustrated minimal bias and lower variability,
1224 suggesting optimal model performance under full identification conditions. As *pID* decreased,
1225 estimated density was less accurate and variability increased (Table 2.4).

1226 **Table 2.3** Badger density per km² and associated standard error (SE), 95% confidence intervals (CI),
1227 and coefficient of variation (CV) estimated from six camera surveys at five sites, using three camera
1228 trap-based methods (the random encounter model (REM), camera trap distance sampling (CT-DS),
1229 and spatial mark-resight (SMR)). SMR analysis was only possible for three of the surveys where a
1230 sufficient number of badgers were uniquely marked and resighted.

Site	Survey	Density estimation method	Density (badgers/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



1231 **Figure 2.5** Badger densities per km² and associated 95% confidence intervals estimated from six
 1232 camera surveys at five sites, using three camera trap-based methods (the random encounter model
 1233 (REM), camera trap distance sampling (CT-DS) and spatial mark-resight (SMR)). SMR analysis was only
 1234 possible for three of the surveys where a sufficient number of badgers were uniquely marked and
 1235 resighted.

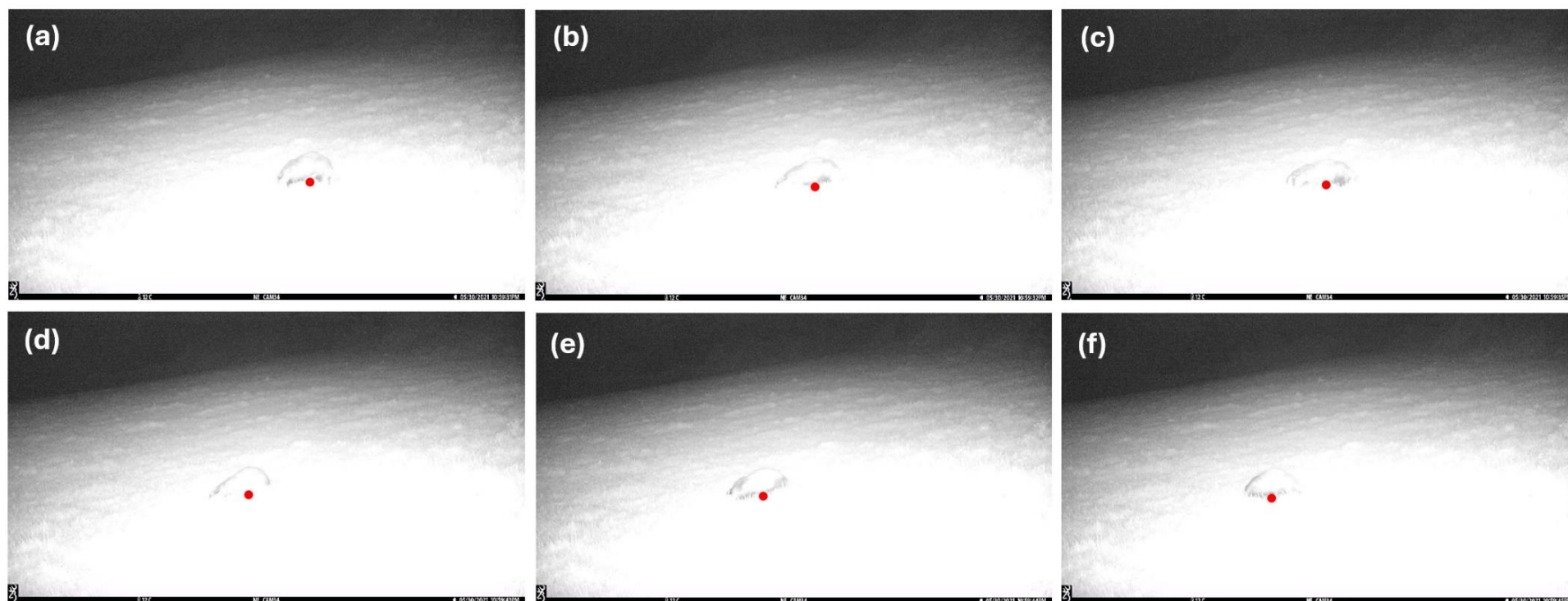
Table 2.4 Estimated animal density per km², with associated standard error (SE), 95% confidence intervals (CI), and coefficient of variation (CV), derived from simulated mark-resight models. Data were simulated with fixed model parameters reflecting observed data from badgers: a density of 10 individuals per km², detection probabilities for marking and sighting occasions of 0.09 and 0.04, respectively, and a spatial scale parameter (σ) of 219.3.

<i>pID</i>	Estimated density (individuals/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

2.5. Discussion

Our study suggests that the REM and CT-DS are reliable methods of estimating the density of animal populations in which individuals are not recognisable. 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 (Palencia *et al.*, 2021; Henrich *et al.*, 2022; 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 (McClintock *et al.*, 2014; Jimenez *et al.*, 2019). On average, we were able to identify 56% of the encounters with marked individuals (Table 2.2) consistent with rates reported in other studies employing camera traps for resighting (Jimenez *et al.*, 2019; Greenspan *et al.*, 2020). Difficulty distinguishing fur clips was often the result of overexposed images (Fig. 2.6), which can occur if the camera's exposure settings are calibrated for subjects at greater distance. We found that overexposure was less problematic for the REM and CT-DS, because we were still able to identify species and locate animals reliably in images (e.g. Fig. 2.6), thereby maximising data usage with these methods.



1261 **Figure 2.6** Illustrative images of an overexposed badger sequence, with red circles representing a digitised mark on the ground directly below the animal's
 1262 centre of mass. In this example, the presence or absence of a fur clip for spatial mark-resight analysis is not discernible, but digitising the animal's position in
 1263 the image, necessary for the random encounter model and camera trap distance sampling, is still possible.

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 2.4). 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 specifically address the challenge of imperfect identification by adding partially known information about identity, such as sex, to probabilistically determine identities obtained from camera trap images, thereby improving density estimate precision (Augustine *et al.*, 2019). Such models may outperform other spatial models (Sun *et al.*, 2022), particularly where 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 spatial partial identity models.

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. SMR models can therefore 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 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 badgers per km² (95% CI 3.15 – 8.15 badgers per km²) in Land Class 1 and 5.98 badgers per km² (95% CI 4.57 – 7.39 badgers per km²) in Land Class 4; Judge *et al.*, 2017). However, the census assumed one main badger sett per km², 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

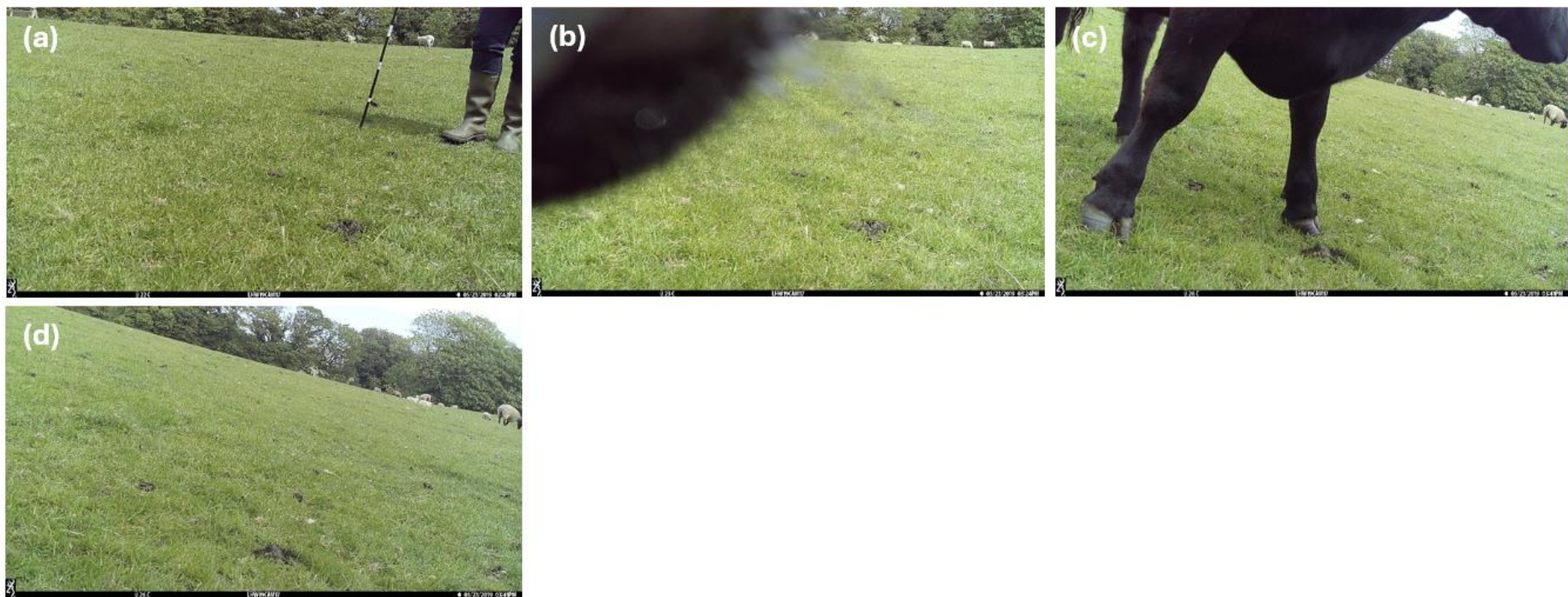
average (Judge *et al.*, 2017). Notably, the REM estimate at site B, survey 2 (20.2 badgers per km² (95% CI 11.8 – 34.4 badgers per km²)) indicates high badger density, comparable to that of Woodchester Park, Gloucestershire, where, at its peak, density was estimated at 47 badgers per km² (Delahay *et al.*, 2013). In the current study, a survey at site B two years later (survey 3) yielded a markedly lower REM estimate (Table 2.3; Fig. 2.5), 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 (Cappelle *et al.*, 2021; Palencia *et al.*, 2021; Bengsen *et al.*, 2022) but falls short of the recommended variance of CV <0.20 suggested for wildlife management (Pollock *et al.*, 1990; Cappelle *et al.*, 2021). Although previous studies have highlighted the suitability of the REM and CT-DS for studying populations at low densities given sufficient survey effort (Rowcliffe *et al.*, 2008; Palencia *et al.*, 2021), 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 recommended 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 moving them during the survey, 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 halved the estimated density, although variance was slightly improved. This result is consistent with previous studies which 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 an excess of animal detections (referred to as '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 reducing bias in 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 (Fig. 2.7), which likely contributed to the imprecision of the estimates due to loss of data. 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.*, 2015b). 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.



1365 **Figure 2.7** A sequence of images showing a camera trap being moved by cattle, adjusting the camera's field of view. Distances calibrated in the first image (a)
 1366 would not be valid for subsequent images (b – d).

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 individually unidentifiable 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 recommend practical considerations to improve the accuracy and precision of density estimates, making the REM and CT-DS more suitable for wildlife management purposes.

1388 **3. Chapter 3: Estimating vaccination coverage using camera traps: insights**
1389 **from badger vaccination operations in Cornwall**



1390 *A badger being weighed during vaccination and sampling operations.*

3.1. Abstract

Wildlife management policy for bovine tuberculosis (bTB) control in England is placing a growing emphasis on badger (*Meles meles*) vaccination. However, the impact of badger vaccination on bTB incidence in UK cattle has not been quantified. Any such impact depends on reducing bTB transmission from badgers, which in turn depends, in part, upon the proportion of the badger population receiving the vaccine. Modelling based on data from the Republic of Ireland suggests that eliminating bTB from badger populations demands vaccinating at least 30% of the population annually, alongside existing bTB control measures. This study presents insights from badger vaccination operations in Cornwall, utilising a novel method involving camera traps to estimate badger density, and, by comparison with the numbers vaccinated, the proportion of badgers vaccinated. Across five surveys at four sites, we achieved an average vaccination rate of 6.6 badgers per km² (range 0.9 – 11.7 badgers per km²) and the mean vaccination coverage ranged from 50.6% – 74.2%. These results indicate the potential of badger vaccination to attain high levels of coverage. Our findings also highlight the value of integrating population monitoring using camera traps into disease management strategies, which is highly relevant to current bTB policy.

3.2. Introduction

Since the mid-1900s, with the introduction of milk pasteurisation, compulsory cattle testing and human immunization using the Bacille Calmette-Guérin (BCG) vaccine, the prevalence of human *Mycobacterium bovis* (*M. bovis*) infection, the causative agent of bovine tuberculosis (bTB), has declined substantially in the UK (de la Rua-Domenech, 2006). Although human cases are now rare (UK Health Security Agency, 2023), bTB persists as a formidable animal health challenge (APHA, 2023). Recent data underscore the ongoing impact, revealing that between 2018 and 2022, over 140,000 cattle were prematurely slaughtered due to bTB in England alone (DEFRA, 2023a). Control efforts for bTB impose substantial financial burdens on both taxpayers and farmers (DEFRA, 2021c, 2022a), and the emotional toll on farming communities is well documented (Butler *et al.*, 2010; Crimes & Enticott, 2019).

Vaccination is a widely practiced and well evidenced method of controlling and eradicating disease in humans, domestic animals, and wildlife (Lombard *et al.*, 2007; Greenwood, 2014; Barnett & Civitello, 2020). Evidence indicates the effectiveness of the BCG vaccine in reducing the risk of testing positive for *M. bovis* infection in captive (Corner *et al.*, 2008; Lesellier *et al.*, 2011) and wild (Chambers *et al.*, 2011) badgers (*Meles meles*), as well as reducing the incidence of bTB in badger populations (Gormley *et al.*, 2017). However, given the complex multi-host dynamics of bTB transmission, it is not clear what impact vaccinating badgers has on the incidence of bTB in cattle.

Preliminary studies suggest a potential decline in bTB incidence among herds in areas where badger vaccination is implemented (APHA, 2016b, c) and a trial conducted in Ireland suggested that badger vaccination is not inferior to badger culling for controlling bTB in cattle (Martin *et al.*, 2020).

Recent changes to bTB policy in England indicate a growing emphasis on badger vaccination (DEFRA, 2014, 2020, 2024d), including the first large-scale government-funded badger vaccination program led by farmers in East Sussex (DEFRA, 2021b) and pilot badger vaccination projects in post-cull zones (DEFRA, 2020). However, the prolonged debate surrounding badger culling, exacerbated by a lack of research on badger vaccination, has led to entrenched viewpoints and concerns about the feasibility and effectiveness of badger vaccination. For example, a social science study examining farmer attitudes revealed apprehensions regarding the effectiveness of badger vaccination, with some participants expressing doubts about the ability to vaccinate a sufficient number of badgers to be effective (Chivers *et al.*, 2022).

Questions regarding how many badgers need to be vaccinated to control bTB in badgers, and hence to reduce incidence in cattle, remain unanswered. Modelling efforts based on data from Woodchester Park, Gloucestershire, suggest that vaccinating 40% of the uninfected badger population might be necessary to eliminate bTB in badgers (Wilkinson *et al.*, 2004), while research from Ireland suggests that bTB could be eliminated in badgers if a minimum vaccination coverage of 30% is maintained (Aznar *et al.*, 2018). However, it is unclear whether such coverages would also reduce bTB incidence in cattle.

A critical gap in scientific understanding concerns not only the necessary vaccination coverage in badgers to reduce bTB incidence in cattle, but also whether such coverage is being effectively achieved. Efforts to estimate badger vaccination coverage are currently limited and lack a standardised framework for comparison. A study conducted in Wales, which utilised genotyping to estimate the badger population size and hence (through comparison with the number vaccinated) the proportion vaccinated, reported an annual vaccination coverage estimate of 50% (95% CI 40% – 60%), although the potential underrepresentation of cubs in the sample suggests this figure may primarily reflect the adult population (Smith *et al.*, 2020). Benton *et al.* (2020) estimated a comparable vaccination coverage of 57% (range 48% – 63%) following a simpler mark-recapture method, utilising the fur-clips applied during badger vaccination in England. However, the authors call attention to several potential biases and suggest that the assumption of population closure may have been violated, emphasising the need for cautious interpretation of the results. Without a consistent and reliable method for estimating population size and vaccination coverage, the ability to evaluate vaccination targets, and compare results, is limited.

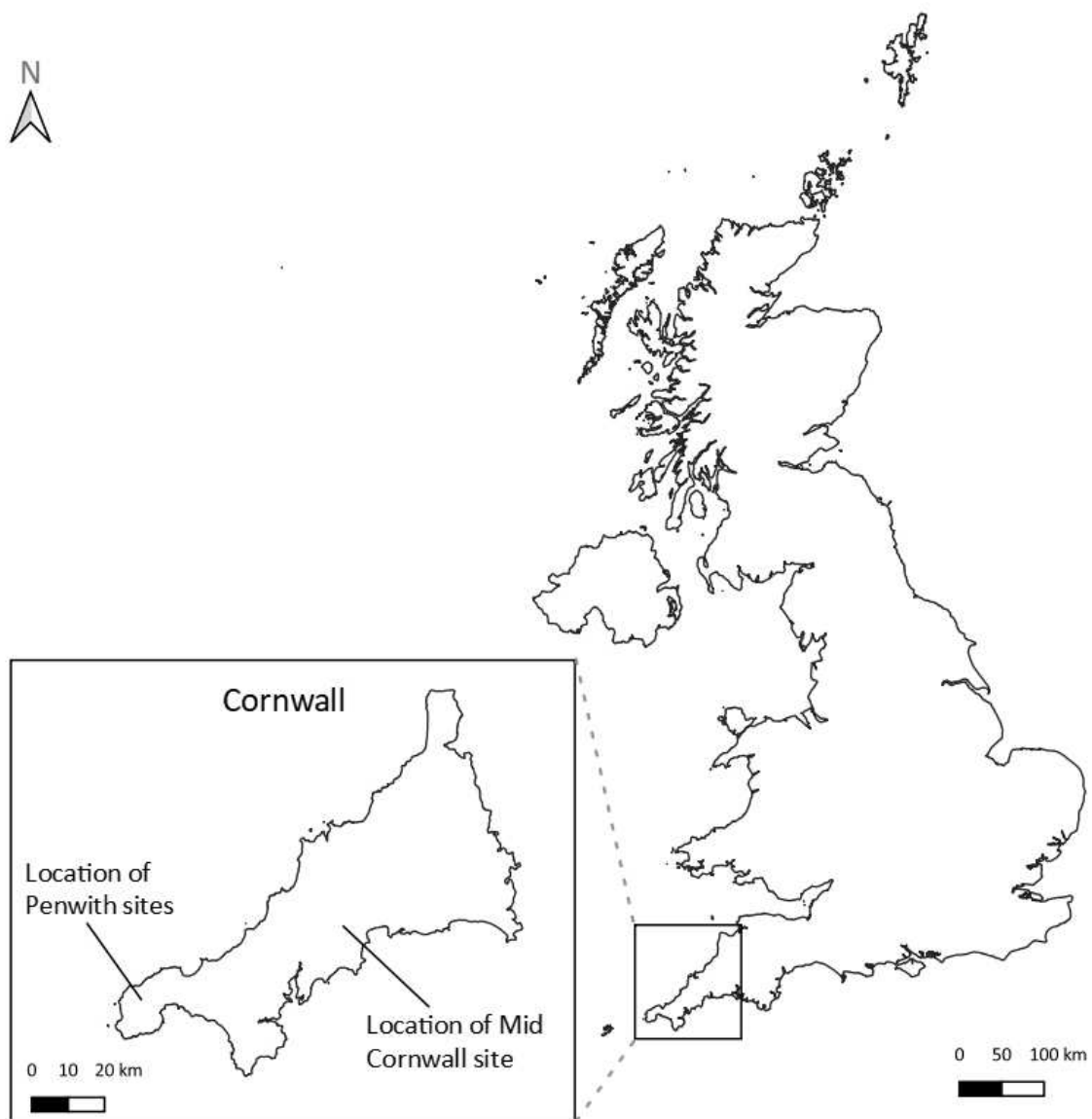
The effectiveness of badger vaccination is largely contingent upon what proportion of the badger population are trapped, which may be influenced by factors such as population density, trapping effort, previous history of trapping, and prior culling activities. For instance, in high-density populations, increased competition for resources might make badgers more attracted to bait, and hence more susceptible to trapping. By comparison, repetitive trapping efforts could result in learned avoidance behaviour, and prior culling operations may inadvertently select for 'trap-shy' animals that are less likely to be captured (Tuytens *et al.*, 1999). In these scenarios, higher trapping probability could be expected as the number of trap-nights per unit area increases, although such effort is usually a response to local badger activity, which is likely related to population density (Woodroffe *et al.*, 2008). Limited government investment in monitoring and evaluation of badger vaccination projects complicates the ability to draw definitive conclusions about these trends.

Understanding the feasibility and effectiveness of badger vaccination in real-world trials is crucial for informing policy decisions. We share outcomes from a badger vaccination initiative at four sites in Cornwall, UK. We employed a novel approach, utilising advances in camera trap-based density estimation to understand the size of the badger population and, by comparison with the number vaccinated, provide an estimate of vaccination coverage. The objective of our research is to inform tactics to control bTB in badgers within the framework of bTB control.

3.3. Materials and methods

3.3.1. Study area

Data were collected from four sites in Cornwall, UK, in 2019 and 2021 (Fig. 3.1; Table 3.1). Site A, located in Mid Cornwall, was surveyed twice, in 2019 and 2021. Sites B, C and D were located in the Penwith region of West Cornwall and were studied in 2021. Each site consisted of at least two farms and formed part of a larger vaccination study. No badger culling took place at any of the study sites during the research period; however, site A fell within an area that was licensed for intensive culling, although the exact distance between the culling activities and the study site is unknown (Woodroffe *et al.*, 2024). All research was conducted with the consent of landowners.



1485 **Figure 3.1** Approximate locations of study sites in Cornwall, UK. Precise site locations and farm
 1486 boundaries are not mapped to preserve participant confidentiality.

1487 **Table 3.1** Details of badger vaccination operations and camera trap surveys at four sites in Cornwall.

1488 Badgers recaptured within the same year are not shown in the counts. The number of camera trap

1489 nights excludes nights affected by cage trapping (defined as nights when cage traps were set to

1490 catch) and the movement of cameras by livestock.

	Survey number				
	1	2	3	4	5
Study sites					
<i>Site</i>	A	A	B	C	D
<i>Year studied</i>	2019	2021	2021	2021	2021
<i>Number of farms</i>	2	2	2	3	4
<i>Combined area of farms (km²)</i>	2.4	2.4	1.8	2.0	4.6
Badger vaccination					
<i>Trapping dates</i>	22 nd May 23 rd May 24 th May 26 th May	15 th June 16 th June 24 th June 1 st July	25 th May 27 th May	8 th June 9 th June	6 th October 7 th October
<i>Cage-trap nights</i>	58	98	52	32	33
<i>Total badgers vaccinated</i>	23	26	21	13	4
<i>Adults</i>	11	11	17	6	3
<i>Cubs</i>	12	15	4	7	1
<i>Badgers vaccinated/trap-night</i>	0.4	0.2	0.4	0.4	0.1
Camera trapping					
<i>Number of cameras</i>	63	56	45	48	75
<i>Camera spacing (m)</i>	155	200	200	195	250
<i>Camera deployment period</i>	23 rd May – 17 th Jul	1 st June – 29 th July	17 th May – 21 st Jun	26 th May – 23 rd Jul	27 th Sep – 4 th Nov
<i>Camera trap-nights</i>	1217	1464	1052	917	2277

1491

3.3.2. Badger distribution surveys

Sites were surveyed for signs of badger activity during winter months, focussing on setts (underground tunnels and chambers used by badgers for shelter, breeding and protection) and latrines (shallow pits above ground where badgers deposit faeces; Neal & Cheeseman, 1996). We recorded the location of active and disused badger setts and the number of active, partially active and inactive holes at each sett. Latrines were mapped and scored based on the number of pits containing fresh and old faeces. We also recorded the location of badger runs (well defined paths that badgers used to travel between setts, latrines and foraging sites). Following best practice guidance for badger vaccination (DEFRA, 2021a), approximately one week prior to deploying cage traps, sites were re-surveyed to check for active signs of badgers and to identify suitable positions to locate cage traps for vaccination.

As these sites formed part of a larger vaccination project following a standardised badger survey protocol (DEFRA, 2021a), several sites were situated within a larger area of surveyed land. Where possible, the locations of active badger setts on contiguous land were used to map badger home ranges, even if they fell outside the camera trapping area.

3.3.3. Badger trapping, sampling and vaccination

All sites were part of an existing badger vaccination research project managed by the Cornwall Badger Project of the Zoological Society London (Woodroffe *et al.*, 2017; Woodroffe *et al.*, 2024), for which blood samples were collected, necessitating the anaesthesia of badgers upon capture. The trapping, sampling and vaccination of badgers were conducted under licence from the UK Home Office (project licence PB32E4DFC) and Natural England (research licences 2019-40177-SCI-SCI and 2021-53121-SCI-SCI) as described in Woodroffe *et al.* (2017).

Badger trapping was conducted for two consecutive nights (weather permitting) at each farm between May and September in 2019 and 2021 (Table 3.1). Following government best practice guidelines (DEFRA, 2021a), cage traps were placed near active badger setts and runs, and were pre-baited with peanuts for 7-10 days prior to trapping. Traps were set late in the afternoon and then checked at dawn the following morning. Upon capture, badgers were given a welfare assessment, followed by anaesthesia via intramuscular injection of medetomidine (approximately 0.03mg per kg) and ketamine (approximately 9mg per kg) (Woodroffe *et al.*, 2016).

Once anaesthetised, individuals with an existing microchip (from previous years' trapping) were identified and any newly caught individuals were fitted with a microchip (DNAChip, Avid PLC, Lewes, UK). Badgers were then vaccinated intramuscularly with the BCG vaccine (Intervax Ltd, Markham, Canada, the "Sofia strain" in 2019; Statens Serum Institut, Denmark, the "Danish strain" in 2021).

Vaccinated animals were then given a temporary fur clip by trimming the guard hairs on the flanks with a unique pattern (Stewart & Macdonald, 1997). This allowed us to distinguish vaccinated individuals so on the second night of trapping, any fur clipped animals were recorded as recaptures and released without anaesthesia. All badgers were returned to the trap after handling and were released after a visual assessment confirmed they had fully recovered from the anaesthetic and were fit for release (DEFRA, 2021a).

3.3.4. Badger density

We used two camera-based methods, the random encounter model (REM; Rowcliffe *et al.*, 2008) and camera trap distance sampling (CT-DS; Howe *et al.*, 2017), to estimate badger density. Camera surveys were designed using a systematic grid with a random origin for each site, where the nodes of the cells represented the predetermined camera locations. Across the sites, we deployed a total of 301 camera traps (Browning StrikeForce HD Pro X; Table 3.1), placing them as close as possible to the predetermined locations using the nearest suitable object (such as a tree, fence post or telegraph pole). Cameras were positioned 30-40 cm high and parallel to the ground, without bait. Once the camera was in its final position, we took a series of calibration images using a 1m calibration pole at varying angles and distances from the camera (Wearn *et al.*, 2022). Cameras were programmed to take photographs 24 hours per day with no time lapse and a 1-second passive infrared trigger interval, and were deployed for approximately 7 weeks (Table 3.1).

During image processing we used a novel computer algorithm, Sherlock (Penn *et al.*, 2024) to remove a large number of 'empty' images (those not containing any animals or moving objects), and tagged the remaining images manually using XnView MP (version 0.99.6; Gougelet, 2020). Images with badgers were then isolated and digitised using AnimalTracker (Vargas Zarco, 2019). We identified sequences where badgers reacted to camera traps, defined as the animal looking directly at the camera and then adjusting their behaviour, such as moving towards or away from the camera or staying in a fixed position staring at it.

Badger densities, along with associated 95% confidence intervals (CI), were estimated using the equations from Rowcliffe *et al.* (2008) and Howe *et al.* (2017) for the REM and CT-DS, respectively, following Miles *et al.* (2024; Chapter 2). All model parameters were estimated from the camera data using digitised animal positions (Wearn *et al.*, 2022). Consistent with Miles *et al.* (2024; Chapter 2), for CT-DS we estimated density in two ways, with reactive sequences both included and excluded, since at present there is no universally accepted way to approach bias arising from reactivity to camera traps (Delisle *et al.*, 2023). Given that badgers were vaccinated during the time cameras were operational, we discarded camera trap data from nights affected by cage trapping

(defined as nights when cage traps were set to catch) when estimating densities (Miles *et al.*, 2024; Chapter 2).

3.3.5. Population size and vaccination coverage

To convert density estimates into estimates of the population size (the number of badgers in the vaccination area) it is necessary to know the size of the area vaccinated. Since vaccination delivery targets farms, the combined area of the farms at each site gives an estimate of the size of the ‘targeted area’. However, at a farm-scale, property boundaries may not accurately reflect social group territories, and the area occupied by the badgers using the targeted area is likely to be larger than the targeted area itself. Thus, detailed knowledge of badger territories becomes valuable in this context. We used the targeted area as a conservative estimate of the size of the area vaccinated (Fig. 3.2 (a)) and also estimated the area occupied by the badgers using the targeted area (hereafter referred to as the ‘area vaccinated using territory boundaries’) by employing a modification of the Dirichlet tessellations method (Doncaster & Woodroffe, 1993; Schlicht *et al.*, 2014) (Fig. 3.2 (b)). Dirichlet tessellations are formed from the perpendicular bisectors of lines connecting neighbouring active main setts; such tessellations are also referred to as Thiessen areas or Voronoi polygons and define regions wherein any given point within a polygon is closer to the sett situated inside that specific polygon than to any other sett. Research suggests that such methods can effectively delineate badger territories, indicated by the alignment of polygons with boundary markers such as latrines (Woodroffe *et al.*, 2009b).

We inferred territories by constructing polygons in QGIS (QGIS Development Team, 2021), using the locations of all active main setts recorded on sites and contiguous land (Fig. 3.2). For coastal sites, polygons were constrained to the coastline. We also used expert knowledge and information from badger surveys to refine the polygons, accommodating barriers such as rivers and urban boundaries. In some areas the locations of badger setts on neighbouring land were unknown. Where this occurred, we avoided unrealistically large territories using the assumption that badgers would not travel further than a certain distance from the sett (Schlicht *et al.*, 2014). We estimated the mean maximum nightly distance that badgers travelled from the sett as recorded by Ham *et al.* (2019) using GPS data from badgers collared at nearby uncultivated sites in Cornwall. This distance, which was estimated at 527m, was used to impose a circular boundary around each sett, limiting the outward extension of the polygons. Territories were considered ‘targeted’ by vaccination operations if cage traps were positioned within that polygon. The total area vaccinated using territory boundaries was estimated using the combined area of all the targeted territories at a site.

We estimated the population size (and associated 95% CI) under all badger density and area scenarios, by multiplying density estimates (and associated confidence limits) by the size of the area vaccinated, estimated using either (i) the targeted area or (ii) territory boundaries. Vaccination coverage (and 95% CI) was calculated by dividing the number of vaccinated badgers by the population size (and the associated confidence limits), expressed as a percentage. We also estimated the mean vaccination coverage for each method, averaging across sites. The variance of the mean was calculated as the square root of the sum of the squared differences divided by n . This variance was used to derive the standard error of the mean and compute the 95% confidence interval (mean $\pm 1.96 \times \text{SE}$).

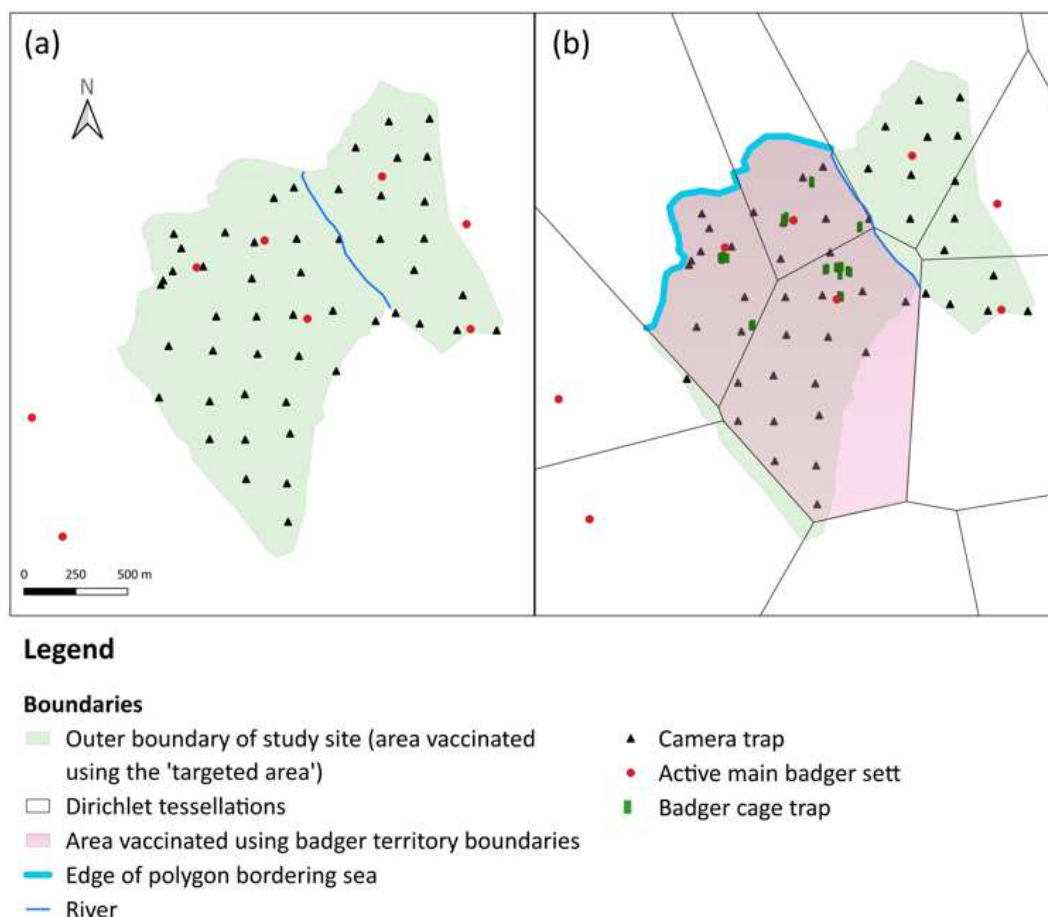


Figure 3.2 Map of site B illustrating the methods used to estimate the area vaccinated, which was delineated using either the targeted area (a) or badger territory boundaries (b). Badger territories were estimated using Dirichlet tessellations, which were refined using contextual information such as land edges and rivers. In instances of missing sett locations on adjacent land, we used the mean maximum nightly distance badgers in local social groups travelled from the sett (527m; Ham et al., 2019) to limit the extension of polygons.

3.4. Results

3.4.1. Badger vaccination

Across the five camera-trapped sites, we vaccinated an average of 0.3 badgers (range 0.1 – 0.4 badgers) per trap night and 6.6 badgers per km² (range 0.9 – 11.7 badgers per km²) of land participating in badger vaccination. Nearly half (44.8%) of the badgers vaccinated were cubs (Table 3.1). For comparison, in the initial year of badger culling operations on land near our study sites, 3.5 badgers per km² were removed in 2022 in licenced cull Area 64 (covering 104 km² in Penwith; Natural England, 2023) and 2.9 badgers per km² were removed in 2019 in licenced cull Area 35 (covering 1021 km² in Mid Cornwall; Natural England, 2020).

3.4.2. Badger density, population size and vaccination coverage

Badger density varied across sites (Table 3.2); the lowest estimated badger density was 1.4 badgers per km² (95% CI 0.6 – 3.0 badgers per km²) estimated from survey 5 at site D using the REM, and the highest estimated badger density was 20.2 badgers per km² (95% CI 18.8 – 34.4 badgers per km²) estimated from survey 2 at site A, also using the REM. Within surveys, densities were generally consistent between the REM and CT-DS when reactive sequences were included. Removing reactive sequences in CT-DS analyses had a substantial impact on density estimates at some sites, reducing the estimated density by an average of 26.8% (range 9.7% – 50.8%; Table 3.2).

Estimates of the area vaccinated, and hence the estimated population sizes, tended to be larger when based on badger territory boundaries than when using the targeted area, which was delineated using farm boundaries. The population sizes varied between sites (Table 3.2), with the smallest estimate being 6.4 badgers (95% CI 2.8 – 13.8 badgers) and the largest estimate being 76.3 badgers (95% CI 44.6 – 129.9 badgers).

Point estimates of vaccination coverage exceeded 30% (range 30.1% – 109.1%; Table 3.2) in all badger population scenarios, with lower coverage generally observed when using badger territory boundaries to define the area vaccinated. All mean estimates of vaccination coverage and their lower confidence intervals exceeded 30% (range 50.6% – 74.2%; Table 3.3).

Table 3.2 Summary of the estimated badger density, population size, area vaccinated, vaccination coverage, and associated 95% confidence intervals (CI; in square brackets), at four sites in Cornwall. Badger density was estimated using the random encounter model (REM) and camera trap distance sampling (CT-DS).

	Density model	Study site (survey number)				
		A (1)	A (2)	B (3)	C (4)	D (5)
Area vaccinated (km²)		2.4	2.4	1.8	2.0	4.6
<i>Targeted area</i>		3.8	3.0	1.6	1.8	5.8
<i>Territory boundaries</i>						
Badger density (badgers/km²) [95% CI]	<i>REM</i>	20.2 [11.8 – 34.4]	11.7 [6.3 – 22.0]	12.1 [7.7 – 18.9]	14.5 [9.1 – 23.1]	1.4 [0.6 – 3.0]
	<i>CT-DS (react. in.)</i>	19.8 [18.8 – 34.4]	14.5 [9.4 – 22.4]	14.3 [7.7 – 18.9]	18.1 [9.1 – 36.2]	2.3 [0.9 – 5.7]
	<i>CT-DS (react. ex.)</i>	13.8 [7.6 – 25.1]	13.1 [8.7 – 19.8]	12.5 [7.8 – 20.0]	8.9 [4.6 – 17.2]	1.6 [0.6 – 4.5]
Population size [95% CI]	<i>REM</i>	48.8 [28.5 – 83.1]	28.3 [15.2 – 53.2]	21.8 [13.9 – 34.0]	29.3 [18.4 – 46.7]	6.4 [2.8 – 13.8]
<i>Targeted area</i>	<i>CT-DS (react. in.)</i>	47.9 [27.6 – 82.4]	35.0 [22.7 – 54.1]	25.7 [16.0 – 39.6]	36.6 [18.4 – 73.2]	10.5 [4.1 – 26.1]
	<i>CT-DS (react. ex.)</i>	33.4 [18.4 – 60.7]	31.7 [21.0 – 47.9]	22.5 [14.0 – 36.0]	18.0 [9.3 – 34.8]	7.3 [2.8 – 20.6]
<i>Territory boundaries</i>	<i>REM</i>	76.3 [44.6 – 129.9]	35.2 [19.0 – 66.2]	19.3 [12.3 – 30.1]	26.0 [16.3 – 41.4]	8.1 [3.5 – 17.5]
	<i>CT-DS (react. in.)</i>	74.8 [43.1 – 128.8]	43.6 [28.3 – 67.4]	22.8 [14.2 – 35.0]	32.4 [16.3 – 64.8]	13.3 [5.2 – 32.9]
	<i>CT-DS (react. ex.)</i>	52.1 [28.7 – 94.8]	39.4 [26.2 – 59.6]	19.9 [12.4 – 31.8]	15.9 [8.2 – 30.8]	9.2 [3.5 – 26.0]
Vaccination coverage (%) [95% CI]						
<i>Targeted area</i>	<i>REM</i>	47.1 [27.7 – 80.6]	91.9 [48.9 – 170.8]	96.4 [61.7 – 151.5]	44.4 [27.8 – 70.7]	62.3 [29.1 – 145.4]
	<i>CT-DS (react. in.)</i>	48.1 [27.9 – 83.5]	74.2 [48.0 – 114.4]	81.6 [53.0 – 131.1]	35.5 [17.8 – 70.7]	37.9 [15.3 – 96.9]
	<i>CT-DS (react. ex.)</i>	69.0 [37.9 – 125.2]	82.1 [54.3 – 123.6]	93.3 [58.3 – 149.6]	72.3 [37.4 – 139.8]	54.5 [19.4 – 145.4]
<i>Territory boundaries</i>	<i>REM</i>	30.1 [17.7 – 51.6]	73.8 [39.3 – 137.1]	109.1 [69.8 – 171.4]	50.1 [31.4 – 79.8]	49.5 [23.1 – 115.6]
	<i>CT-DS (react. in.)</i>	30.8 [17.9 – 53.4]	59.6 [38.6 – 91.9]	92.3 [60.0 – 148.3]	40.1 [20.1 – 79.8]	30.2 [12.2 – 77.1]
	<i>CT-DS (react. ex.)</i>	44.1 [24.3 – 80.1]	65.9 [43.6 – 99.3]	105.6 [66.0 – 169.2]	81.6 [42.2 – 157.8]	43.3 [15.4 – 115.6]

Table 3.3 Mean badger vaccination coverage (and associated mean 95% confidence intervals (CI)) across five surveys conducted at four sites in Cornwall. Badger density was estimated using the random encounter model (REM) and camera trap distance sampling (CT-DS).

Area vaccinated delineation method	Density model	Mean vaccination coverage (mean 95% CI)
Targeted area	REM	68.4 (48.1 – 88.7)
	<i>CT-DS (reactive sequences included)</i>	55.5 (40.3 – 70.6)
	<i>CT-DS (reactive sequences excluded)</i>	74.2 (52.5 – 95.9)
Territory boundaries	REM	62.5 (44.6 – 80.4)
	<i>CT-DS (reactive sequences included)</i>	50.6 (36.6 – 64.6)
	<i>CT-DS (reactive sequences excluded)</i>	68.1 (48.0 – 88.2)

3.5. Discussion

This study examines the use of camera traps to estimate badger vaccination coverage and reports the coverage achieved across four sites in Cornwall, helping to assess the feasibility of badger vaccination on a localised scale. Our findings indicate that vaccinating a sufficient proportion of the badger population is both achievable and practical. Notably, all point estimates of vaccination coverage were in the range of 30.1% to 109.1%, and the mean vaccination coverage ranged from 50.6% – 74.2%. These levels of coverage address concerns that badger vaccination might not capture enough individuals to be effective (Chivers *et al.*, 2022) and suggest that badger vaccination could be a feasible strategy for bTB management.

We vaccinated more badgers per km² than culling efforts on nearby land, and the mean vaccination coverage surpassed 30% in all population size scenarios (Table 3.3). All point estimates of vaccination coverage also exceeded 30% (Table 3.2), even in low-density populations, although the results had wide confidence intervals. Nonetheless, these findings are reassuring, as they suggest that a substantial proportion of the badger population were trapped and vaccinated, even where density was low, challenging suggestions that vaccine delivery may be difficult in low-population density scenarios (Byrne *et al.*, 2012). However, it is important to note that this study did not account for variation in environmental factors, leaving some uncertainty about their potential impact on the results. For example, in the UK, badgers preferentially forage for earthworms (*Lumbricus terrestris*) (Kruuk, 1978; Kruuk *et al.*, 1979) unless climatic conditions such as low rainfall force earthworms to be less available at the soil surface, making them harder to find (Macdonald *et al.*, 2010). Consequently, badgers may be easier to trap during dry spells if they are hungrier and more

attracted to bait (Tuytens *et al.*, 1999). Additionally, the small sample size in this study limited our ability to draw meaningful conclusions about the effect of trapping effort on vaccination coverage. Future analyses of vaccination programs would benefit from considering these variables to better understand how to maximize the effectiveness of badger vaccination efforts.

Our estimates of vaccination coverage align with those from previous studies such as Benton *et al.* (2020) and Smith *et al.* (2020) where mark-recapture approaches were used to estimate population size. Unlike mark-recapture, our use of camera traps offers a feasible method of estimating vaccination coverage in both small and large target areas. The mark-recapture approach employed by Benton *et al.* (2020) is appealing because it relies solely on data gathered in the course of the vaccination process, including the numbers of animals trapped, marked, and subsequently recaptured. However, this model relies on the Lincoln–Petersen estimator and precision increases with the number of recaptures. As such, the method may be less suitable for small vaccination areas where achieving the necessary number of recaptures may be challenging. Our approach utilising camera traps may provide an advantage over mark-recapture studies by generating density estimates that represent the entire population rather than just a trappable subset. Sophisticated mark-recapture methods that adjust for variation in detectability generally require repeated sampling to ensure precise estimates in the presence of heterogeneity in capture probability (Palmero *et al.*, 2023), likely exceeding the two trapping opportunities mandated by best practice guidance for badger vaccination (DEFRA, 2021a) and thus making them unsuitable for this purpose. In addition, camera traps facilitate simultaneous density estimation of a range of species, enabling monitoring of potential wider ecosystem responses to changes in management.

The wide confidence intervals in our results arise from the uncertainty associated with density estimates, emphasising the need to improve precision in density estimation. This can be achieved by increasing the camera effort through additional deployments or prolonged deployment times. We found that the REM tended to have narrower confidence intervals than CT-DS (Table 3.2), highlighting the potential advantage of using the REM for this purpose. In addition, the REM has a standardised method for controlling bias arising from reactivity to camera traps, a critical factor given the observed reactivity of badgers in our study. The lack of such a standardised approach in CT-DS analyses can have a substantial effect on density estimates, as evidenced here and in previous studies (Bessone *et al.*, 2020; Miles *et al.*, 2024, Chapter 2). Furthermore, the demonstrated scalability of camera trap methods (Mason *et al.*, 2022) is advantageous in the context of current policy because a bTB eradication strategy emphasising vaccination is likely to need to operate over very large scales.

1692 Estimated population sizes were generally larger, and hence vaccination coverage was
1693 estimated to be lower, when delineating the area vaccinated using badger territory boundaries
1694 rather than farm boundaries. The greatest disparities in estimates of the area vaccinated emerged in
1695 locations where badger territories and farm boundaries were not aligned. This outcome is expected
1696 given the localized nature of our study, and badger territory-based estimates might offer more
1697 accurate insights at such scales. Employing Dirichlet tessellations to map home ranges offers a
1698 valuable approach for accurately defining the size of the area occupied by the badgers within the
1699 area targeted for vaccine delivery, and thus population sizes, in small-scale projects, however, across
1700 broader landscapes, the edge effects associated with badger home ranges decrease in relative terms,
1701 reducing the necessity for such precise adjustments.

1702 In summary, our study provides valuable insights for shaping badger-focussed bTB
1703 management policies. Our findings suggest that badger vaccination can achieve substantial coverage
1704 in various density scenarios. They also highlight the value of integrating camera traps in bTB
1705 eradication strategies to facilitate estimating vaccination coverage. Using camera traps for this
1706 purpose would enable monitoring of changes in badger density and vaccination coverage over time,
1707 supporting the long-term assessment of a badger vaccination strategy. The practical feasibility of
1708 badger vaccination, as shown by our study, suggests that an evaluation of badger vaccination on a
1709 broader scale would be warranted to estimate the effect on bTB incidence among cattle populations.

1710 **4. Chapter 4: Balancing effort and precision in camera trap surveys**



1711 *A roe deer suckles a fawn at Woodchester Park.*

4.1. Abstract

Camera traps are valuable tools for studying wildlife, with abundance assessment often being the primary objective. Advances in statistical methods allow for density estimation of individually unidentifiable species, but these estimates often lack the precision needed for conservation and management. Precision may be improved with increased survey effort but balancing the two is challenging, with little empirical guidance available. We evaluated the relationship between camera trapping effort, and the precision and accuracy of population density estimates obtained using the random encounter model (REM) and camera trap distance sampling (CT-DS) for four mammal species in Woodchester Park, Gloucestershire. Using badgers (*Meles meles*) as a relatively low-population density case study, we estimated the survey effort required for adequate precision (coefficient of variation (CV) $\leq 20\%$) by subsampling the data to simulate varying the number of camera placements and deployment durations. We also used these camera-based methods to assess the potential temporal changes in badger density resulting from culling on nearby land. Our density estimates aligned well with each other and with estimates from the literature. We found that the REM was more precise and demanded less survey effort than CT-DS, in terms of the deployment durations required to reach adequate precision. Both methods required a minimum of 100 camera placements to obtain a CV of $\leq 20\%$, and sampling times of three weeks (REM) or four weeks (CT-DS) were sufficient with 140 cameras. Our results suggest that precise density estimates are obtainable with achievable survey effort, even for relatively low-density populations, supporting the integration of the REM and CT-DS in animal management strategies. We also found that badger density in Woodchester Park has declined significantly over a 10-year period, likely due to local culling, with our results reflecting the lowest published density to date for this site.

4.2. Introduction

Camera traps have become invaluable tools for wildlife research, as evidenced by their extensive use in recent decades (Burton *et al.*, 2015; Delisle *et al.*, 2021). Remotely triggered cameras offer a non-intrusive means of monitoring a range of wild species and are particularly beneficial in the otherwise difficult study of species that are rare, cryptic and/or elusive in nature (Brassine & Parker, 2015; Perera *et al.*, 2022; Nazareth *et al.*, 2024). Surveys benefit from collecting substantial amounts of data across large spatial scales and simultaneously capturing information on multiple species, allowing a range of research questions to be addressed. Although initial investment can be high, camera traps may be more cost-effective than labour-intensive survey methods for assessing species diversity and abundance in the long term (Djekda *et al.*, 2020; Welbourne *et al.*, 2020). The

1745 integration of artificial intelligence is also helping to streamline image processing, although these
1746 technologies are still evolving (Vélez *et al.*, 2023).

1747 Estimating population density is a common objective in camera trapping studies (Trollet *et al.*,
1748 *al.*, 2014; Burton *et al.*, 2015). Various methods have been developed to estimate abundance for
1749 species which are uniquely patterned (e.g. Karanth, 1995; Hedges *et al.*, 2015; Whittington *et al.*,
1750 2018), or can be artificially marked (e.g. Efford & Hunter, 2018; Jimenez *et al.*, 2019; Taylor *et al.*,
1751 2022). Alternative approaches are needed for species which lack unique identifiers (Nakashima *et al.*,
1752 2020; Mason *et al.*, 2022; Morrison *et al.*, 2022), of which the random encounter model (REM) and
1753 camera trap distance sampling (CT-DS) have received the most attention. These models have
1754 demonstrated effectiveness in simulations and field trials (Rowcliffe *et al.*, 2008; Howe *et al.*, 2017),
1755 and through validation with independent measures (e.g. Pettigrew *et al.*, 2021; Twining *et al.*, 2022).
1756 Comparative analyses of the REM and CT-DS have also been performed, examining their accuracy,
1757 precision, cost-effectiveness, and practical implementation (Palencia *et al.*, 2021; Hayashi & Iijima,
1758 2022; Santini *et al.*, 2022). These studies have concluded that, while both methods are effective and
1759 produce accurate and precise results in many circumstances, each exhibits distinct advantages and
1760 limitations and further model refinement would be beneficial (Palencia *et al.*, 2021).

1761 A common limitation of using camera traps for estimating population density is the precision
1762 of the resulting estimates, which often falls short of the threshold necessary to inform management
1763 decisions. Many studies have adopted a threshold of a coefficient of variation (CV) $\leq 20\%$ to indicate
1764 an acceptable level of precision (e.g. Pollock *et al.*, 1990; Williams *et al.*, 2002; Cappelle *et al.*, 2021).
1765 However, recent studies suggest that methods such as the REM and CT-DS rarely meet this standard
1766 without substantial camera trapping effort (Cappelle *et al.*, 2021; Palencia *et al.*, 2022). This issue is
1767 amplified for species living at low densities, or in scenarios where the detection rate is highly variable
1768 in space or time (Rowcliffe *et al.*, 2008). Consequently, there is a critical need to improve the
1769 precision of estimates from camera trap studies using these methods, particularly for low-density
1770 wildlife populations.

1771 When planning a camera trap survey, practitioners should ideally determine the optimal
1772 amount of effort, balancing precision against cost (in terms of number of cameras and duration of
1773 deployment). Provided there is adequate sampling across the range of habitats occupied by the
1774 target species, the scale over which camera surveys are carried out is not critical and is not explicitly
1775 modelled in the REM and CT-DS. While fewer cameras deployed for longer durations may be
1776 preferential in terms of equipment costs and field labour, sampling more locations is likely to better
1777 capture environmental heterogeneity. As such, a survey achieving 1,000 camera trap-days with 50

cameras deployed for 20 days will likely outperform (in terms of both accuracy and precision) a survey with a single camera deployed for 1,000 days (Rowcliffe *et al.*, 2008). However, few studies have empirically examined the minimum effort needed to achieve acceptable precision or assessed the impact on accuracy and precision of increasing the number of cameras and deployment times. Simulations by Rowcliffe *et al.* (2008) suggest that as few as 20 cameras may suffice in conditions with low variability in trap rate (contacts per camera per day), although this figure could rise to at least 100 in settings with greater heterogeneity in image capture rate. For CT-DS, as many as 150 cameras, or deployment times of longer than six months, may be necessary to achieve a CV of $\leq 20\%$ (Cappelle *et al.*, 2021). Further empirical research is needed to understand the trade-offs between achieving precise estimates and resource requirements, as well as to identify the most effective survey designs for optimising precision (Palencia *et al.*, 2021).

Camera traps could aid in the surveillance of terrestrial mammal species that are often difficult to detect but important for management purposes. In the UK, deer populations have substantially increased in size and geographic range (Ward, 2005). High densities of species such as muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*) are routinely controlled due to their negative impact on woodlands and damage to crops (Putman *et al.*, 2011). Roe deer are also managed as a valuable source of meat and revenue (Hare *et al.*, 2021). Culling populations of carnivores such as red foxes (*Vulpes vulpes*) and badgers (*Meles meles*) is also widespread in the UK, with foxes primarily culled for conservation and game management, and badgers to mitigate potential impacts on livestock through their role in the transmission of zoonoses (Reynolds & Tapper, 1996; Artois *et al.*, 2001).

In the British Isles, badger management, conducted in response to human-wildlife conflict arising from the transmission of bovine tuberculosis (bTB), is a source of longstanding scientific and public debate (Bourne *et al.*, 2007). Though the transmission of *Mycobacterium bovis*, the causative agent of bTB, to cattle is primarily from other cattle, badgers contribute to the maintenance of infection (Donnelly & Nouvellet, 2013; Crispell *et al.*, 2019; van Tonder *et al.*, 2021). Consequently, badgers have been a central focus of the UK government's bTB eradication strategy for the last 50 years (DEFRA, 2020), by managing badger populations in areas at risk of bTB herd breakdowns through culling and, to a lesser extent to date, vaccination. Accurate and precise estimates of badger density are valuable for devising and assessing these management strategies, and for monitoring temporal changes in populations. As most badgers are not uniquely identifiable, camera trap methods which do not rely on individual identification, such as the REM and CT-DS could be valuable

for this purpose. However, they require refinement for application in low-density populations, such as those which may result from intensive culling.

This study aimed to estimate the population densities of four mammal species using the REM and CT-DS. Densities were anticipated to range from low (badgers and red foxes) to high (roe deer and muntjac) densities due to different management practices at the study site and on neighbouring land. We compared the results of these methods with each other and evaluated how well the density estimates aligned with previously published literature. Additionally, for badgers, we utilised data from a long-term capture-recapture study to estimate the minimum number alive (MNA) density for comparison with the REM and CT-DS estimates. By deploying a relatively large number of cameras for two months, we sought to estimate the spatial and temporal survey effort needed for the REM and CT-DS to achieve accurate and precise results for species across different densities. Anticipating a low badger density due to nearby culling, we used the badger as a case study to estimate the survey effort required to achieve adequate precision in a relatively low-density population. Additionally, we assessed potential temporal changes in badger density as a result of local culling operations, providing insights that may be useful for monitoring population responses to animal management.

4.3. Materials and methods

4.3.1. Study area

Camera surveys were conducted from 20th June to 18th August 2022, over a 2.3km² area of Woodchester Park, Gloucestershire, South West England (Fig. 4.1). The park features a steep-sided, heavily wooded valley, consisting largely of broadleaved woodland and conifer plantation, with small open fields grazed by sheep and cattle, and a series of lakes in the centre (Rogers *et al.*, 1998; Delahay *et al.*, 2006). This core area is managed by the National Trust and is surrounded mostly by private arable and grazed farmland. The site is frequently visited by the public, with most activity restricted to footpaths running east to west through the centre of the park.

Woodchester Park is located within a region of England considered high risk for bTB (APHA, 2024). At the time of camera deployment, surrounding land was subjected to supplementary badger culling, following completion of four years of intensive culling which began in 2018 (DEFRA, 2023c), although no culling was conducted in the project area itself.

4.3.2. Camera trap surveys

Both density methods necessitate random camera placement. To achieve this, we deployed 149 cameras (Browning StrikeForce HD Pro X) across a grid with a random origin and a predetermined

1843 spacing of 120m (Fig. 4.1), planned using GridMaker (Rowcliffe, 2021c). Cameras were fixed to the
1844 nearest tree or fence post, aiming to keep within $\leq 20\%$ (24m) of the spacing between planned
1845 locations, and facing a direction with a clear field of view (FOV). If cameras could not be situated at
1846 the precise predetermined coordinates, they were placed within the same broad habitat as the
1847 planned location and positioned to face the planned coordinates. Cameras were fixed approximately
1848 60cm above the ground to target large mammals and were not baited. Where necessary, we cleared
1849 vegetation directly within the camera's FOV to prevent interference with camera vision while
1850 minimising alteration of the habitat. Cameras were programmed to take still images and were active
1851 24 hours a day with no time lapse, a 1-second passive infrared trigger interval, and an infrared flash
1852 during low light conditions. At each camera deployment we recorded the coordinates of the final
1853 location, vegetation type, aspect, time, and date, and took an image of these details on each camera
1854 to enable the time and date to be verified during data analysis.

1855 Once cameras were in their final position, we calibrated deployments using an object of
1856 known size, which was a 1m pole marked at 20cm intervals, taking a series of images of the pole at
1857 various angles and distances from the camera (Wearn *et al.*, 2022). We also repeated this in a
1858 controlled setting – a flat area with a clear FOV – using a single camera and the same calibration pole,
1859 placing the pole at known distances measured from the camera. This process enabled construction
1860 of calibration models required to estimate radial distances and angles of animals from the cameras.
1861 Cameras were deployed for approximately eight weeks. Batteries and SD cards were replaced half
1862 way through the study period (where necessary) and deployments were recalibrated in case of
1863 camera movement by people or animals. Upon collection, all camera deployments were recalibrated
1864 for a final time.

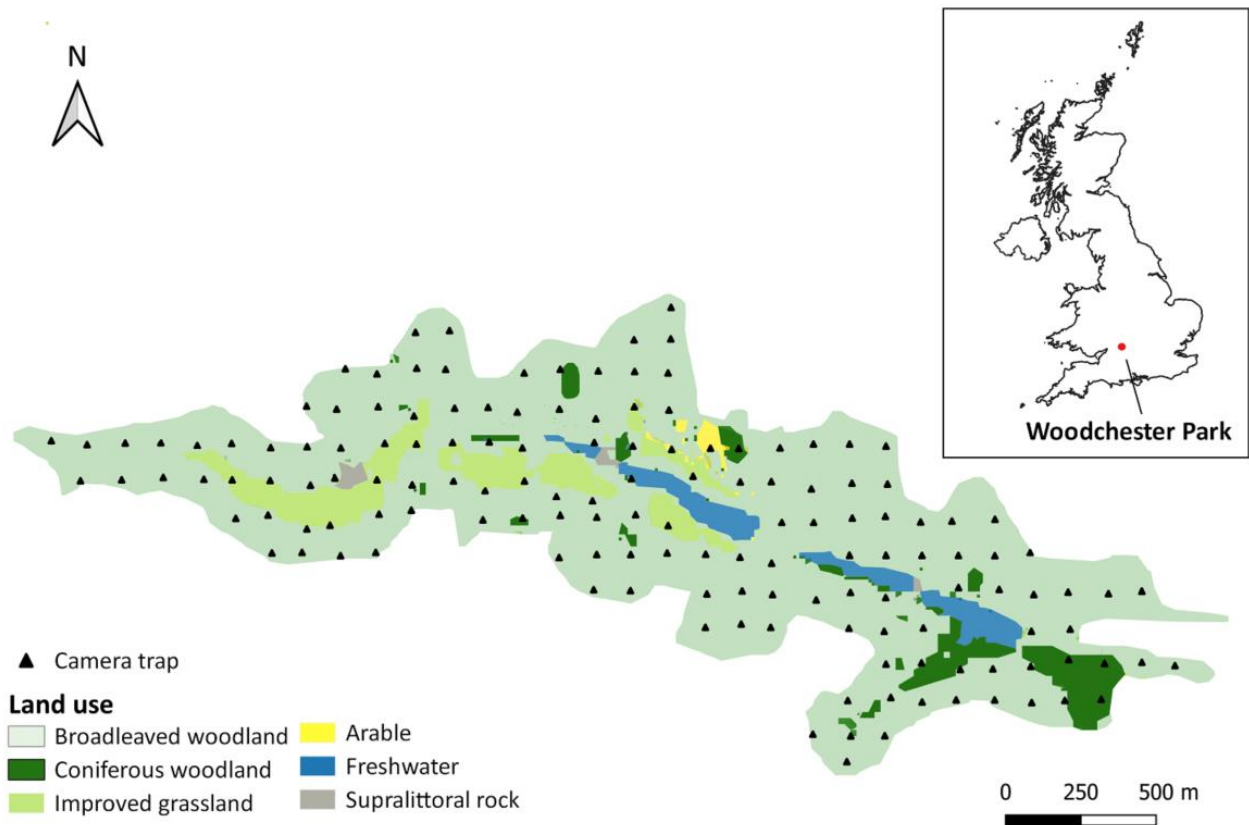


Figure 4.1 Location and habitat characteristics of the study site. Panels show the site location in Gloucestershire, England (inset), and the detailed land use within Woodchester Park, overlaid with the locations of 149 camera traps deployed during the survey (main image). Habitat data from Land Cover Map 2021 (10m classified pixels; Marston *et al.*, 2022).

4.3.3. Estimating model parameters

The REM and CT-DS are fundamentally similar methods and share several model parameters. Here we outline the shared data analysis methods and how we obtained the model parameters for each approach. We estimated data for all terrestrial mammals large enough to be reliably detected by the chosen camera height, and with a sufficient number (≥ 20 ; Rowcliffe *et al.*, 2008) of images to allow estimation of population density. In practice, these criteria restricted our analyses to badgers, muntjac, red foxes, and roe deer. In applying these methods, we treated individual animals as the unit of observation across all species, due to their generally solitary nature outside of setts, dens and refuges. An exception was noted for the two deer species, where pairs – typically a mother and her fawn – were occasionally observed. However, as the majority of deer were seen alone, individuals remained the primary unit of observation. All analyses were conducted in R (R Core Team, 2021), unless otherwise specified.

Images were tagged manually using XnView MP (version 0.99.6; Gougelet, 2020). Tagging involved recording the species, count (the number of individuals of each species present) and contact (the first image in each unique sequence, where a sequence is defined as an individual entering and exiting the FOV) for all images containing animals. Tagged images were then digitised using AnimalTracker (Vargas Zarco, 2019) in order to obtain data on the animals' positions relative to the camera, which is required for both density estimation methods. We digitised animals' locations by finding their approximate centre of mass in every image and marking the corresponding position on the ground directly beneath it, unless the animal was hidden from view so that the position could not be determined reliably.

Images of calibration poles were digitised by marking the minimum and maximum heights of two visible intervals on each pole, ensuring poles were upright and on the ground. For camera calibration images, which were taken in the controlled setting as described above, we also recorded the distance of each calibration pole from the camera. These data were used to build camera calibration models which were fitted to data from camera deployments to estimate the real-world radial and angular distances of animals in images, using the 'CTtracking' package (Rowcliffe, 2021b).

Data on the distances of animals from the camera were used to estimate density model parameters of both methods. The effective detection angle of camera traps was estimated by fitting distance sampling detection functions to the angular distance observations of the position of animals in the first image of each sequence (Rowcliffe *et al.*, 2011). The full angle of the FOV, expressed in degrees, was then used to estimate the proportion of a circle covered by the camera for CT-DS analyses. We also fitted distance sampling detection functions to radial distance data to estimate the effective detection radius for both models and used sequential animal positions to estimate the average speed while active for the REM, by dividing the total distance travelled in each animal sequence by the duration of the sequence. For CT-DS, distance data were used to fit distance sampling models to estimate density (detailed under 'density estimation').

Activity level, defined as the proportion of time spent active (Rowcliffe *et al.*, 2014), is used in both the REM and CT-DS. We estimated the activity level for each species by fitting a circular kernel model to radian time of day distributions of animal contacts using the 'activity' package (Rowcliffe *et al.*, 2014). For REM analyses, we estimated the average daily distance travelled, or 'day range', by multiplying the average speed while active by the activity level. The associated standard error was calculated using the variance of products formula (Goodman, 1960), following Rowcliffe *et al.* (2016).

Both density models are calibrated according to temporal effort and spatial coverage (the angle and radius of the detection zone). For the REM, survey effort is defined as the total number of camera trap-days, calculated by summing the deployment durations of all cameras. For CT-DS, an additional parameter is required; temporal effort is estimated as the number of 'snapshot moments' during the survey, or the total time cameras were available to take images. Although our cameras were continuously operational, there is a short interval after each trigger during which the camera cannot take another image. We set the trigger interval to the minimum available time (1 second) but also estimated it using the mean duration of animal sequences divided by the mean number of intervals between sequential images, resulting in an estimated trigger interval of 2 seconds. The number of snapshot moments was calculated by dividing camera deployment time by the trigger interval.

During camera deployment, badger cage trapping occurred on four occasions, in different parts of the study area, as part of a long-term study of badger ecology and bTB epidemiology (Cheeseman *et al.*, 1987). During trapping events, badger traps were placed near setts and prebaited with peanuts for 7-10 days. Traps were then set to catch on two consecutive 'trapping nights', with any badgers caught, examined and then subsequently released at the point of capture. We assumed that the random placement of cameras mitigated any potential bias from non-random movement of badgers in response to pre-baiting. However, on trapping nights, a proportion of the badger population was restricted, making them undetectable by camera traps. Consequently, we excluded trapping nights from the analysis of badger density by removing the hours when cage traps were set to catch from the effort calculations of both models, and excluding any badgers detected during these times from the analyses. An alternative would have been to exclude 24-hour periods since there are relatively few badger encounters between 8:00 and 18:00. However, given the large number of usable trap nights (Table 4.1) in each time interval, the difference would have been minimal. This adjustment was not applied to other species since no red foxes or deer were unintentionally caught in cage traps during the study.

Both density estimation methods can be biased by animals reacting to camera traps, such as investigative, freeze, or fleeing behaviours in response to novel objects or the infrared flash. During a reactive sequence, an animal may alter its natural movement and speed, potentially biasing model parameters. The most substantial bias likely arises from attraction to cameras (Henrich *et al.*, 2022; Delisle *et al.*, 2023). If an animal is attracted to the camera before detection in the FOV, this attraction can result in more observations close to the camera (referred to as 'spikes' in the distribution of distance data). In the REM, such attraction could result in an elevated overall trap rate

and bias in the distance observations used to estimate the detection zone parameters. However, if the attraction were to occur after the camera had been triggered, it would not affect the first contact which is used in the REM to estimate trap rate and detection zone parameters. Similarly, avoidance behaviours, which are only detectable after the first encounter, are unlikely to affect trap rate or the detection zone parameters but could cause an upward bias in speed estimates in the REM. By contrast, avoidance prior to detection – which is, by definition, undetectable – would lead to a downward bias in trap rate. Freezing is also more likely to cause a downward bias in estimated speed. In CT-DS models, all observations in an animal sequence are used to fit detection models. Therefore, attraction to the camera, whether before or after the first detection, is likely to introduce bias, evident as spikes in the data at very short distances, which may affect the choice of detection function. Delisle *et al.* (2023) suggest that the hazard rate detection function should be avoided where attraction behaviours are abundant because such models can introduce negative bias to the detection probability and overestimate density. In contrast, freezing and fleeing are more likely to result in detections at further distances within the camera's detection zone.

To address the potential bias caused by reactions to the camera, we identified reactive sequences and categorised them as follows: attraction (animals looking and moving towards the camera, distinguishing between those attracted before (Fig. 4.2) and after (Appendix 2, Fig. S2) detection in the FOV), freeze (animals looking towards the camera and remaining still), flee (animals looking towards the camera then moving away rapidly) or a mixture of these behaviours (Fig. 4.2). Looking at the camera was crucial to distinguish between reactions that might have been triggered by other disturbances and similar behaviours exhibited when the animal was perceived to be unaware of the camera. We then explored methods to control bias based on the detection of such behaviours, following the approaches for both models outlined by Delisle *et al.* (2023). Hazard rate models were considered for CT-DS models if spikes near zero were not evident upon inspecting the frequency distributions of animal distances from the camera. Avoidance before detection was not explored in these analyses.

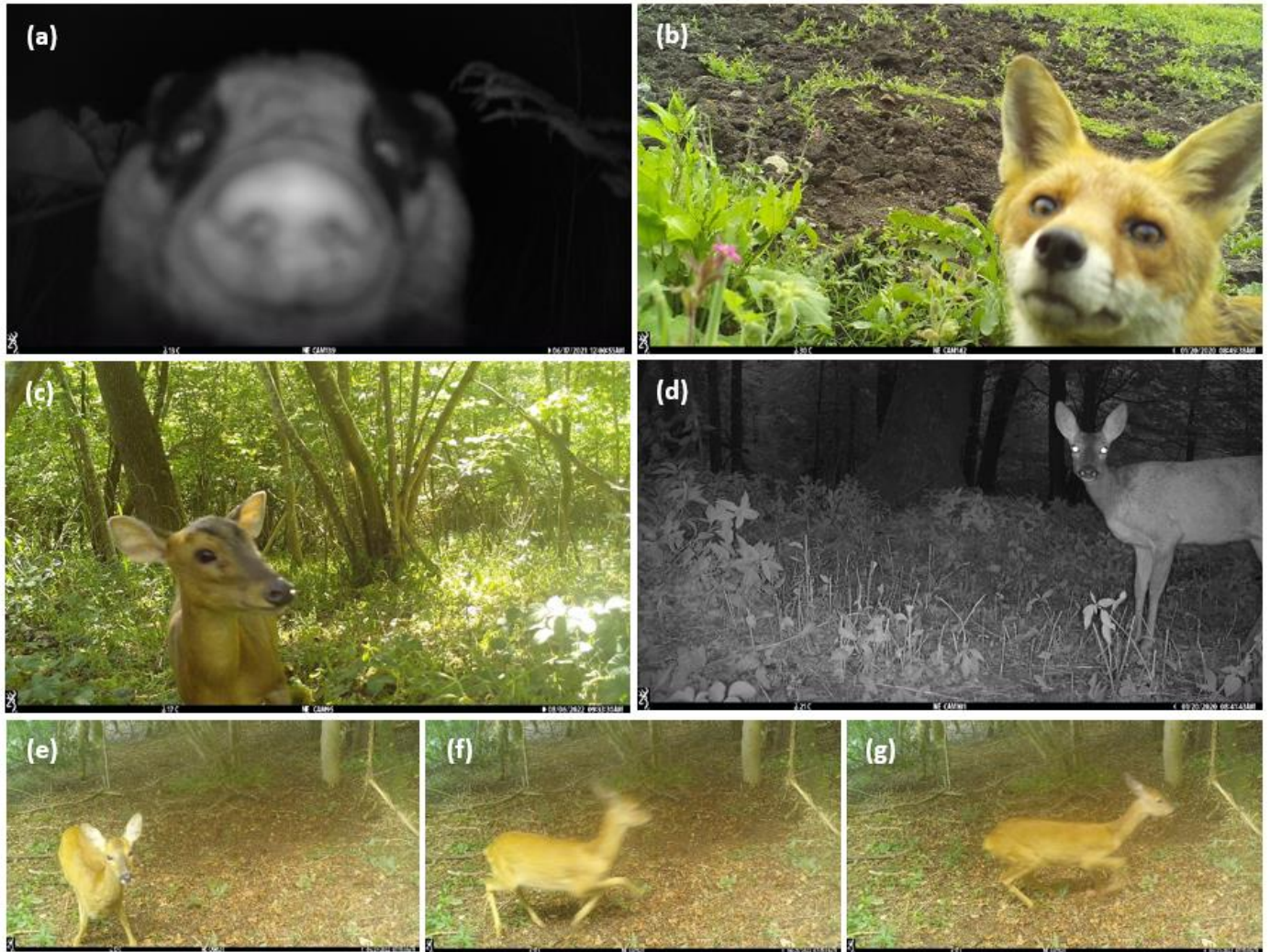


Figure 4.2 Representative images of animals reacting to camera traps, which was recorded in the four focal species: badger (a), red fox (b), muntjac (c) and roe deer (d – g). Reactive behaviour was categorised as attraction (a and b), freeze (c and d), flee (e – g), or a mixture of these behaviours. Where animals were looking at the camera and were very close to it upon first detection (a and b) the behaviour was categorised as attraction before detection in the camera's field of view. Examples of attraction after detection, whereby normal behaviour preceded attraction to the camera, are shown in Appendix 2, Fig. S2.

4.3.4. Density estimation

Density was estimated for each of the focal species independently using the REM and CT-DS equations detailed by Rowcliffe *et al.* (2008) and Howe *et al.* (2017), respectively. As the badger population was not closed, due to badger culling on nearby land, we assumed that density estimates represented a mean density across the survey period.

For the REM, the variance associated with the trap rate was estimated by bootstrapping, resampling camera deployments with replacement. We incorporated the variance of all model parameters in the overall variance of density estimates using the ‘camtools’ package (Rowcliffe, 2021a). We fitted CT-DS models using the ‘Distance’ package (Miller *et al.*, 2019), following the process outlined by Howe *et al.* (2019) for model selection. We left-truncated the data where there was a paucity of observations, to account for animals passing under the camera without being detected, and right-truncated the data where the probability of detection was lower than 0.15 (Buckland *et al.*, 2001). We discarded models where the detection function did not decline monotonically in relation to the detection distance (Howe *et al.*, 2017).

The Woodchester badger population has been the subject of long-term monitoring, including the routine capture, marking, and release of resident animals as part of a comprehensive study on badger ecology and disease dynamics, detailed in McDonald *et al.* (2018). We therefore had a unique opportunity to assess camera surveillance methods in an area where a wealth of information already exists about the badger population. We utilised mark-recapture records of badgers trapped between 2013 and 2023 to estimate population size using the MNA method (Rogers *et al.*, 1997), restricting capture records to those within the region that was also camera trapped. To estimate the area over which the MNA was calculated, we used the combined size of the territories of social groups within the camera trapped region of the park (2.3km²). Territories were mapped using a bait marking technique (Delahay *et al.*, 2000). The total area of the combined territories was slightly smaller than the ‘core’ study area of 7km² reported in McDonald *et al.* (2018) as the southern region outside of Woodchester Park was not camera trapped in our study (Fig. 4.1). Removing this region from our analyses resulted in an area of 6.2 km² over which the MNA was estimated. To convert the MNA into a density estimate, we divided the MNA population size by the area. The 2022 MNA density estimate was used as a comparison for our camera-based badger density estimates.

We also compared the camera-based density estimates for all species with those in the literature. As density is likely to change over time and vary between habitats, we prioritised the most up-to-date estimates and those in similar habitats to the study site. Where possible, we focused on camera-based methods, but also included trapping-based capture-recapture studies and relative indices of density if camera-based estimates were unavailable.

4.3.5. Detecting changes in badger density

Badger culling is not permitted in Woodchester Park. However, the park is situated within an area which has been licensed for badger culling since 2018. Our survey, which took place from 20th June to 18th August 2022 was within the period licensed for supplementary badger culling (1st June 2022 to

13th January 2023; DEFRA, 2023c) and therefore, culling occurring on nearby land at the time of the camera survey may have reduced badger density during the survey period. To assess whether the camera-based methods could detect culling-related short-term changes in badger density, we subdivided the camera trap data into three roughly equal time intervals in terms of survey effort (Table 4.1), accounting for nights excluded due to badger cage trapping, and estimated badger density for each time interval. We presumed that the camera parameters were unaffected by culling operations and therefore used the complete dataset to estimate the mean detection radius and angle to ensure the highest precision for these parameter estimates. However, since badger activity and ranging behaviour are known to change in response to culling (Riordan *et al.*, 2011; Ham *et al.*, 2019), animal parameters might have been impacted. We therefore assessed the impact of fitting the density models under two different scenarios: firstly, with the activity level and speed parameters fixed at the mean across all periods, and secondly, with these parameters estimated specifically for each time interval. Trap rate for the REM, and distance data and truncation decisions for CT-DS, were also considered separately for each time interval.

To evaluate the impact of nearby culling on badger density over a longer period, we calculated the annual MNA from 2017 (the year preceding culling) to 2022 (the year supplementary culling started) and fitted a simple linear regression to test if there was a significant change in the population size over the 5-year period.

Table 4.1 Details of three sequential time intervals used to divide data into roughly equal segments based on survey effort for estimating badger density. Total effort shown is the number of camera trap-nights excluding the hours when badger cage trapping occurred.

	Time interval 1	Time interval 2	Time interval 3
Deployment start (dd/mm/yy hh:mm:ss)	Specific to each camera; earliest start 20/06/22 10:36:17	11/07/22 13:00:01	27/07/22 20:00:01
Deployment end (dd/mm/yy hh:mm:ss)	11/07/22 13:00:00	27/07/22 20:00:00	Specific to each camera; latest end 18/08/22 14:12:00
Number of camera deployments	149	149	149
Mean deployment time/camera (days)	17	16	19
Total effort (camera trap-nights)	2464	2427	2525

4.3.6. Effort precision analysis

To estimate the minimum temporal and spatial effort required to obtain accurate and precise results, we examined how variations in the number of camera placements and deployment durations affected the accuracy and precision of model parameters and estimates of badger population density. We focused our analyses on badgers due to the potential value of camera-based density estimation methods in informing bTB management policies, particularly in areas such as this where badger density was expected to be low as a result of nearby culling operations.

We simulated reduced survey effort by systematically subsampling the observed badger camera data, varying the number of camera placements (20 to 140 cameras, in increments of 20) and durations (7 to 56 days, in increments of 7) included in our analyses. Data were selected by sampling both the camera placements and the days of camera deployment at random, repeating this process 1,000 times for each combination of camera number and deployment duration. Where a camera selected for inclusion in a particular subset was one which stopped collecting data before the selected deployment duration (due to battery failure, memory limitations, or disturbance), the true

deployment duration was used. This adjustment accounted for practical limitations such as battery life or SD card capacity, which typically affect longer deployment periods.

Following the methods described previously for estimating the model parameters for the REM and CT-DS, we calculated the mean and standard error (SE) for each parameter across the 1,000 simulated datasets for each effort combination. These values were then applied to the density models to estimate mean density, SE, and CV for each effort combination using the REM and CT-DS. A CV of $\leq 20\%$ was adopted as an indicator of adequate precision.

4.4. Results

4.4.1. Camera survey and animal density

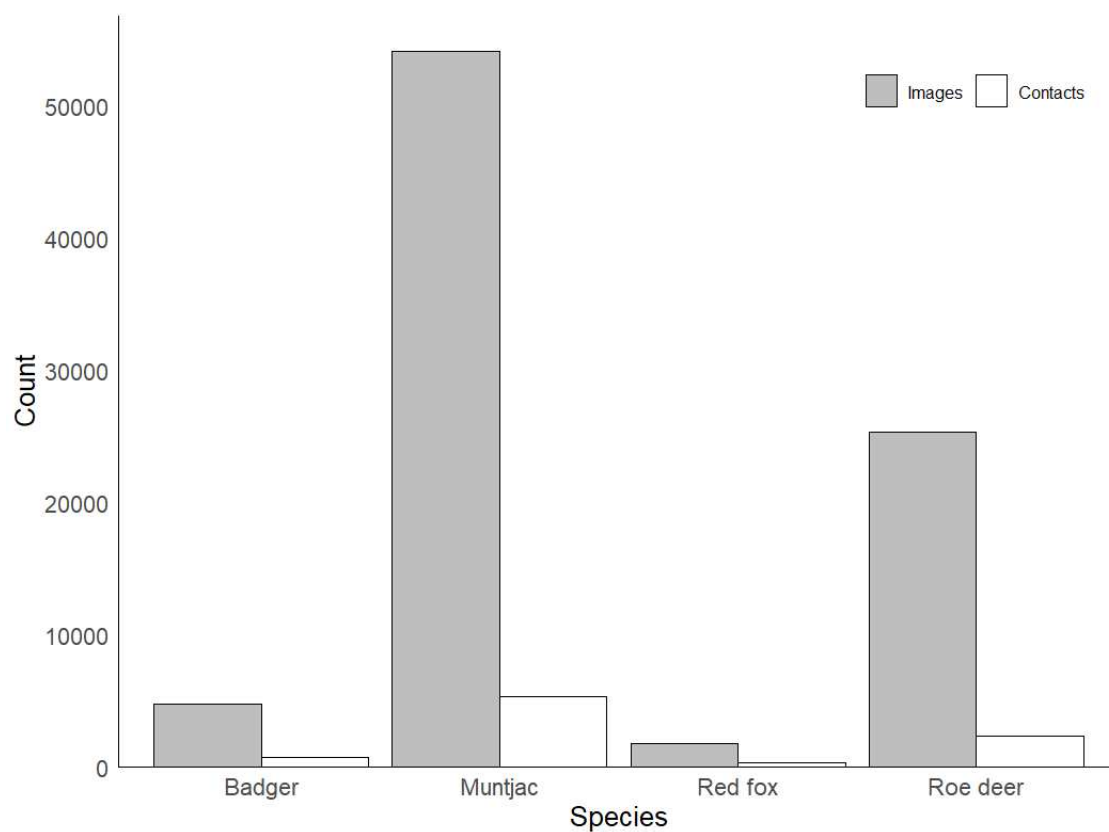
We deployed all 149 cameras and largely adhered to the predetermined camera grid due to the availability of trees for camera attachment in the dense woodland covering most of the study site. The average deviation from the planned location was 11.9m (range 0.5m – 64.2m), with 91.3% of cameras positioned within 20% of the distance between planned locations (24m). Larger deviations occurred in pasture where fewer structures were available for attaching cameras, necessitating placement at field edges. The average deviation from planned locations in pasture was 20.3m (standard deviation (SD) 18.8m) compared to 11.1m (SD 8.0m) in woodland habitats.

Cameras were deployed for eight weeks with 94.6% of cameras remaining active for at least seven weeks. The average deployment time per camera was 53.1 days (SD 2.9 days, range 39.2 – 57.9 days), amounting to a total survey effort of 7,909 camera trap-days. One camera was displaced by cattle and had to be repositioned during the survey.

We obtained 742,087 images during the survey. Of these, 208,468 images contained a wild animal, and 167,495 featured a domesticated animal (cats, dogs or livestock). We recorded nine confirmed species of wild mammal (badger, grey squirrel *Sciurus carolinensis*, brown hare *Lepus europaeus*, hedgehog *Erinaceus europaeus*, muntjac, rabbit *Oryctolagus cuniculus*, red fox, roe deer and stoat *Mustela erminea*), as well as unconfirmed polecat or polecat-ferret, and unidentified bat and rodent species (Fig. 4.3). Our analyses focused on the largest-bodied and most numerous mammals (Fig. 4.4). Of 149 camera traps, 144 recorded at least one of the focal species. Muntjac were recorded on the greatest percentage of cameras (91%), followed by roe deer (87%) and badgers (77%), with red foxes recorded on the fewest (63%). Trap rates followed a similar pattern, with muntjac having the highest average trap rate and red foxes the lowest (Table 4.2).



Figure 4.3 Images representing the range of mammals recorded at Woodchester Park: (a) badger (wearing a GPS collar), (b) grey squirrel, (c) hare, (d) hedgehog, (e) muntjac, (f) polecat/ferret, (g) rabbit, (h) red fox, (i) roe deer (j) stoat, (k) unidentified bat species, (l) unidentified rodent species.



2088 **Figure 4.4** Summary of the representation of the focal species in the camera trap dataset. Unique
 2089 sequences are defined as records in which an animal enters and exits the field of view, with the first
 2090 image in each sequence representing a 'contact'.

Table 4.2 Species-specific density model parameters and density estimates, showing the mean and the associated standard error (in square brackets).

Also shown are the log-normal 95% confidence intervals (CI) and coefficient of variation (CV) of density estimates. All parameters for the random encounter model (REM) and camera trap distance sampling (CT-DS) were estimated from camera trap data.

	Species			
	Badger (<i>Meles meles</i>)	Muntjac (<i>Muntiacus reevesi</i>)	Red fox (<i>Vulpes vulpes</i>)	Roe deer (<i>Capreolus capreolus</i>)
Model parameters				
Shared				
Activity level	0.30 [0.01]	0.34 [0.01]	0.56 [0.05]	0.62 [0.03]
Effective detection angle (radians)	0.66 [0.02]	0.75 [0.01]	0.81 [0.06]	0.84 [0.01]
REM				
Trap rate (contacts/camera/day)	0.09 [0.01]	0.66 [0.08]	0.04 [0.01]	0.29 [0.03]
Speed (m/s)	0.22 [0.02]	0.09 [0.003]	0.33 [0.04]	0.07 [0.01]
Day range (km/day)	5.70 [0.55]	2.67 [0.12]	16.01 [2.42]	3.72 [0.56]
Effective detection radius (m)	5.50 [0.10]	6.08 [0.07]	5.36 [0.19]	5.22 [0.08]
CT-DS				
Truncation distances (left, right; m)	2.0, 7.5	1.5, 8.5	1.7, 9.0	2.0, 7.5
Probability of detection	0.36 [0.01]	0.32 [0.02]	0.34 [0.01]	0.29 [0.01]
Density				
REM				
Estimate (individuals/km ²)	3.6 [0.6]	45.5 [6.1]	0.5 [0.1]	16.4 [2.6]
Log-normal 95% CI	2.6 – 4.9	35.1 – 59.1	0.4 – 0.8	12.1 – 22.3
CV (%)	16	13	22	16
CT-DS				
Estimate (individuals/km ²)	6.0 [1.1]	48.0 [7.7]	0.5 [0.1]	15.1 [7.2]
Log-normal 95% CI	4.4 – 8.8	36.7 – 66.9	0.3 – 0.8	9.4 – 37.7
CV (%)	17	15	24	44

The spatial distribution of camera trap observations across the site showed clear patterns for each species (Fig. 4.5). Badgers and red foxes were observed most frequently (i.e. had the greatest trap rate) in the south-west region. While red foxes were often recorded in the centre of the park near the lakes, badgers were more frequently recorded at the edges of the site, closer to the surrounding farmland. Both deer species tended to avoid the central region of the park. Muntjac were most observed in the southern centre of the park and least observed in the west. In contrast, roe deer showed a more even distribution across the park, with two hotspots in the north and east, not overlapping with the muntjac distribution (Fig. 4.5).

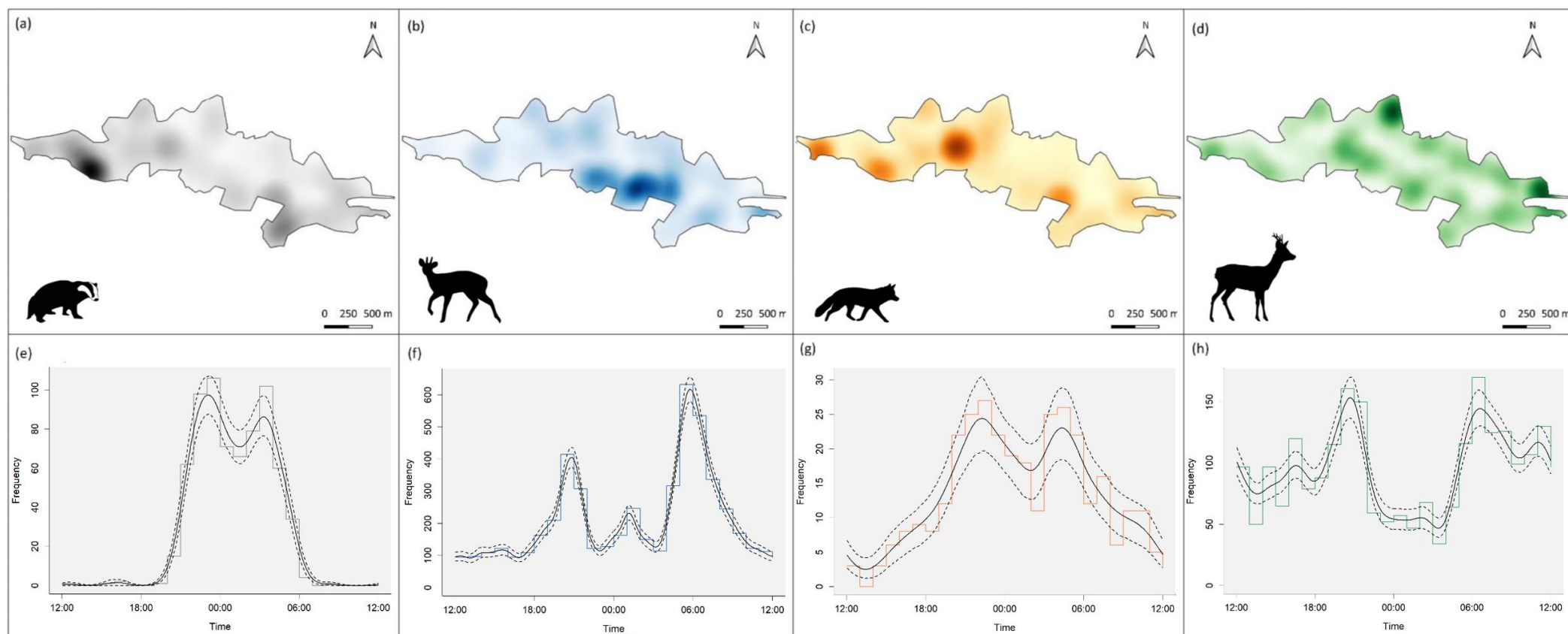
The activity patterns for each species were distinct and aligned with expectations (Fig. 4.5). Badgers were largely nocturnal, while red foxes were also most active at night but exhibited an extended activity period relative to badgers. Both deer species were predominantly crepuscular, although muntjac showed a small peak of activity in the middle of the night.

Roe deer exhibited the largest reactivity to camera traps, with 5.4% of sequences showing reactive behaviour, while badgers showed the least reactivity, at 1.0% of sequences (Table 4.3). The most commonly recorded reactive behaviour was attraction to cameras. Notably, most of the attraction behaviour was observed after the first detection (Table 4.3) and was therefore unlikely to affect the overall trap rate for REM analyses. Consequently, for the REM, we excluded reactive sequences from the estimation of speed and camera trap parameters, but not overall trap rate. Upon inspecting the frequency distributions of animal distances from the camera for CT-DS, we did not observe spikes near zero (Appendix 2, Fig. S3). The final selected CT-DS models were the unadjusted hazard rate model for muntjac and red fox, the hazard rate model with one polynomial adjustment for badgers, and the half-normal model with one polynomial adjustment for roe deer.

Density estimates from the REM and CT-DS methods were similar (Table 4.2; Fig. 4.6) and aligned well with estimates from previously published data, both at this site and sites with similar habitats (Table 4.4). The MNA density estimate for badgers in 2022 was 6.5 badgers per km², comparable to the CT-DS estimate of 6.0 badgers per km² (95% CI 4.5 – 8.9 badgers per km²), but significantly higher than the REM estimate of 3.6 badgers per km² (95% CI 2.6 – 4.9 badgers per km²).

Estimates obtained using the REM were more precise than those from CT-DS, with a CV below 20% for most species, except for red foxes, which also had the highest variability in trap rate and the lowest estimated density. The CT-DS density estimate for roe deer was the least precise estimate and exceeded the 20% CV threshold (Table 4.2). This was likely due to spikes in the frequency distribution of roe deer distances from the camera at 2.8m, 3.8m and 4.2m (Appendix 2, Fig. S4), which resulted in a poor fit of detection functions. As expected, badger density was

2126 substantially lower than previous published estimates for Woodchester Park (Table 4.4). By contrast,
2127 deer were abundant, with muntjac having a particularly high estimated density (Table 4.2).



2128 **Figure 4.5** Species distribution across Woodchester Park (a – d) and activity patterns (e – h) for badgers, muntjac, red foxes and roe deer (left to right). Heat
 2129 maps (above) show species' distribution across the study site, with darker colours representing high trap rate and lighter colours representing low trap rate.
 2130 Activity patterns (below) were characterised by fitting circular kernel models to radian time distributions of camera trap records. Coloured lines represent
 2131 observed frequencies, black curves are fitted circular kernel distributions, and dashed lines show the 95% confidence limits. Species silhouettes were
 2132 sourced from Anthony Caravaggi, Gabriela Palomo-Munoz (licence CC BY-NC-SA 3.0; <https://creativecommons.org/licenses/by-nc-sa/3.0/>) and Ferran Sayol
 2133 (licence CC0 1.0).

2134 **Table 4.3** Species-specific breakdown of animals' reactive behaviour to camera traps. Attraction to cameras was defined as occurring before detection in the
2135 camera's field of view (FOV) if the first image in the sequence was very close to the camera. Behaviour was classified as attraction after detection in the FOV
2136 if normal behaviour preceded looking at the camera and moving towards it.

	Species			
	Badger (<i>Meles meles</i>)	Muntjac (<i>Muntiacus reevesi</i>)	Red fox (<i>Vulpes vulpes</i>)	Roe deer (<i>Capreolus capreolus</i>)
Number of images	4,825	54,178	1,776	25,358
Number of reactive images [proportion of total]	49 [1.02%]	803 [1.48%]	48 [2.70%]	1,366 [5.39%]
Number of unique sequences	782	5,366	328	2,412
Number of reactive sequences [proportion of total]	5 [0.64%]	19 [0.35%]	7 [2.13%]	37 [1.53%]
Category of reactive sequences [proportion of total]				
Attraction (before detection in the FOV)	1 [0.13%]	2 [0.04%]	0 [0.00%]	14 [0.58%]
Attraction (after detection in the FOV)	2 [0.26%]	6 [0.11%]	0 [0.00%]	16 [0.66%]
Freeze	0 [0.00%]	7 [0.13%]	4 [1.22%]	3 [0.12%]
Flee	0 [0.00%]	0 [0.00%]	0 [0.00%]	1 [0.04%]
Mixture of behaviours	2 [0.26%]	4 [0.07%]	3 [0.91%]	3 [0.12%]

2137

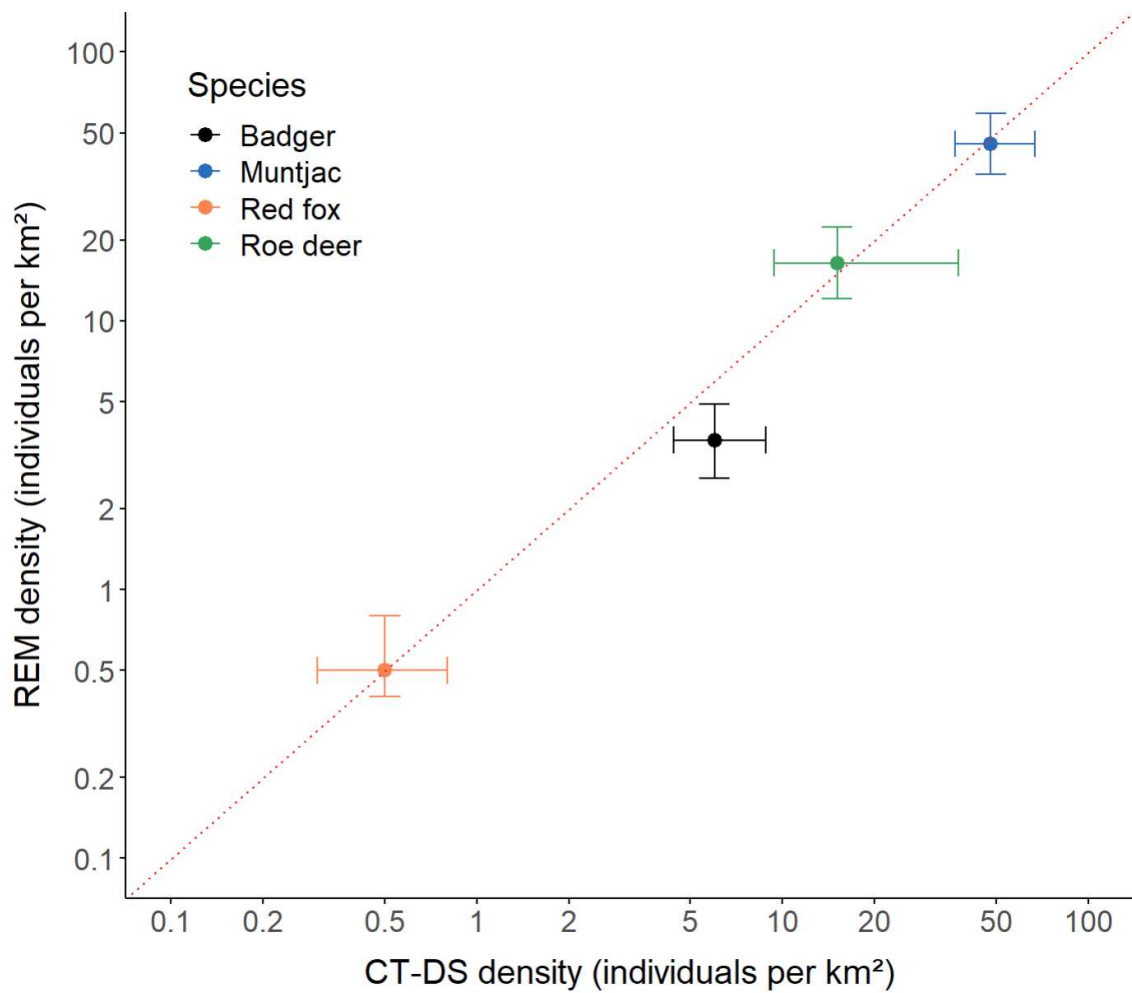


Figure 4.6 Comparison of mammal density estimates using the random encounter model (REM) and camera trap distance sampling (CT-DS) methods, plotted on a log scale. Error bars indicate 95% log-normal confidence limits, and the dotted red line represents the line of equality ($y = x$).

Table 4.4 Density estimates for the four focal species from previously published literature and estimates from the present study included for reference. Literature cited: [1] Delahay *et al.* (2013); [2] Webbon *et al.* (2004); [3] Hemami *et al.* (2007); [4] Hemami *et al.* (2005); [5] Parrott *et al.* (2012); [6] Mason *et al.* (2022); [7] Miles *et al.* (2024; Chapter 2).

Location	Survey area	Habitat	Year(s) studied	Density method(s)	Reference density estimate/km ² [95% CI]				Citation
					Badger (<i>Meles meles</i>)	Muntjac (<i>Muntiacus reevesi</i>)	Red fox (<i>Vulpes vulpes</i>)	Roe deer (<i>Capreolus capreolus</i>)	
Woodchester Park, South West England	6.2 km ²	Broadleaved woodland and pasture	2022	REM	3.6 [2.6 – 4.9]	45.5 [35.1 – 59.1]	0.5 [0.4 – 0.8]	16.4 [12.1 – 22.3]	Present study
				CT-DS	6.0 [4.5 – 8.9]	48.0 [36.7 – 66.9]	0.5 [0.3 – 0.8]	15.1 [9.4 – 37.7]	
Woodchester Park, South West England	7 km ²	Broadleaved woodland and pasture	1982–2005	Capture-recapture	18.4; 39.9 [†]				1
Various pastoral sites across England	31,332 km ²	Pastural, Land Class Group 1*	1999-2000	Faecal density counts	1.9 [1.0–2.7]				2
Thetford Forest, East England	12.8 km ²	Lowland pine forest	2001	Distance sampling	20 [12 – 28]				3
Thetford Forest, East England	185 km ²	Lowland pine forest	2002	Standing crop count	64 [51 – 77]				4
Various sites in Gloucestershire, South West England	242 km ²	Open farmland, predominantly pasture	2006	Distance sampling	4.42 [3.18 – 6.14] 2.41 [1.77–3.26]				5
County Durham, North East England	2725 km ²	Varied including mountainous, grassland, arable and urban habitats	2018	CT-DS	1.3 [0.8 – 4.2] 5.97 [1.37 – 21.15] 5.67 [2.67 – 10.52]				6
Mid-Cornwall, South West England	2.4 km ²	Lowland pasture, arable farmland and woodland	2021	REM; CT-DS; mark-resight	11.7 [6.3 – 22.0]; 13.1 [8.7 – 19.8]; 16.8 [10.4 – 27.1]				7

[†] Densities given are for 1982 and 2005, the first and last years of the study, respectively.

* Woodchester Park is situated within Land Class Group 1, based on the Land Classification System designated by the Centre for Ecology and Hydrology (Bunce *et al.*, 1981)

4.4.2. Changes in badger density

Activity level and badger speed remained consistent throughout the survey period (Appendix 2, Table S5), so we fitted REM and CT-DS models with these parameters fixed at the mean for all time intervals. Both the REM and CT-DS density point estimates indicated no consistent trend in badger density, and the confidence intervals of all density estimates overlapped substantially (Fig. 4.7).

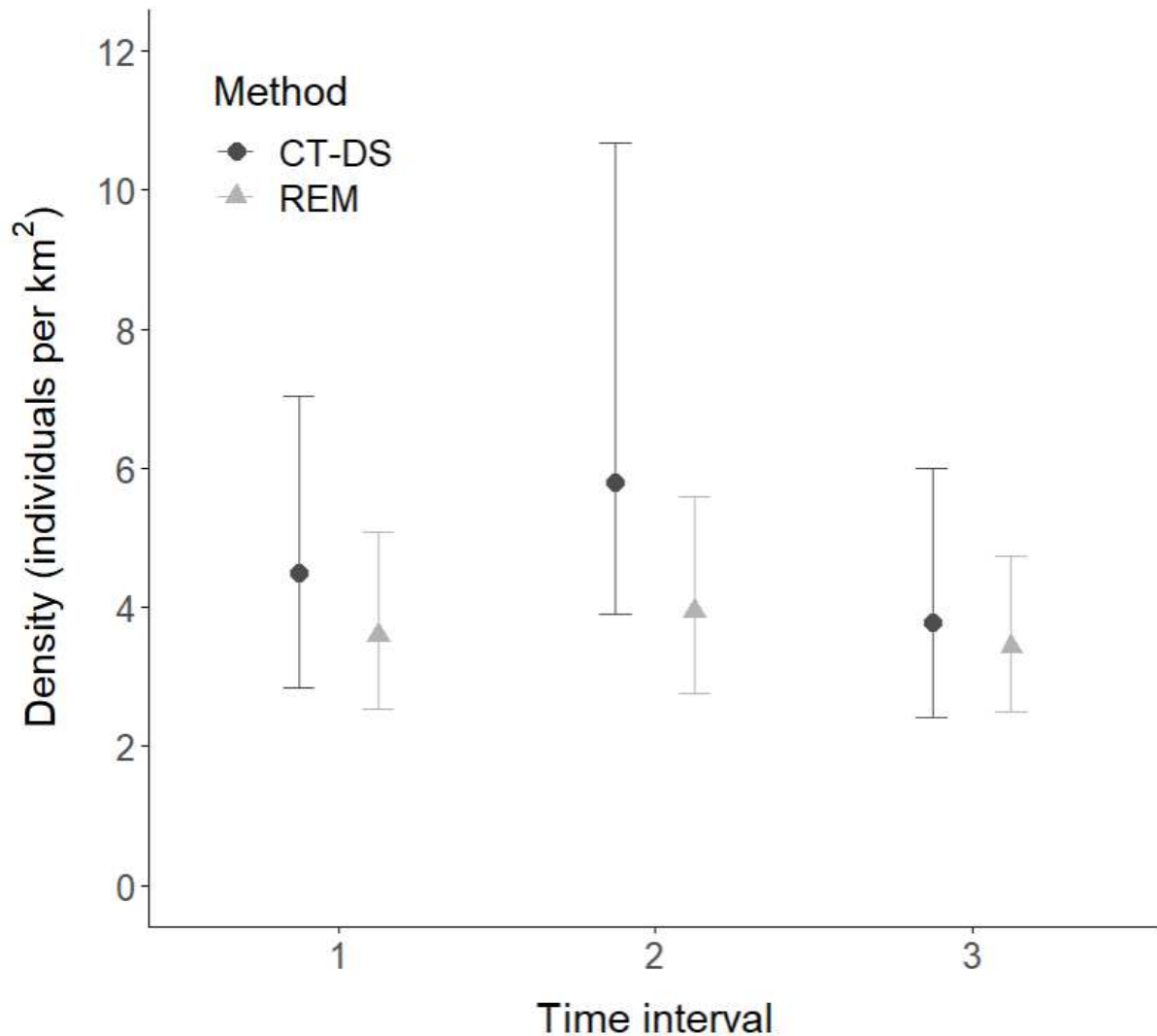
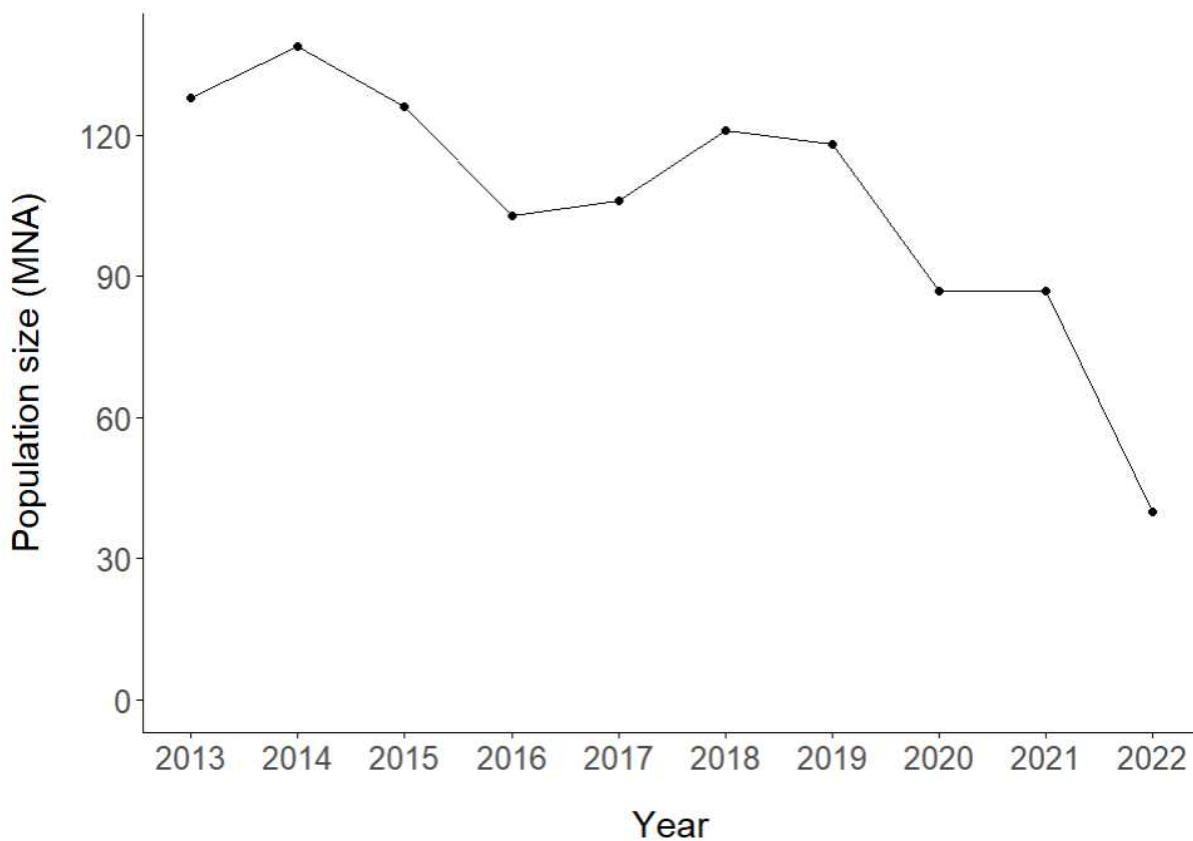


Figure 4.7 Badger density estimated for three consecutive subdivided time intervals of roughly equal survey effort using the random encounter model (REM) and camera trap distance sampling (CT-DS). Each point shows the estimated density (individuals per km²) for a given method, with error bars representing the log-normal 95% confidence limits.

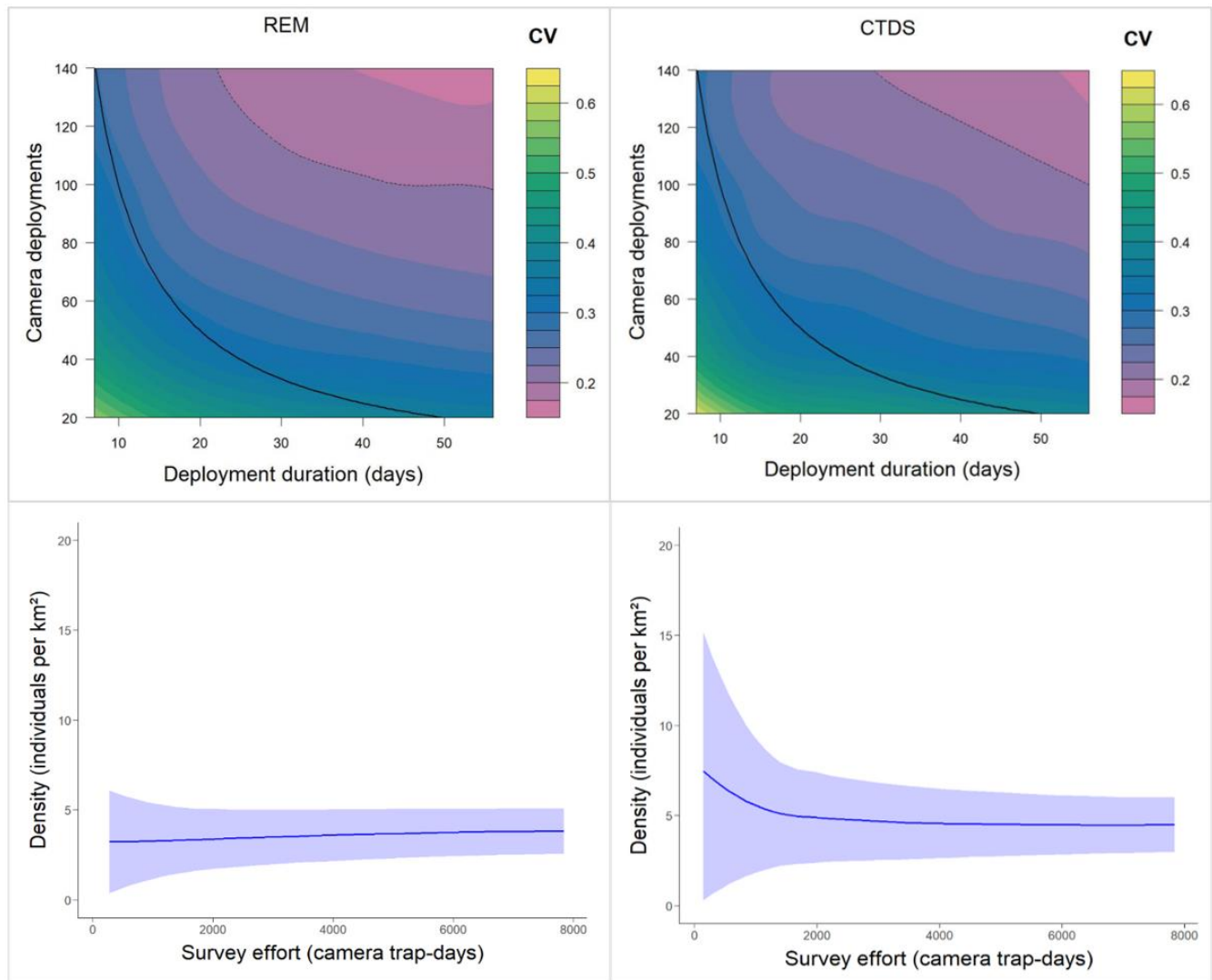
2152 In 2017, before the beginning of culling on nearby land, the MNA population estimate was
 2153 106 badgers. The population declined significantly over a 5-year period from 2017 to 2022 ($R^2 =$
 2154 0.687 , $F(1,4) = 8.77$, $p = 0.004$), declining by 62% over this time, with the steepest decline occurring
 2155 between 2021 and 2022 (Fig. 4.8).



2156 **Figure 4.8** Estimated population size of badgers at Woodchester Park over a ten-year period, using
 2157 capture-recapture data to estimate the minimum number alive (MNA). Trapping occurred
 2158 systematically across the site from May to January each year and badgers were marked with unique
 2159 tattoos to identify individuals (a detailed description of the methodology can be found in McDonald
 2160 *et al.*, 2018). Culling on nearby land started in 2018. From 2018 to 2021 culling operations took place
 2161 over six-weeks annually in the autumn and in 2022, supplementary culling was licensed to take place
 2162 from June until December.

4.4.3. Effort precision analysis for badger density

As expected, analyses of subsets of the data showed that the CV associated with estimates of badger density declined with increasing survey effort (Fig. 4.9), as did the variance of all model parameters. Both density methods required a minimum of 100 camera deployments to achieve a CV of $\leq 20\%$, but the REM required shorter deployment times, achieving a CV of 20% with 100 cameras deployed for 42 days, whereas CT-DS required deployment times of 56 days to reach the same value (Fig. 4.9). Shorter deployment times of 21 days for the REM and 28 days for CT-DS were sufficient when using 140 cameras. Density estimates using the REM were less sensitive to variation in survey effort, in terms of both the number of cameras and deployment times (Fig. 4.9). For a given effort, increasing the number of camera deployments had a greater impact on precision than increasing the deployment duration. There were insufficient data to obtain a standard error estimate for the radius parameter using 20 camera placements with a deployment duration of 7 days, so REM models were not fitted for this effort combination.



2176 **Figure 4.9** Minimum camera survey effort required to reach adequate precision, signified by a
 2177 coefficient of variation (CV) of ≤ 0.20 . Contour plots (above) indicate the precision of badger density
 2178 estimates obtained from the random encounter model (REM) and camera trap distance sampling
 2179 (CT-DS) with varying numbers of camera placements and deployment durations. The dashed black
 2180 line represents a CV of 0.20 and the solid black line represents equal camera effort. Data for each
 2181 combination of cameras and deployment days were subsampled from the observed dataset 1000
 2182 times and used to estimate model parameters and associated standard errors. Line plots (below)
 2183 show the mean badger density estimated using the subsampled models (blue line) and the
 2184 associated 95% confidence limits (ribbon) as a function of overall effort, expressed as camera trap-
 2185 days, covering the ranges of both variables shown in the upper panel.

4.5. Discussion

Our results show that the REM consistently outperformed CT-DS. Across four different species, varying in their trophic level, activity pattern, and estimated density, point estimates for the REM were comparable with those from CT-DS, but invariably more precise (Table 4.2). This greater precision helps to explain why subsampling the data to simulate lower survey effort showed that acceptable levels of precision ($CV \leq 20\%$) could be obtained with fewer cameras and/or shorter deployment times for the REM compared with CT-DS (Fig. 4.9). The badger population in Woodchester Park has declined significantly since 2017 (Fig. 4.6) and density estimates were low relative to previous MNA estimates, likely due to culling activities on nearby land. We discuss these results within the context of wildlife management and the potential implications for policy decisions.

For density estimates to be useful for wildlife management, CV values of $\leq 20\%$ are generally considered necessary (Pollock *et al.*, 1990). However, in planning a survey, predicting the survey effort required to attain this precision is challenging. In practice, the actual effort expended is often dictated by resource availability. From the study of a relatively low-density badger population, we found that the REM density estimates were consistent across a range of effort, with just variation in precision, whereas CT-DS appeared to over-estimate density where survey effort was low (Fig. 4.9). For the REM, precision worsened as survey effort declined, while for CT-DS both accuracy and precision declined. Both density methods required a minimum of 100 camera deployments to reach adequate precision, with the REM achieving a CV of 20% with shorter deployment durations (Fig. 4.9). Specifically, for the REM, 100 cameras deployed for 42 days were necessary to achieve a CV of $\leq 20\%$. Shorter deployment durations of 21 days were sufficient with at least 140 cameras. For CT-DS, achieving a CV of $\leq 20\%$ necessitated 100 cameras deployed for 56 days, or 140 cameras deployed for 28 days. These results are consistent with the recommendations of Rowcliffe *et al.* (2008) and Cappelle *et al.* (2021), who advise using a minimum of 100 cameras for these methods. We also found that, for a given total survey effort, increasing the number of cameras had a greater impact on precision than increasing deployment durations, aligning with the results of these studies (Rowcliffe *et al.*, 2008; Cappelle *et al.*, 2021). Where possible, we recommend using more cameras with shorter deployment durations to maintain the assumption of population closure during monitoring. While a survey comprising 100 cameras requires substantial initial investment, camera surveys are generally cost-effective over time (Welbourne *et al.*, 2015).

Our results suggest that greater survey effort may be necessary to achieve accurate and precise density estimates in low-density populations or in areas with spatial heterogeneity in animal distribution. For the four mammal species studied, both methods mostly met the $\leq 20\%$ CV threshold.

Exceptions included the CT-DS model for roe deer, likely due to poorly fitting detection functions caused by spikes in the frequency distribution of animal distances from the camera at 3 – 4m (Appendix 2, Fig. S4), and the estimates for red foxes, which had the lowest estimated density (Table 4.2) and the highest variability in trap rate. In these cases, a CV of $\leq 20\%$ was not achieved even with 149 cameras deployed for an average of 53 days per camera. This contrasts with Miura *et al.* (2022) who found 50 cameras deployed for three weeks to be sufficient for achieving a CV of 20% using the REM in a comparable low-density (0.5 individuals per km² (95% CI 0.17 – 1.08 individuals per km²)) Asiatic black bear (*Ursus thibetanus*) population. In comparison, Cappelle *et al.* (2021) found that estimates for a population of the western chimpanzee (*Pan troglodytes verus*) with a similar density (≈ 0.5 individuals per km²) did not reach a CV of 20% with 200 cameras deployed for 130 days. These results highlight the importance of spatial distribution, as aggregated data from cameras which vary in their capture rate can lead to imprecise estimates for a given density. While our results provide guidance on the requisite survey effort, we recommend utilising prior ecological knowledge of density and animal distribution, as a result of factors such as social behaviour and habitat selection, to inform survey design. Bias could also be mitigated with stratified survey designs if heterogeneity is linked to specific habitat variables, by estimating density within specific habitat types and calculating a weighted mean based on the proportional area or time spent in each habitat (Cusack *et al.*, 2015b).

The density estimates of the four mammal species were similar between the REM and CT-DS (Fig. 4.6; Table 4.2), supporting previous studies which found consistency between these methods (Jayasekara *et al.*, 2021; Palencia *et al.*, 2021). However, the REM badger density estimate was significantly lower than the MNA badger density. Given cage-trapping may only represent a trappable subpopulation and MNA estimates are likely to be biased low, these results suggest that the REM may have underestimated badger density. However, it is possible that the MNA estimate in our study actually reflects an over estimate of the number of animals alive during time the site was surveyed with camera traps. Our MNA estimates denote the minimum number of badgers alive during a given year. In 2022, supplementary culling on nearby land started on 1st June, and a number of marked badgers were removed before the camera trap survey began on 20th June (the exact number of animals killed is not reported in this thesis due to data privacy restrictions). These badgers could have therefore been trapped in May and contributed to the population estimate but have been removed from the population before the camera survey. Similarly, cubs, which can be trapped and marked from 1st May (DEFRA, 2021a), may have contributed to population estimates but could have died before the camera surveys started, as juvenile mortality rate is high (Rogers *et al.*, 1997). As such, although the CT-DS point density estimate was closer to the MNA density estimate than the REM, we cannot be certain which result is the most accurate.

Independent validation of the density methods for species other than badgers was not possible, but our results align with previously published data (Table 4.4), supporting the use of these methods to estimate the density of unmarked mammals. Exceptions were noted with the badger density estimates from Delahay *et al.* (2013) and the fox density estimate from Mason *et al.* (2022), which were both considerably higher than our density estimates for these species. However, both species in our study were likely impacted by culling operations on nearby land (detailed subsequently in this discussion), which may explain the lower densities. Similarly to Palencia *et al.* (2021) and Twining *et al.* (2022) we found that both methods had similar precision, although the REM slightly outperformed CT-DS and may therefore be the preferred method when precision is critical.

Our study provides the lowest density estimate for badgers in Woodchester Park to date, likely due to culling on nearby land. Our MNA calculations suggest that the badger population declined by 62% between 2017 to 2022, with the largest decline noticed between 2021 and 2022 (Fig. 4.8). Thus, despite not targeting the park itself, culling appears to have significantly reduced the badger population in Woodchester Park, particularly after the initiation of supplementary culling. This highlights the broad impact that badger culling can have, extending beyond the boundaries of the cull zone, as documented in the proactive areas of the Randomised Badger Culling Trial (RBCT) (Woodroffe *et al.*, 2006a). Though the exact number of badgers removed on land adjoining Woodchester Park is unknown, during the study period a number of GPS collars were returned from badgers which had been shot on nearby land but collared in the park, suggesting the population may have been reduced. As such, our finding that there was no detectable decline in badger density during the survey period (Fig. 4.7) may not be accurate. However, since culling disrupts badger social structure and movement behaviour (Woodroffe *et al.*, 2006a; Ham *et al.*, 2019), this result could be explained by more badgers moving into vacated territories within the park in response to local culling.

We found a comparatively low density of red foxes in the park (Table 4.2), which is surprising. During the RBCT, fox numbers doubled in areas where large-scale badger culling occurred (Trewby *et al.*, 2008). Foxes and badgers may compete for food and den sites (Neal & Cheeseman, 1996), and our data indicate similar activity patterns and spatial usage between the two species. Since fox numbers are not managed within Woodchester Park, we hypothesise that the low fox density may result from population management on surrounding farms, potentially differing from the RBCT scenario where only badgers were controlled. However, data suggest that foxes are generally declining across the UK (BTO, 2023). Without prior fox density estimates for the park, it is unclear whether the current relatively low density reflects a longer-term pattern.

Our results suggest that the population density of muntjac in Woodchester Park was approximately three times that of roe deer (Table 4.2), with both species exhibiting high densities despite population control measures. Higher densities have been recorded for both species in similar landscapes (e.g. Gill *et al.*, 1996; Hemami *et al.*, 2005; Harris & Yalden, 2008) and the densities at Woodchester Park align with high deer numbers reported across England (Harris *et al.*, 1995; Fuller & Gill, 2001; Ward, 2005; Ward *et al.*, 2021). Such high population densities could threaten local biodiversity, as deer can have a negative impact on woodland vegetation, bird diversity, and many rodent species (Flowerdew & Ellwood, 2001; Morecroft *et al.*, 2001; Gill & Fuller, 2007). Additionally, deer contribute to the transmission of range of infectious diseases (Böhm *et al.*, 2007), including Lyme's disease, which is spread by the tick *Ixodes ricinus*. Since the density of *I. ricinus* is strongly correlated with the abundance of suitable hosts (Andersen *et al.*, 2018), the high deer densities in Woodchester Park could create a potential public health risk, though both species tended to avoid areas of the park frequented by people (Fig. 4.5).

Although camera traps are widely viewed as minimally intrusive, their presence can still alter animal behaviour which challenges this assumption (Fig. 4.2). We observed some reactive behaviour to camera traps, with 'attraction' being the most common, though this pattern varied between species (Table 4.3). Generally, the proportion of reactive sequences was lower than that reported for the same species elsewhere (Henrich *et al.*, 2020; Miles *et al.*, 2024, Chapter 2). Reactivity to camera traps can introduce bias in both the REM and CT-DS methods, which both assume random animal movement relative to cameras. The best approach to mitigate this bias depends on the observed behaviour type. For example, attraction to the camera is likely the most substantial source of bias in both methods, while freezing does not seem to affect density estimates (Delisle *et al.*, 2023). For the REM, the standard approach is to exclude reactive sequences from the estimation of speed and camera detection zone parameters (Rowcliffe *et al.*, 2008; Palencia *et al.*, 2021). Delisle *et al.* (2023) also recommend removing these encounters from the overall trap rate, assuming animals are attracted to the camera before detection in the FOV, thus affecting the first contact. However, in our study, most 'attraction' occurred after the animal was already detected by the camera, with normal behaviour preceding the point at which the animal looked at the camera (Appendix 2, Fig. S2). Since attraction before detection in the FOV affected only 0.19% of encounters (Table 4.3), we concluded that removing all reactive sequences from the trap rate parameter was unnecessary.

For CT-DS, attraction to camera traps can lead to an excess of observations close to the camera. To address this issue, it is recommended to left truncate the data (Cappelle *et al.*, 2019), remove reactive sequences completely (Bessone *et al.*, 2020; Houa *et al.*, 2022), and avoid using the

hazard rate detection function, which may better accommodate spikes near zero (Delisle *et al.*, 2023). Given that attraction was the primary source of reactivity in our study (Table 4.3), we intended to follow the corrective strategy outlined by Delisle *et al.* (2023). However, detection function models should decline monotonically, since the probability of detection is assumed to decline with distance from the camera. We found that, for badgers and red foxes, alternatives to hazard rate models did not decline with increasing distance, therefore necessitating the use of hazard rate models in these cases. For muntjac, freezing constituted the highest proportion of reactive sequences (37%) and we did not observe spikes near zero in our data, so we included hazard rate models in our selection process. Although roe deer exhibited the most attraction to camera traps, we observed several spikes in the detection distance data between 3 – 4m (Appendix 2, Fig. S4). This suggests that roe deer might be deterred by the cameras, maintaining a distance without displaying clear reactive behaviours. Consistent with this hypothesis, similar to Henrich *et al.* (2020), we found that roe deer rarely looked directly at the camera. If this is the case, such behaviour, akin to complete avoidance of camera traps, is more challenging to detect, and to adjust for the resulting bias (Delisle *et al.*, 2023).

Our study demonstrates that accurate and precise ($CV \leq 20\%$) density estimates can be achieved using camera-based methods, and near-acceptable precision ($CV 22\%$) is achievable where the density is as low as 0.5 individuals per km^2 (Table 4.2). This finding is crucial for monitoring rare, cryptic and/or elusive species and managing wildlife populations effectively. Implementing similar survey designs in animal management strategies may enhance the monitoring of population changes. Additionally, our results provide practical guidance on the required effort for camera trap field surveys, and the choice of analysis methods, based on resource availability. By refining these techniques, we can better inform conservation and wildlife management efforts and ensure more accurate assessments of wildlife populations.

- 2342 **5. Chapter 5: Application of camera-based population monitoring to estimate**
2343 **vaccination coverage of badgers (*Meles meles*) following repeated**
2344 **widespread badger culling**



- 2345 *A camera trap deployed on a cattle farm.*

5.1. Abstract

The control of bovine tuberculosis (bTB) is a formidable animal health challenge. In England, the bTB eradication policy is shifting emphasis from badger culling to badger vaccination, with rapid expansion of vaccination into previously culled areas anticipated in coming years. However, post-cull badger vaccination is a novel approach, and its effectiveness has not yet been evaluated empirically. The effectiveness of any vaccination approach depends in part on achieving sufficient coverage, but previous studies have found that badger capture rates are lower in populations with a recent history of culling, potentially reducing the ability of vaccination to curb transmission. In this study, we estimated vaccination coverage at two post-cull sites in Gloucestershire, UK. We compared the number of vaccinated badgers with population estimates derived from two camera-based methods, the random encounter model (REM) and camera trap distance sampling (CT-DS). We also evaluated the monitoring effort required to estimate badger density over several years and the suitability of integrating these methods into vaccination projects, considering financial costs and resource constraints. While apparently high vaccination coverage was achieved in some analysis scenarios, the small geographic scale of the study and imprecision in density estimates resulted in high statistical uncertainty. This uncertainty could be reduced by monitoring coverage over larger temporal and spatial scales. Camera traps proved to be an effective tool for monitoring changes in badger density, as the methods explored could detect increases in density with sufficient statistical power ($\geq 80\%$; when population growth rate was 25% annually) and were cost-effective relative to alternative methods. However, surveys spaced 24 or 36 months apart were necessary to detect such changes, suggesting long-term monitoring is required. Overall, our findings support the integration of population monitoring in post-cull badger vaccination efforts over large areas, with badger density assessed in surveys conducted at least every 24 months, to fully evaluate the effectiveness of this strategy.

5.2. Introduction

In Britain, the spread of bovine tuberculosis (bTB), a zoonotic respiratory disease of cattle caused by the bacterium *Mycobacterium bovis* (*M. bovis*), is a chronic animal health problem (Krebs, 1997). Current policy in England stipulates that if bTB is suspected or confirmed in a cattle herd (referred to as a 'bTB breakdown') the reactors² must be slaughtered and the entire herd placed under restriction, affecting the movement and sale of cattle and milk products (DEFRA, 2024c). Although compensation is available for any compulsorily slaughtered cattle, the expenses associated with

² An animal which has failed a tuberculin skin test, a gamma interferon blood test, or other approved bTB test, or has had two consecutive inconclusive test results.

2378 complying with testing regulations and movement restrictions, which often represent the biggest
2379 costs, are borne by farmers (Barnes *et al.*, 2023).

2380 Badgers (*Meles meles*) were identified as wildlife hosts for *M. bovis* in 1971 (Muirhead *et al.*,
2381 1974) and subsequent research has provided strong evidence that they can contribute to the
2382 persistence of the disease (Griffin *et al.*, 2005; Donnelly *et al.*, 2007; Donnelly & Hone, 2010;
2383 Donnelly & Nouvellet, 2013; Crispell *et al.*, 2019; van Tonder *et al.*, 2021). As a result, over the last 50
2384 years, policy to control bTB has focused on managing the disease in cattle by mandatory test and
2385 slaughter and attempting to control bTB transmission from badgers to cattle through badger culling
2386 and, to a much lesser extent, badger vaccination (Benton *et al.*, 2020). England is categorised into
2387 three epidemiological areas, and the intensity of bTB measures, such as badger control and herd
2388 testing, are determined by the expected risk of infection (DEFRA, 2014). Under the current bTB
2389 eradication strategy, which was introduced in 2013 (DEFRA, 2014), intensive badger culling can be
2390 licensed in any of these risk areas but is carried out most extensively in high risk and edge areas
2391 (those in between high and low risk areas where there is an intermediate incidence of bTB) (DEFRA,
2392 2014). Intensive industry-led culls aim to remove $\geq 70\%$ of the badger population in the first year and
2393 maintain a reduced population density in successive years (DEFRA, 2023b). Following the completion
2394 of four years of intensive culling, supplementary culling may then be licensed, with the aim of
2395 preventing badger populations from recovering. In the policy, badger vaccination was considered an
2396 exit strategy from badger culling (DEFRA, 2011) and policy updates have put greater emphasis on this
2397 approach in recent years, with the intention of gradually phasing out intensive culling and expanding
2398 government-supported and farmer-led badger vaccination (DEFRA, 2020, 2024d). To date, a limited
2399 number of four-year government-led badger vaccination initiatives have been established in former
2400 cull areas which have completed intensive culling requirements (DEFRA, 2024a). Cattle herd testing is
2401 maintained in badger vaccination areas, and further research is intended to analyse the impact of
2402 badger vaccination on bTB incidence in cattle (DEFRA, 2024d).

2403 Modelling suggests that post-cull badger vaccination could be more effective than either
2404 culling or vaccination conducted independently (Smith & Budgey, 2021). However, there has been
2405 limited empirical assessment of the impact of badger vaccination (post-cull or otherwise) on herd
2406 incidence (APHA, 2016c, b; Martin *et al.*, 2020). Whether vaccination influences disease transmission
2407 depends on, among other factors, the efficacy of the vaccine and what proportion of the population
2408 receives it (or 'vaccination coverage'). Three known studies to date that have attempted to estimate
2409 vaccination coverage in uncultured badger populations found that coverages of $\geq 50\%$ can be achieved
2410 (Benton *et al.*, 2020; Smith *et al.*, 2020; Woodroffe *et al.*, 2024), surpassing the minimum coverage of
2411 30% estimated to be necessary to eliminate bTB from badger populations (Aznar *et al.*, 2018).

2412 However, there are concerns that post-cull badger vaccination may fail to achieve the coverage
2413 needed to reduce *M. bovis* transmission (Benton *et al.*, 2023). Vaccination delivery to badgers relies
2414 on live trapping, since injection with the Bacille Calmette-Guérin (BCG) vaccine is the only method
2415 currently licensed for badgers in the UK (DEFRA, 2011). Trappability (the percentage of all individuals
2416 known to be alive in the population that are captured; Tuytens *et al.*, 1999) will therefore have a
2417 major impact on vaccine delivery, and consequently the effectiveness of this approach. Tuytens *et*
2418 *al.* (1999) found that trappability decreased the year following badger culling operations. If culling
2419 were to make badgers more difficult to trap, vaccination would potentially be less effective in post-
2420 cull populations than in undisturbed populations.

2421 Estimating vaccination coverage requires comparison of the number of vaccinated badgers
2422 with an estimate of the number of badgers present, but this process is often hindered by reliance on
2423 estimates of badger density, which can be biased and imprecise (Woodroffe *et al.*, 2008; Benton *et*
2424 *al.*, 2020). Achieving sufficient precision is likely to be particularly challenging immediately post-cull,
2425 when previous studies have found badger numbers to be substantially reduced (Woodroffe *et al.*,
2426 2008). However, population size and vaccination coverage are both expected to increase in
2427 successive years after culling stops, as the population recovers, and less ‘trap-shy’ cubs are recruited
2428 into the population (Tuytens *et al.*, 1999; Byrne *et al.*, 2012). These larger numbers are likely to
2429 generate more precise estimates of density and coverage. As such, estimating badger density and
2430 vaccination coverage as a snapshot in the first-year post-cull may be insufficient; monitoring over
2431 several years is likely necessary to assess the effectiveness of badger vaccination (Byrne *et al.*, 2012).

2432 Within this context, we aimed to estimate (1) the vaccination coverage achieved at two post-
2433 cull sites in England, (2) the level of monitoring needed to detect increases in badger density over
2434 four years post-cull, and (3) the financial costs of conducting such assessments. We assessed
2435 vaccination coverage by comparing the numbers vaccinated with population size estimates derived
2436 from two camera-based methods of estimating badger density – the random encounter model (REM)
2437 and camera trap distance sampling (CT-DS). Building on evidence of the accuracy and precision of
2438 camera-based methods for population estimates at a single time point (Miles *et al.*, 2024, Chapter 2;
2439 Chapter 4), we evaluated their suitability for long-term population monitoring. First, we assessed
2440 their power to detect increases in badger density over four years, given the survey design and
2441 sample size (the number of cameras and days of image collection) used in this study. We also
2442 analysed the expected cost and resource requirements of integrating camera-based population
2443 monitoring in a post-cull badger vaccination framework.

5.3. Materials and methods

5.3.1. Study area

Two areas within the high risk area of England (Fig. 5.1), had been selected for badger vaccination delivery over four years, following several years of widespread industry-led culling (DEFRA, 2024a). We identified a study site within each of these areas (Table 5.1), each consisting of contiguous farms where landowners consented to take part in a camera trapping survey in addition to badger vaccination. Site A consisted of farms totalling 5.05km² within a vaccinated area of 357km² in Gloucestershire and Wiltshire. Site B consisted of farms totalling 1.98km² within a vaccinated area of 109km² in Gloucestershire (Fig. 5.1). This study was conducted in the first-year post-cull at site A and the second-year post-cull at site B.

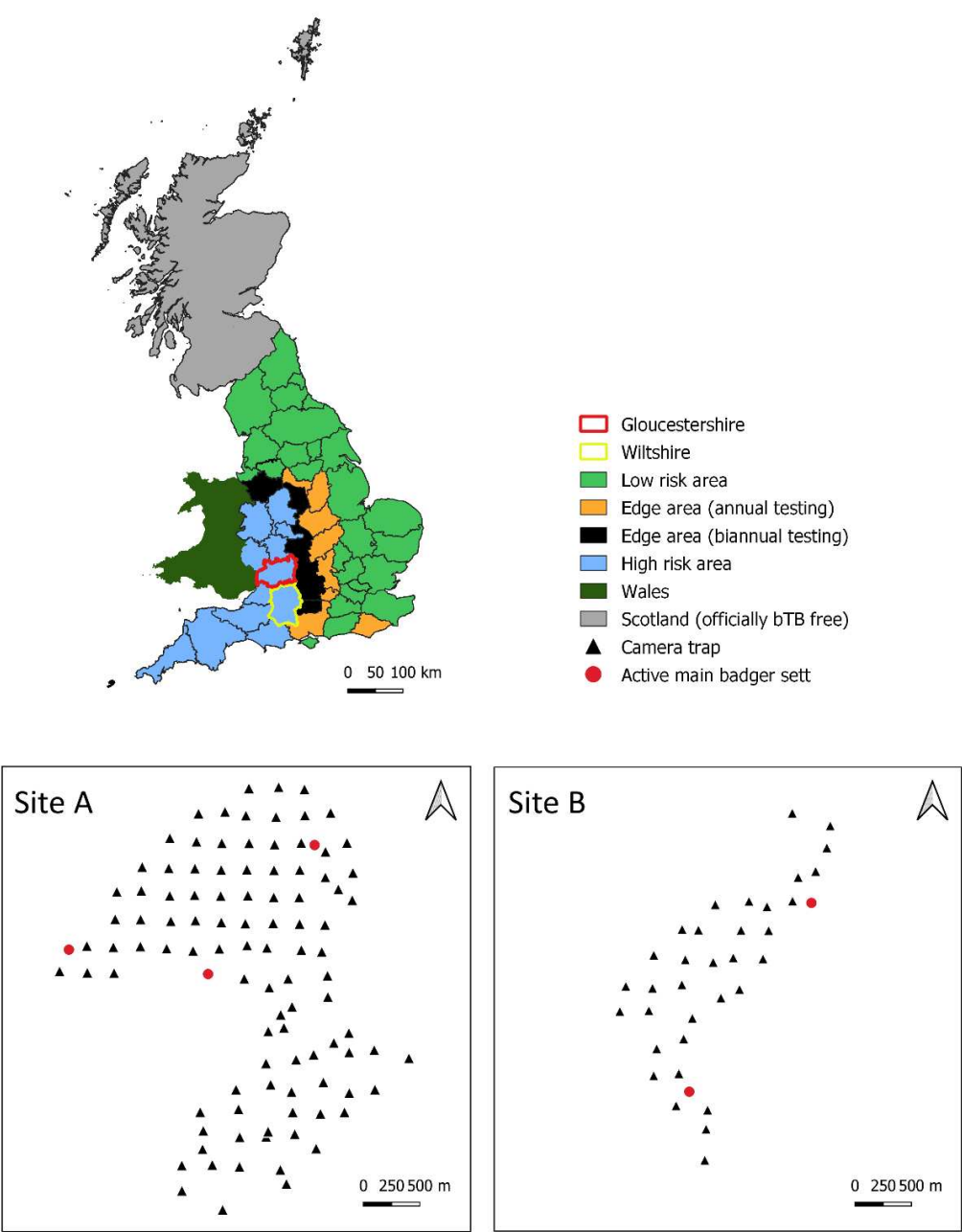
5.3.2. Camera trap surveys

Camera trap surveys were conducted prior to vaccination, from 6th March until 27th April 2023, to avoid interference with vaccination-related badger cage trapping, which was permitted from 1st May (DEFRA, 2021a). Both the REM and CT-DS necessitate random camera placement. To adhere to this requirement, camera locations were planned using GridMaker (Rowcliffe, 2021c) to generate a grid of randomised origin for each site, with the nodes of the grid representing camera locations. These grids comprised 100 camera locations spaced 225m apart at site A, and 34 camera locations with a spacing of 245m at site B.

In the field, we located the coordinates of each planned camera placement then attached cameras (Browning Strike Force HD Pro X) to the nearest suitable object. We aimed to keep cameras within 20% of the distance between planned coordinates, which was 45m at site A and 49m at site B. Cameras were fixed at a height of approximately 40cm, facing a direction with a clear field of view (FOV). Where necessary, we removed vegetation within the FOV which could falsely trigger the camera. We did not use bait, to minimise any influence of the cameras on animal behaviour. Cameras were programmed to take a single still image with each trigger, for 24 hours per day, with no time lapse and a 1-second passive infrared trigger interval. Once each camera was in its final position, the deployment was calibrated by taking images of a calibration pole (a 1m pole marked at intervals of 20cm) placed at ≥20 positions, at a range of angles and distances from the camera (Wearn *et al.*, 2022). All SD cards and batteries were replaced after 24 days, around the midway point of the survey, and then deployments were recalibrated in case of any small shifts in the FOV caused by opening the camera case. Deployments were also recalibrated a final time upon collecting cameras.

To calculate the real-world radial and angular distances of badgers and calibration poles from the camera, we took a series of images in a controlled setting from which to build calibration models.

2477 This involved setting up one camera in a flat location with a clear FOV, at a height of 40cm. We
 2478 measured fixed distances from the camera (1m – 6m) and moved around the FOV with the
 2479 calibration pole to obtain images of the pole at a range of angles and fixed distances.



2480 **Figure 5.1** Classification of bTB risk areas in England and the location of Gloucestershire (outlined in
 2481 red) and Wiltshire (outlined in yellow) within the high risk area (top). Insets (bottom) show realised
 2482 placements of camera traps at site A (100 cameras in 5.05km²) and site B (34 cameras in 1.98km²),
 2483 each located within wider areas included in badger vaccination delivery, and the locations of active
 2484 main badger setts. Precise locations of study sites are not mapped to ensure landholder
 2485 confidentiality.

2486 **Table 5.1** Details of two sites selected for badger vaccination and camera surveys to estimate badger
2487 density. Intensive culling operations took place for six weeks from October to November annually;
2488 supplementary culling was licensed from June to January annually. Camera trap surveys were
2489 conducted in 2023.

	Study site	
	A	B
Study site area	5.05km ²	1.98km ²
Number of years of intensive culling prior to vaccination	4	4
Number of years of supplementary culling prior to vaccination	2	5
First year vaccinated	2023	2022
Habitat and farming practices	Farmland; semi-managed woodland	Farmland; flood plain
Farming practices	Arable; sheep grazing	Arable; sheep and cattle grazing

2490

2491

2492 5.3.3. Image processing

2493 Images were annotated (or ‘tagged’) manually using XnView MP (version 0.99.6; Gougelet, 2020).
2494 Those containing identifiable people and vehicles were then removed before further image
2495 processing. For images containing wild mammals, we tagged the species, the first image in each
2496 unique sequence (defined as an individual animal entering and exiting the FOV, referred to as a
2497 ‘contact’), and the total number of each species present in each image. We also differentiated images
2498 in which animals appeared to be reacting to the camera, and classified such reactive behaviour as
2499 one of four categories: attraction (the animal looks at the camera and moves towards it); freeze (the
2500 animal looks at the camera and remains in a fixed position); flee (the animal looks at the camera and
2501 is startled by it, moving rapidly away); or a mixture of these behaviours.

2502 Badger and calibration images were isolated and then digitised using AnimalTracker (Vargas
2503 Zarco, 2019) to obtain position data used for further analyses. For calibration images, we marked the
2504 lowest and highest visible 20cm measures on each pole placed on the ground in a unique position.
2505 For badger images, we recorded the positions of badgers in each image by marking the point on the
2506 ground directly below each animal’s centre of mass. If the camera was moved during deployment
2507 (for example, as a result of being knocked by cattle or people) and the new position did not have a

corresponding set of calibration images, we stopped digitising badger sequences after this point as it was not possible to estimate angles and distances accurately. Camera calibration images taken in the controlled setting were digitised similarly, with the additional step of recording the radial distances of poles from the camera.

5.3.4. Badger density

We estimated badger density using two camera-based methods for unmarked animals, the REM and CT-DS, following the equations detailed in Rowcliffe *et al.* (2008) and Howe *et al.* (2017), respectively (Miles *et al.*, 2024; Chapter 2). These approaches share some model parameters, as detailed below, which were estimated using data from camera images exclusively. Since camera traps were deployed in March and April, typically before badger cubs explore beyond the den site or ‘sett’ (Neal & Cheeseman, 1996), we assumed that the estimates represented the density of the adult population. All analyses were completed in R (R Core Team, 2021) unless otherwise stated.

Both density models utilised data from the positions of badgers in images to estimate model parameters. To estimate radial and angular distances, we used the digitised camera calibration data to build camera calibration models and fitted these to calibration data from digitised deployment images using the ‘CTtracking’ package (Rowcliffe, 2021b). Using the ‘Distance’ package (Miller *et al.*, 2019), we fitted detection function models to badger position data from the first image of each sequence to estimate the effective detection angle and radius, which are used in both models. In addition, for the REM, we used badger positions to estimate average speed while active. After removing any reactive sequences from the data (following Miles *et al.*, 2024; Chapter 2), we divided the total distance badgers travelled in each sequence by the duration of each sequence using the time stamp on the images, and then used the ‘camtools’ package (Rowcliffe, 2021a) to find the harmonic mean of these speed observations (Rowcliffe *et al.*, 2016).

The proportion of time spent active (hereafter referred to as ‘activity level’) is employed by both models to account for the amount of time that animals were available for detection. We used the ‘activity’ package (Rowcliffe *et al.*, 2014) to fit circular kernel distribution models to the radian times of day of the first image of each badger sequence. Following the method detailed by Rowcliffe *et al.* (2014), we assumed that the entire population was active and potentially detectable on cameras when the activity probability density function was at its peak in the daily cycle. To estimate day range (the daily distance travelled) for the REM, travel speed (in metres per second) was first converted to km per day by multiplying travel speed by the number of seconds in a day and dividing that value by 1,000. The resulting travel distance (km per day) was then multiplied by the activity level to calculate the estimated day range (Rowcliffe *et al.*, 2016).

Temporal survey effort is considered in both density estimation models but is calculated differently in each. In the REM, effort is given by the number of camera trap-days, which is a function of the number of camera traps and the time for which each was operational. Trap rate is then given by dividing the number of badger contacts by the temporal survey effort in camera trap-days. By contrast, in CT-DS, each image of an animal in a sequence is regarded as a unique detection record, and temporal effort is given by the time each camera was available to capture data. In our study, cameras were operational 24h per day and were programmed to take still images. Since there is usually a short delay or 'interval time' between successive image triggers, cameras cannot take images for the entire period they are operational. Temporal effort is therefore given by the time each camera was operational (in seconds) divided by the interval time, which gives the number of 'snapshot moments' when each camera was able to take images. Though we programmed the interval time to be 1s, we also estimated it empirically by taking the duration of each badger sequence divided by the number of intervals between images within the sequence.

5.3.5. Badger vaccination

Cage trapping and vaccination of badgers were carried out by the Animal and Plant Health Agency under licences issued by DEFRA and Natural England, following best practice guidance (DEFRA, 2021a). Badger ecologists surveyed sites for signs of badger activity in winter months, before each camera survey, recording the location of active badger setts, runs and latrines. Badger cage trapping and vaccination occurred the following May – August after the camera surveys and during the open season for badger vaccination. We deployed 22 cage traps at Site A and 5 cage traps at site B, and pre-baited each with peanuts for 7-10 days. Following this acclimatisation period, traps were baited and set for two (or three, when necessary) consecutive nights and checked at first light each morning. Any captured badgers were given a welfare assessment, before being vaccinated intramuscularly using 1ml of the BCG vaccine reconstituted with Sauton diluent (AJ Vaccines, Denmark). Before being released, each vaccinated animal was given a temporary mark by clipping a small patch of fur on the middle of the back and spraying the mark with livestock marking spray. After the first morning of vaccination, any previously marked badgers were released without being re-vaccinated, and any unmarked badgers were vaccinated, marked and released. For each captured badger, we recorded the location, age class (i.e., cub or adult), any welfare concerns, and the recapture status.

5.3.6. Vaccination coverage

To estimate what proportion of each badger population was vaccinated, it was first necessary to delineate the size of the area used by the badgers which inhabit the farms. This is challenging at the farm-scale because badger social group home ranges seldom align with farm boundaries and, in this study, methods of delineating social group home ranges directly, such as bait marking (Delahay *et al.*, 2000) or GPS collaring (Ham *et al.*, 2019; Barbour *et al.*, 2024) were not implemented. Social group territories can be approximated using the locations of main setts and latrines, following the Dirichlet tessellations method developed by Doncaster and Woodroffe (1993). However, we decided this approach was not suitable for this analysis for two reasons. Firstly, the Dirichlet tessellations method assumes a stable territorial structure which is unlikely to exist in a post-culling landscape due to the disruption caused by reducing the population density of badgers (Woodroffe *et al.*, 2006a; Woodroffe *et al.*, 2009a; Ham *et al.*, 2019). The impacts of badger culling, including increases in badger home range size and home range overlap, may endure for several years after culling ends (Tuytens *et al.*, 2000a; Woodroffe *et al.*, 2006a; Carter *et al.*, 2007; Bielby *et al.*, 2014). Secondly, information which can improve the reliability of Dirichlet tessellations, such as the locations of badger setts in the wider landscape, the locations of badger latrines, and knowledge of habitat features which might restrict badger movement, were not available for these study sites.

We therefore adopted three alternative methods for estimating the extent of the area occupied by badgers in the area vaccinated. First, we used the size of the study site delineated by the outermost farm boundary (the ‘targeted area’; method 1, Table 5.2), assuming this represented the smallest possible area vaccinated, as vaccination operations target farms. However, since badgers may have ranged beyond farm boundaries, the area occupied by the badgers using the targeted area is likely to be larger than the targeted area itself. In our second method of estimating the area vaccinated, we assumed a circular home range around each active main sett, using post-cull social group home range estimates from Bielby *et al.* (2014) (included in Appendix 3, Table S6) to limit the size of the circles (method 2; Table 5.2). Active main setts were identified using badger survey data and trapping records, with the number of active holes and badgers caught at each sett used as indicators of sett activity. The radius of the circular home range was calculated as the square root of the estimated home range divided by π . The total area occupied by the badgers targeted for vaccination was the combined area of these circles. In cases where circular home ranges overlapped, we used the outermost boundary of the combined circles to estimate the total area vaccinated. For the third method of estimating the area vaccinated, we added a buffer around the outermost farm boundary, where the buffer’s width was equal to the radius of the average post-cull home range size,

2604 using estimates from Riordan *et al.* (2011) (method 3; Table 5.2). Using this method, the total area
2605 vaccinated was delineated by the outermost boundary of the buffer.

2606 Vaccination coverage was estimated under two density scenarios, using the REM and CT-DS.
2607 We estimated population size by multiplying the estimated badger density (and associated 95%
2608 confidence limits) by the estimated area vaccinated, as described above. The number of badgers
2609 vaccinated at each site was then divided by the estimate of population size and multiplied by 100 to
2610 estimate the percentage vaccinated. We estimated the variance associated with vaccination coverage
2611 using parametric bootstrapping, assuming a Poisson distribution for the numerator (the number of
2612 badgers vaccinated), and a log-normal distribution for the density component of the denominator
2613 (population size), resampling the data 100,000 times.

Table 5.2 Details of methods used to estimate the area vaccinated during post-cull badger vaccination operations at two sites in South West England. The area vaccinated was either taken as the area targeted by vaccination operations, delineated by the outermost boundary of study sites (method 1), or based on badger home range estimates, which were used to draw circular home ranges around badger setts (method 2), or to add a buffer around the study site (method 3). Since the home ranges of badgers at these sites are not known, we used two previously published estimates from populations impacted by culling. Results use information from badger surveys which identified three main setts at site A and two at site B.

Area vaccinated delineation method	Method details	Study details			Estimated post-cull home range (km ²)	Estimated area vaccinated (km ²)	
		Location	Type of culling	Home range estimation method		Site A	Site B
1	Study site boundary	n/a	n/a	n/a	n/a	5.05	1.98
2	Circular home range around active main setts, using the mean home range size of social groups within 500m from culling in the previous ≤ 2 years (Bielby <i>et al.</i> , 2014)	East Midlands, West Midlands and South West England	Widespread	Dirichlet tessellations, supplemented with capture data	1.81	5.12	3.62
3	Buffer added to the study site boundary, using the radius of the mean home range size of badgers surviving reactive culling (Riordan <i>et al.</i> , 2011)	South West England	Localised	Radio collars; 95% minimum convex polygons	0.41	9.43	5.15

5.3.7. Power analysis

We used power analysis to assess the camera survey effort required to detect increases in badger density if population monitoring were repeated for four years post-cull, with surveys spaced either 12, 24, or 36 months apart. Power analysis is a statistical method that can be used either to improve study designs by determining the sample size necessary to detect a given effect size with adequate power, or retrospectively to assess the probability of detecting a given effect size with a given sample size (Cohen, 1988). More specifically, statistical power is equal to $1 - \beta$, where β is the probability of a

Type II error, or the probability of not rejecting a null hypothesis that is false (Steidl *et al.*, 1997).

Therefore, power is the probability of correctly rejecting a false null hypothesis (Cohen, 1988).

Four elements are necessary in power analysis: α , the probability of falsely rejecting a null hypothesis (usually set at 0.05); effect size, a measure of the expected degree of change (which here refers to the change in badger density and is estimated using the difference in the means divided by the standard deviation); power, where a value of ≥ 0.80 is often considered adequate (but see Di Stefano, 2003); and n , sample size. In our study, the density estimates are composed of several component estimates each with an associated sample size and standard error (trap rate, speed, activity level, angle and radius for the REM, and trap rate, activity level and the probability of detection for CT-DS). The overall coefficient of variation (CV) of the density estimates is derived using the delta method: the squared CV is equal to the sum of the squared component CVs, so a component's contribution to overall effective sample size should be proportional to its squared CV. We therefore estimated the sample size using the mean sample size of the component estimates weighted by their contribution to the overall error, using the equation:

$$n = \frac{\sum(n_i CV_i^2)}{\sum CV_i^2}$$

where n_i is the sample size for the i -th component of the density estimate and CV_i is the coefficient of variation for the i -th component. This approach is conservative in that it gives more weight to the sample size contributing more (scaled) variance. The standard deviation, used to calculate the effect size, was then estimated using the equation:

$$SD = SE\sqrt{n}$$

We compared the statistical power of the REM and CT-DS to detect increases in badger density over four years following the cessation of culling and assessed the sample size necessary for monitoring population recovery in future surveys. Studies of badger population dynamics suggest growth rates of between 6% and 25% annually (Anderson & Trewhella, 1985; Macdonald & Newman, 2002; Macdonald *et al.*, 2009). Recovery is likely to be slow after widespread removal (Anderson & Trewhella, 1985; Cheeseman, 1993; Krebs, 1997; Tuytens *et al.*, 2000b), though the UK government anticipates a 20% population growth rate following the first year of culling (DEFRA, 2023b). We therefore estimated the sample size required to detect a statistically significant ($p \leq 0.05$) increase in badger density under annual population growth scenarios of 5%, 10% and 25% with a statistical power of 0.80, 0.95 and 0.99, assuming camera deployment times remained the same as in our

surveys. To convert the overall sample size from the power analysis, n' , into an estimate of the number of camera traps, we used the following formula:

$$n_i' = n_i \frac{n'}{n}$$

which is weighted by the scaled variances and assumes that the ratios of component-specific sample sizes remain constant. Power was calculated using two-tailed paired-sample t-tests, pairing years one and two, one and three and one and four, assuming that each camera survey was repeated as in the first year. Analyses were conducted using the 'pwr' package (Champely, 2020).

5.3.8. Cost-effort analysis

We calculated the total costs of estimating badger density using the REM and CT-DS in these post-cull areas, accounting for the costs of equipment, materials, and staff time required for data collection and analysis. Costs were classified as either start-up or recurring annually and were estimated for two surveys using 100 and 34 camera traps. The costs associated with labour included preparation for camera surveys, training, deploying, checking and collecting cameras, image processing, and data analyses. Labour costs were calculated using the 2023 National Living Wage of £10.42 per hour (Low Pay Commission, 2023) for reference purposes.

5.4. Results

5.4.1. Camera surveys and density estimation

Cameras were deployed over three days, including time spent on training, by a team of 20 field staff. Due to constraints of the farmland habitat, which mainly consisted of large open fields, it was not possible to position every camera at the planned location. However, 71 of 100 cameras at site A (71%) and 22 of 34 cameras at site B (65%) were deployed within the target maximum distance (45m site A; 49m site B) from the pre-determined location at sites A and B, respectively. The average deviation from predetermined locations at site A was 21.5m (standard deviation (SD) 42.2m; range 2.3m – 178.3m) and at site B was 41.3m (SD 32.6m; range 1.4m – 125.1m). The field team spent one day checking and recalibrating cameras, and another day recalibrating and collecting them, totalling 100 person-days overall.

Cameras were deployed for an average of 51.2 days (range 49.8 – 52.0 days) at site A and 50.1 days (range 27.9 – 51.1 days) at site B. Over this time, we obtained 352,246 images from the cameras at site A and 226,486 images from site B, with an average of 4,319 images per camera. Of these, 3,778 (0.7%) images contained a badger. There were 529 unique badger contacts at site A and 263 at site B. Reactivity to camera traps was observed in 28 (5.3%) badger sequences at site A and 1

(0.4%) sequence at site B. The most commonly observed reactive behaviour was ‘freeze’ which accounted for 32.1% and 100.0% of the reactive sequences at sites A and B, respectively.

Estimated parameters for the REM and CT-DS models were similar at both sites (Table 5.3), but the effective detection radius was higher at site A (6.60m (95% CI 6.25m – 7.00m)) than site B (4.46m (95% CI 4.15m – 4.77m)). Density estimates aligned between the REM and CT-DS methods (Table 5.3). The estimated badger density at site A was lower than that of site B.

Table 5.3 Model parameters and badger density estimates from two sites in Gloucestershire, UK, using the random encounter model (REM) and camera trap distance sampling (CT-DS). Results shown are the mean and the associated standard error (in square brackets). All parameters were estimated from camera trap data.

	Site A	Site B
Model parameters		
Shared		
Activity level	0.34 [0.02]	0.35 [0.03]
Effective detection angle (radians)	0.79 [0.05]	0.55 [0.03]
REM		
Trap rate (contacts/camera/day)	0.10 [0.02]	0.15 [0.04]
Speed (m/s)	0.43 [0.03]	0.49 [0.08]
Day range (km/day)	12.6 [1.15]	14.8 [2.70]
Effective detection radius (m)	6.60 [0.18]	4.46 [0.16]
CT-DS		
Truncation distances (left, right; m)	2.0, 9.5	1.5, 6.5
Probability of detection	0.34 [0.01]	0.27 [0.01]
Density		
REM		
Estimate (individuals/km ²)	1.39 [0.23]	2.86 [0.91]
Log-normal 95% CI	1.01 – 1.91	1.55 – 5.27
CV	0.16	0.32
CT-DS		
Estimate (individuals/km ²)	1.13 [0.27]	4.72 [1.63]
Log-normal 95% CI	0.64 – 1.70	2.08 – 8.23
CV	0.27	0.35

5.4.2. Badger vaccination

At site A, we vaccinated eight badgers over 42 cage-trap nights and at site B, we vaccinated two badgers over 15 cage-trap nights. In total, we vaccinated 10 badgers over 57 cage-trap nights, an average of 1.4 badgers vaccinated per km² and 0.2 badgers vaccinated per cage-trap night. All badgers trapped and vaccinated were adults.

We identified three main setts at site A and two main setts at site B. The number of badgers considered in our analyses of vaccination coverage were small, resulting in wide confidence intervals for all coverage estimates (Fig. 5.2; Table 5.4). At site A, all point estimates of vaccination coverage exceeded 100%, except when the area vaccinated was estimated using a buffer around the farm boundaries. Coverage was lower at site B, where all point estimates were within the range of 8% – 35%.

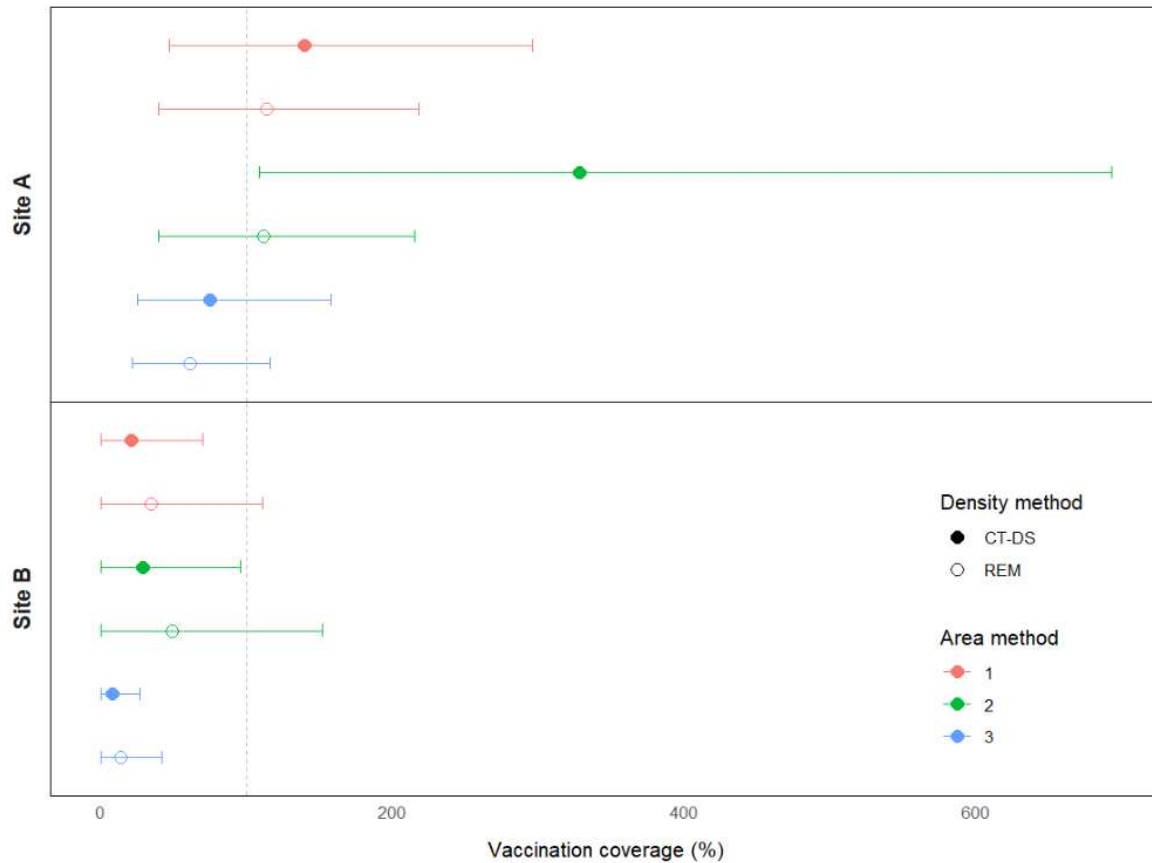


Figure 5.2 Estimated vaccination coverage and associated 95% confidence intervals at two post-cull badger vaccination sites, using the random encounter model (REM) and camera trap distance sampling (CT-DS) to estimate badger density. Population size was estimated by multiplying the estimated badger density by the area vaccinated. As the area vaccinated is uncertain, we used three methods for estimating the extent of the area used by badgers targeted for vaccination. These methods were either based on the area targeted by vaccination operations, delineated by the outermost boundary of study sites (method 1), or the estimated social group home ranges of badgers from setts on vaccinated land (methods 2 and 3). The grey dashed vertical line indicates 100% coverage.

Table 5.4 Summary of badger abundance and vaccination coverage estimates at two post-cull sites in South West England. Density was estimated at each site using the random encounter model (REM) and camera trap distance sampling (CT-DS). The area vaccinated was either taken as the area delineated by the boundary of study sites (method 1) or based on the estimated social group home ranges of badgers in setts on vaccinated land (methods 2 and 3). Results show the mean and associated 95% confidence intervals (CI; in square brackets).

Site A								
Area vaccinated estimation method	Estimated area vaccinated (km ²)	Number of badgers vaccinated	REM			CT-DS		
			Density (badgers/km ²) [95% CI]	Population size (badgers) [95% CI]	Vaccination coverage (%) [95% CI]	Density (badgers/km ²) [95% CI]	Population size (badgers) [95% CI]	Vaccination coverage (%) [95% CI]
1	5.05	8	1.39 [1.01 – 1.91]	7.0 [5.1 – 9.6]	114 [40 – 218]	1.13 [0.64 – 1.70]	5.7 [3.2 – 8.6]	140 [47 – 296]
2	5.12			7.1 [5.2 – 9.8]	112 [40 – 214]		5.8 [3.3 – 8.7]	138 [46 – 293]
3	9.43			13.1 [9.5 – 18.0]	61 [22 – 116]		10.7 [6.0 – 16.0]	75 [25 – 158]
Site B								
Area vaccinated estimation method	Estimated area vaccinated (km ²)	Number of badgers vaccinated	REM			CT-DS		
			Density (badgers/km ²) [95% CI]	Population size (badgers) [95% CI]	Vaccination coverage (%) [95% CI]	Density (badgers/km ²) [95% CI]	Population size (badgers) [95% CI]	Vaccination coverage (%) [95% CI]
1	1.98	2	2.86 [1.55 – 5.27]	5.7 [3.1 – 10.4]	35 [0 – 111]	4.72 [2.08 – 8.23]	9.3 [4.1 – 16.3]	21 [0 – 70]
2	3.62			10.3 [5.6 – 19.1]	19 [0 – 61]		17.1 [7.5 – 29.8]	12 [0 – 38]
3	5.15			14.7 [8.0 – 27.1]	14 [0 – 42]		24.3 [10.7 – 42.4]	8 [0 – 27]

5.4.3. Power analysis

Using our study design at site A (100 cameras deployed for an average of 51.2 days), both the REM and CT-DS could detect increases in badger density with sufficient statistical power ($\geq 80\%$) when annual population growth was 25% and surveys were spaced 24 months apart (Table 5.5). Given a 10% annual population growth, the REM had sufficient power to detect an increase with surveys spaced 36 months apart, but CT-DS did not have sufficient power to detect such changes under the same conditions. Under the scenario of 5% annual population growth, neither method had sufficient power to detect increases in density, even with surveys spaced 36 months apart. To detect such changes with sufficient power after 36 months, a minimum of 396 camera traps were required for the REM and 755 for CT-DS (assuming average deployment times remained fixed; Table 5.6).

Despite using fewer camera traps, the higher estimated densities at site B, combined with the similar standard deviation estimates, meant that the same percentage increase at both sites reflected a larger absolute increase at site B (Appendix 3, Table S7). Consequently, the power to detect a given percentage change in density was higher at site B than site A. Following our survey design at site B (34 cameras deployed for an average of 50.1 days), under the scenario of 25% annual population growth, CT-DS could detect an increase in badger density with sufficient power with surveys spaced 24 months apart (Table 5.5). The REM required surveys spaced at 36 months to detect the same changes. Given a 10% annual growth rate, increases in density could be detected with sufficient power with surveys spaced 24 months (CT-DS) or 36 months (REM) apart. Similarly to site A, under a scenario of 5% annual population growth, neither method had sufficient power to detect an increase in density, even with surveys spaced 36 months apart. However, compared to site A, fewer additional cameras were required at site B to detect such changes after 36 months (99 cameras for the REM and 46 cameras for CT-DS; Table 5.6).

2756 **Table 5.5** Statistical power to detect a significant ($p \leq 0.05$) increase in badger density over four years
 2757 under three population recovery rate scenarios, using the random encounter model (REM) and
 2758 camera trap distance sampling (CT-DS). We assumed that camera trap surveys were conducted either
 2759 12, 24 or 36 months apart, using the same number of cameras and deployment durations as used in
 2760 year one.

				Power to detect stated annual increase in badger density		
Site	Sample size	Method	Paired years	5%	10%	25%
A	100	REM	1 ~ 2	0.11	0.20	0.63
			1 ~ 3	0.20	0.51	1
			1 ~ 4	0.34	0.83	1
		CT-DS	1 ~ 2	0.08	0.14	0.41
			1 ~ 3	0.14	0.33	0.94
			1 ~ 4	0.23	0.60	1
B	34	REM	1 ~ 2	0.12	0.23	0.74
			1 ~ 3	0.24	0.61	1
			1 ~ 4	0.42	0.92	1
		CT-DS	1 ~ 2	0.17	0.39	0.96
			1 ~ 3	0.30	0.89	1
			1 ~ 4	0.69	1	1

2761

2762 **Table 5.6** Sample size (number of cameras) required to detect 5%, 10% and 25% increases in badger density per annum (*p.a.*) over four years using the
 2763 random encounter model (REM) and camera trap distance sampling (CT-DS). We assumed that camera surveys were conducted either 12, 24 or 36 month
 2764 apart, at the same time each year, and cameras were deployed for the same number of days (on average, 51.2 days at site A and 50.1 at site B).

2765

Site	Method	Paired years	Sample size necessary to detect stated annual increase in badger density								
			Statistical power: 80%			Statistical power: 95%			Statistical power: 99%		
			5% <i>p.a.</i>	10% <i>p.a.</i>	25% <i>p.a.</i>	5% <i>p.a.</i>	10% <i>p.a.</i>	25% <i>p.a.</i>	5% <i>p.a.</i>	10% <i>p.a.</i>	25% <i>p.a.</i>
A	REM	1 ~ 2	3932	984	158	6882	1721	276	10029	2508	402
		1 ~ 3	936	224	32	1638	391	55	2387	569	80
		1 ~ 4	396	90	12	693	158	20	1010	230	28
	CT-DS	1 ~ 2	7500	1876	301	13128	3283	526	19130	4783	766
		1 ~ 3	1785	426	60	3124	745	105	4553	1085	152
		1 ~ 4	755	172	22	1322	300	37	1926	437	53
	REM	1 ~ 2	983	246	40	1719	430	69	2505	627	101
		1 ~ 3	234	56	8	410	98	14	597	143	20
		1 ~ 4	99	23	3	174	40	5	253	58	8
B	CT-DS	1 ~ 2	442	111	19	772	194	32	1125	282	46
		1 ~ 3	106	26	5	185	45	8	269	65	10
		1 ~ 4	46	11	3	79	19	4	114	27	5

5.4.4. Cost-effort analysis

The resource requirements and financial cost of obtaining density estimates using the REM and CT-DS were equivalent (Table 5.7). Image tagging was the most resource-intensive part of both methods, followed by camera deployment. The total cost of using both methods to estimate badger density was estimated at £96,400 over four years, averaging £24,000 per year and £3,400 per km² per year. The first year of study was the most expensive due to the purchase of equipment. The initial investment of equipment totalled £29,300, while the labour costs associated with every year of population monitoring were estimated at £16,800. If badger density was estimated twice, with two surveys conducted either 24 or 36 months apart, the total cost was £58,800.

Table 5.7 Costs and resources required to estimate badger density at two sites over four years using the random encounter model (REM) and camera trap distance sampling (CT-DS). Costs associated with labour were estimated by multiplying the total staff time by the hourly rate, using the National Living Wage (£10.42 per hour in 2023) for comparative purposes. Where tasks are repeated annually, we multiplied the annual cost by 4, without accounting for inflation. Units of stationery and personal protective equipment (PPE) are not shown as these categories constituted several items.

Category	Description	Units	Frequency type	Team size [total hours]	Cost over 4 years (£)
Equipment	Cameras	134	Start up	n/a	13,667
	SD cards	268	Start up	n/a	1,367
	Batteries	162	Annual	n/a	8,095
	Security cases	134	Start up	n/a	3,245
	Locks	134	Start up	n/a	2,135
	Calibration poles	10	Start up	n/a	27
	Stationary	n/a	Start up	n/a	317
	PPE	n/a	Start up	n/a	248
	Hard drives	4	Start up	n/a	228
Time	Survey preparation	n/a	Annual	1 [75]	3,126
	Training	n/a	Annual	21 [84]	3,501
	Camera deployment	n/a	Annual	20 [400]	16,672
	Camera checking	n/a	Annual	20 [140]	5,835
	Camera collection	n/a	Annual	20 [140]	5,835
	Data processing	n/a	Annual	1 [21]	875
	Image tagging (all species)	n/a	Annual	14 [700]	29,176
	Digitising (just badgers)	n/a	Annual	1 [21]	875
	Data analysis (REM)	n/a	Annual	1 [14]	584
	Data analysis (CT-DS)	n/a	Annual	1 [14]	584
Total cost over 4 years (£)					96,391

5.5. Discussion

We report the estimated vaccination coverage achieved at two sites following widespread industry-led badger culling. Although high coverage was apparently achieved under certain density scenarios, our results exhibit a large degree of statistical uncertainty due to the imprecision of the density estimates and the small size of the badger population within the area considered in this research. Studies involving more badgers would likely reduce variability in coverage estimates. Consequently, longer-term assessments across larger geographic scales may be necessary to fully evaluate the effectiveness of a post-cull badger vaccination strategy. Furthermore, our power analyses show that surveys assessing badger density, from which vaccination coverage is derived, should be spaced 24 (or more) months apart to have sufficient statistical power to detect biologically plausible growth in badger population density. These findings have important implications for evaluating the effectiveness of post-cull badger vaccination strategies, which are becoming increasingly relevant in England and Northern Ireland.

Badger density estimates at our study sites were lower than estimates from similar habitats (e.g. McDonald *et al.*, 2018), likely due to several years of industry-led culling intended to achieve and maintain a 70% reduction in the population (DEFRA, 2023b). Despite this low density, our results suggest that high vaccination coverage was achieved in some population size scenarios (Table 5.4). However, at site A, most point estimates exceeded 100% (Fig. 5.2), suggesting the population size was underestimated (by underestimating density, the area vaccinated, or both). Furthermore, statistical uncertainty in the results limited the ability to precisely estimate vaccination coverage. This uncertainty arose from two main sources: (1) imprecision in our population density estimates; and (2) the small size of the badger population within the area vaccinated, which introduced stochastic variation. There are several ways to address these sources of uncertainty. Firstly, the precision of the density estimates could be improved by increasing the number of camera placements, either by deploying more camera traps or moving them during the survey to sample more locations. Secondly, broadening the study site to sample a larger area of the vaccinated land could increase both the number of badgers vaccinated (the numerator of the coverage estimate) and the population within the area vaccinated (the corresponding denominator), likely improving the precision of the estimated proportion vaccinated. For example, at site B, we vaccinated 2 badgers over an area of 1.98km² from an estimated population of 5.7 (using the REM density estimate), yielding a vaccination coverage estimate of 35%, with a 95% confidence interval of 0% – 111%. If the study area were increased tenfold, with the density estimate (2.86 badgers per km²) remaining constant, but assuming the number vaccinated scaled proportionally, 20 badgers would be vaccinated from a population of 57. While the central vaccination coverage estimate would remain 35%, the confidence interval would

2817 narrow to 16% – 72%, reflecting improved precision due to the larger number of vaccinated badgers
2818 and the larger population estimate, both of which reduce stochastic variation.

2819 Long-term population monitoring could also help address the uncertainty associated with
2820 the small number of badgers considered in the study. As the badger population recovers post-cull,
2821 the number of badgers vaccinated and considered in the population estimate would increase. More
2822 cubs that have not had any previous exposure to cage traps would also be recruited into the
2823 population, so trappability is expected to increase (Tuytens *et al.*, 1999; Byrne *et al.*, 2012). This
2824 would likely result in more (and a higher proportion of) badgers being vaccinated and, through a
2825 larger underlying population size, improve the precision of future estimates. Our power analyses
2826 suggest that monitoring badger density with surveys undertaken 36 months apart (with our level of
2827 survey effort) would be needed to provide sufficient statistical power to detect population recovery
2828 at $\geq 10\%$ per year (Table 5.5). Surveys conducted more than 36 months apart were required when the
2829 annual growth rate was 5%. It is worth highlighting, however, that if the population were recovering
2830 along a logistic growth curve, the period of exponential growth may generate absolute increases
2831 large enough to be detected by more frequent surveys. Additionally, as the growth rate slows, power
2832 is likely to decline. Overall, these findings suggest that, to understand the vaccination coverage
2833 achievable by post-cull badger vaccination, population monitoring must be conducted over larger
2834 spatial and temporal scales.

2835 In addition to statistical uncertainty arising from imprecise density estimates, there is
2836 uncertainty in the accuracy of the area vaccinated. This parameter is challenging to estimate at the
2837 farm-level scale, because it requires knowledge of the spatial use of the habitat by badgers (Benton
2838 *et al.*, 2023), though our estimates reflect the most accurate approximation given data limitations.
2839 Due to the small geographical scale of our study and the likely impact of culling on badger ranging
2840 behaviour, it is possible that we trapped and vaccinated badgers whose home-range centres were
2841 outside the boundaries of the study site. If so, some of our estimates of the area vaccinated may be
2842 too low, leading to an overestimation of vaccination coverage. In larger-scale studies however, this
2843 edge effect would be less pronounced as a proportion of the study area, and thus detailed
2844 knowledge of home ranges may not be critical. Therefore, conducting similar studies of vaccination
2845 coverage over larger areas would not only mitigate the effects of stochastic variation, but would also
2846 reduce uncertainty about the size of the area to include in analyses.

2847 When evaluating the suitability of our specific surveys for long-term population monitoring,
2848 we found that both survey designs had sufficient sampling effort to detect increases in badger
2849 density with $\geq 80\%$ power, when surveys were conducted 36 months apart, under population

recovery rate scenarios of $\geq 10\%$ annually. An exception was noted at site A, where 172 camera traps were required to detect increases in density over the same time period using CT-DS. However, under a 5% annual population growth rate scenario, more camera traps were necessary at both sites: a minimum of 396 at site A and 46 at site B (Table 5.6). At site A in particular, the number of cameras required to detect such changes was exceptionally high, far exceeding what would be considered achievable effort for monitoring, unless annual population growth rate was 25%. While our results provide valuable guidance for future study design, previous research recommends a minimum of 100 camera placements to ensure adequate precision for these methods, and highlights the importance of considering the focal species' expected density, day range, and spatial distribution when deciding on the number of camera traps to use (Rowcliffe *et al.*, 2008; Cappelle *et al.*, 2021). Therefore, our results should be interpreted as a minimum guide, and we recommend aiming for at least 100 camera placements where precision is critical.

Due to the shared model parameters and methodologies, the costs of obtaining density estimates using the REM and CT-DS were equivalent (Table 5.7). Using either method would cost an estimated £3,400 per km² per year. This is comparable to the cost of vaccinating badgers, depending on the type of labour used. For example, a badger vaccination programme led by the Welsh Government cost £3,100 per km² per year (Llywodraeth Cymru, 2016), while projects utilising volunteers are more cost-effective at £600 per km² per year (Zoological Society of London, 2018). Like vaccination programmes, the cost of camera surveys can be reduced by drawing on volunteer assistance. Since the REM and CT-DS are both scalable to large areas (e.g. Cusack *et al.*, 2015b; Mason *et al.*, 2022), the cost of conducting an identical survey with a greater camera spacing (allowing the same number of cameras to cover a larger area) would be similar those estimated here. Such an approach would only increase the cost of camera deployment, checking, and retrieval, because field teams would have to travel further between camera locations. Based on the costs presented in Table 5.7, a 50% increase in the cost of camera deployment, checking, and retrieval would only lead to a 16% increase in the overall budget, suggesting this is a cost-effective way to increase the geographical size of the study (Fig. 5.3). Spacing surveys further apart in time would be another effective way of reducing monitoring costs, as annual surveys may not be necessary for detecting density trends.

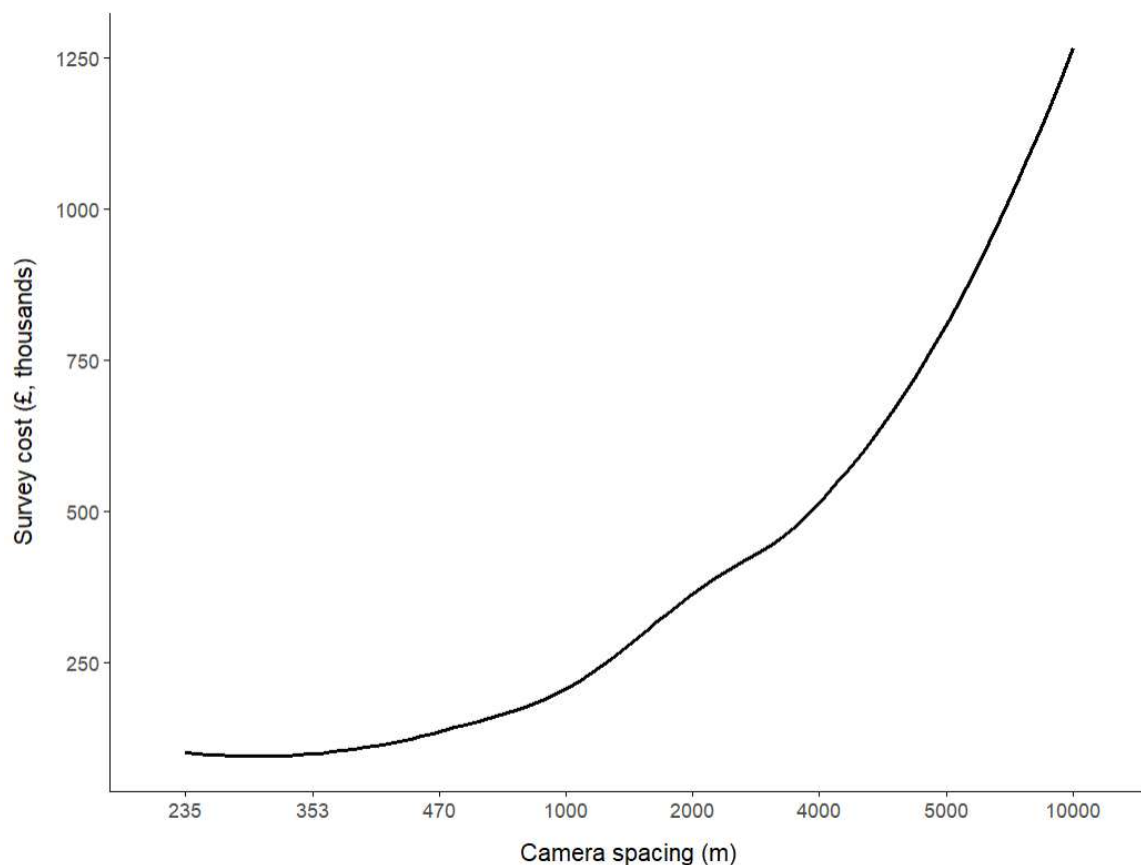


Figure 5.3 Projected cost of conducting similar camera trap surveys (in terms of the number of cameras and deployment durations) over larger spatial scales by increasing the distance between camera traps.

The most resource-intensive part of the process was tagging camera images (Table 5.7). We chose not to employ artificial intelligence (AI) technologies, which could have made image processing more efficient, due to staff availability during the closed season of badger vaccination. Using AI software such as Conservation AI, which can process approximately 50,000 images per hour (Vélez *et al.*, 2023), would have reduced tagging time from 700 hours to approximately 7 hours, though additional time would likely be needed for further processing. Manual tagging has resulted in a labelled dataset specific to our study site which could be used to train AI classification models such as MegaDetector (Beery *et al.*, 2019) in future years of the study. It is also worth highlighting that we chose to tag every species in our dataset, despite only estimating density for badgers. This approach enabled density estimation of other species in future, though processing times would have been reduced if efforts were focussed exclusively on badgers.

Our results suggest that camera traps might be used to identify culling-induced changes in badger behaviour. For example, our estimates of badger day range (12.6km per day (95% CI 10.3 – 14.9km per day) at site A and 14.8km per day (95% CI 9.5 – 20.1km per day) at site B) were high in comparison with estimates presented by Kowalczyk *et al.* (2006) and those used to derive density estimates in Miles *et al.* (2024; Chapter 2), where the mean day range was 5.3km per day (range 4.3 – 7.3km per day). This difference could be explained by the effect of culling on badger behaviour, as surviving badgers have previously been shown to move faster, to travel further from their setts, and to have larger home ranges (Ham *et al.*, 2019), patterns which are likely to be reflected in larger day range estimates. In this study, short-term movement speed (0.43m/s (95% CI 0.37 – 0.49 m/s), site A; 0.49m/s (95% CI 0.33 – 0.65 m/s), site B) tended to be high compared to estimates from similar analyses of uncultured populations in Cornwall (mean speed 0.22m/s (range 0.20 – 0.24m/s); Miles *et al.*, 2024, Chapter 2). This supports suggestions from Ham *et al.* (2019) that culling is associated with an increase in short-term movement speed, estimated by the 20-minute step length interval of GPS-collared badgers. However, both short- and long-term movement speed can be highly variable within species (ENETWILD-consortium *et al.*, 2023), so these results could be related to local habitat, rather than prior badger culling. Given the small-scale of our study and lack of controls, it was not possible to determine the cause of the observed patterns, but continued population monitoring would help detect any behavioural changes as the population recovers.

The results of our study will serve as a baseline for comparing badger density and vaccination coverage at the two sites over the planned four years of vaccine delivery. Our density estimates likely represent the adult population as cameras were deployed in April and May, before cubs typically explore beyond the sett (Neal & Cheeseman, 1996). The absence of cubs in images supports this; although determining age class from images can be difficult, cubs would likely appear with adults at this stage, making size comparison possible. Only adult badgers were trapped and vaccinated at these sites, but if cubs are vaccinated in future years, they should be excluded from coverage estimates, unless subsequent camera surveys occur when cubs can be seen above ground.

Our findings have important implications for bTB control policy. In England, badger culling is being phased out in favour of badger vaccination (DEFRA, 2024d), yet there is limited understanding of how badger population recovery affects trapping efficiency and hence vaccine coverage (Byrne *et al.*, 2012). Although our results carry some uncertainty, the high coverages achieved at site A are promising and suggest that, despite the potential impact of culling on trappability (Tuytens *et al.*, 1999), sufficient coverage may be attainable in the first- and second-years post-cull. However, the absence of cubs in our study raises questions about whether vaccinating immediately after culling is

2927 the optimal strategy. Trappability is expected to improve over time as the badger population recovers
2928 (Tuytens *et al.*, 1999), with more cubs – which are less likely to have been exposed to *M. bovis*
2929 (Woodroffe *et al.*, 2006b) – recruited into the population. This suggests that vaccine coverage, and
2930 hence vaccination effectiveness, are likely to improve with time, and resources could potentially be
2931 allocated more efficiently when success is most probable. Furthermore, we found that estimating
2932 vaccination coverage in the first- or second-year post-cull may not precisely estimate the coverage
2933 achievable and thus fail to fully capture the long-term implications of this strategy. We recommend
2934 that post-cull vaccination efforts be integrated with population monitoring over larger spatial scales
2935 than considered here, and that vaccination coverage be monitored with density assessments
2936 conducted 24 to 36 months apart, or at even longer intervals if the badger population recovers
2937 slowly.

2938 **6. Chapter 6: General discussion**



2939 *Badgers foraging in the long grass at sunset.*

6.1. Overview

This thesis explores the application of camera-based methods for estimating the density of unmarked animals, and their suitability for informing disease management policies. Specifically, it aimed to: evaluate the reliability of the random encounter model (REM) and camera trap distance sampling (CT-DS) across several species and density ranges; assess the survey effort, financial costs and resources necessary for application of these models; and test these methods within a disease management framework. I explored these objectives within the context of badger vaccination for the control of bovine tuberculosis (bTB), discussing the implications of the findings for current bTB control strategies.

Obtaining reliable estimates of animal density is valuable for effective wildlife management and conservation, but particularly challenging for species in which individuals are not easily identifiable. Camera traps and the associated statistical tools have become valuable for this purpose, but methods such as the REM and CT-DS are still in relative infancy and further testing in novel contexts is advised (Palencia *et al.*, 2021). In this thesis, I assessed the accuracy and precision of these two camera-based methods and explored how to control potential sources of bias. Given the demand to make best use of limited resources, I also investigated the minimum survey effort necessary to achieve reliable density estimates. Additionally, I evaluated whether the survey designs of current population monitoring efforts would be statistically powerful enough to detect population trends, and provide practical suggestions for improving data utilisation in camera surveys more broadly.

The implications for wildlife management are a key focus of this thesis. As one of the UK's most serious animal health challenges, the control of bTB through badger management provided an ideal context for the research because badgers are notoriously difficult to count, due to their nocturnal and fossorial nature, and abundance estimates are important for informing management plans. In England, strategy for controlling bTB in wildlife is shifting from badger culling to a policy focused on badger vaccination, and yet the post-cull landscape is not well studied. I aimed to assess the feasibility of this approach for contributing to bTB elimination by estimating vaccination coverage in culled and uncultured badger populations. I also compared the accuracy, precision, costs, resource requirements, and practical considerations of using the REM and CT-DS for population monitoring within a disease management framework. The findings provide valuable guidance for the camera-trapping community and for policymakers wishing to utilise such methods to inform management decisions.

In this discussion I synthesise the main findings of this thesis, emphasising how the results are relevant to conservation and animal management, whilst paying particular attention to bTB eradication policy. As both camera-based methods and bTB policies are evolving rapidly, I discuss important recent developments in these areas and address the remaining challenges, highlighting where there are opportunities for further research.

6.2. Validating the methods

Previous studies comparing density estimates from the REM and CT-DS with known populations or independent density methods generally support their accuracy (e.g. Rowcliffe *et al.*, 2008; Howe *et al.*, 2017; Palencia *et al.*, 2022), though some substantial differences have been reported (Chauvenet *et al.*, 2017; Santini *et al.*, 2022) and several potential biases identified. For example, as both models assume the independent movement of animals with respect to camera traps, non-random behaviour or habitual space used can bias density estimates (Cusack *et al.*, 2015a; Cusack *et al.*, 2015b). Under this assumption, cameras should not influence animal movement, and yet reactivity to novel objects and the infrared light used in most modern cameras is a well-documented problem (Henrich *et al.*, 2020; Houa *et al.*, 2022). Providing such behaviours are measurable, the bias can be quantified and controlled. In this context, further testing of the REM and CT-DS to new scenarios and species, and against independent approaches, is recommended to improve the applicability of the methods. A key objective of our research was to evaluate the performance of the REM and CT-DS within a badger management framework, to identify any potential biases relating to badger behaviour or the farming landscape in order to assess the suitability of integrating these methods into bTB control policy.

In **Chapter 2** I assessed the accuracy of the REM and CT-DS, using an independent method for comparison. By taking advantage of a vaccination study in which badgers were anaesthetised for blood sampling, I was able to mark badgers with individually identifiable fur clips, enabling density estimation under a spatial mark-resight (SMR) framework. A key assumption of SMR is that marked animals remain identifiable for the duration of study. Recent research highlights that badger fur clips may become less detectable on camera traps over time, particularly during summer months (Benton *et al.*, 2024). However, based on model predictions by Benton *et al.* (2024), during our study, the probability of detection is unlikely to have declined substantially due to the relatively short deployment durations (46.6 days, on average), supporting the use of this technique for comparative analyses. I found consistency in the density estimates obtained from all methods, validating the accuracy of the REM and CT-DS and their application to badgers.

I further examined the accuracy of these methods in **Chapter 4** by assessing how well the density estimates of four mammal populations in Woodchester Park aligned with reference estimates

from the literature, and a minimum number alive (MNA) density estimate obtained for badgers using data from a long-term capture-recapture at the same site. Generally, I found correspondence between our results and the reference densities. However, badger density estimated using the REM (3.6 badgers per km² (95% confidence interval (CI) 2.6 – 4.9 badgers per km²)) was significantly lower than the MNA density estimate (6.5 badgers per km²), suggesting the REM may have underestimated badger density. However, while MNA is generally understood to be biased low, it is possible that in our study it actually represents an overestimate of the number of badgers present during the camera survey period. The MNA estimate is a count of the minimum number of badgers that were alive at any point during the year based on live capture records. However, supplementary badger culling operations occurring on nearby land started on the 1st June 2022, and a number of marked badgers were removed before the beginning of the camera survey on the 20th June (exact numbers are not published in this thesis due to data privacy restrictions). Though these animals would have contributed to the MNA estimate for the year, they would have been absent from the population by the time the camera survey started. Furthermore, the greatest mortality in badgers tends to occur in the first year of life (Neal & Cheeseman, 1996). Therefore, some cubs, which are most frequently born in February (Neal & Cheeseman, 1996) and can be trapped and marked from 1st May (DEFRA, 2021a), could have been included in the MNA estimate but may have died before the initiation of camera trapping in June. This could explain the apparent underestimate of the REM badger density in this survey.

In **Chapter 4** I also found that our estimated densities of badgers and foxes were notably lower than those published in Delahay *et al.* (2013) and Mason *et al.* (2022), respectively. However, this result is likely explained by the occurrence of badger removal near our study site, and the possible culling of foxes on nearby land, rather than reflecting model inaccuracy. Given the general consistency between the density estimates presented in this thesis, I suggest that both the REM and CT-DS are reliable methods of estimating the density of individually unidentifiable animal populations but encourage the continued testing of the methods in novel contexts.

I explored several potential sources of bias which could have affected the accuracy of the density results. The assumption of random camera placement is fundamental to both models and failure to achieve this can skew density estimates (Rowcliffe *et al.*, 2008; Howe *et al.*, 2017). Obvious violations include camera placement directed by knowledge of the focal species' use of habitat, for example, by deliberately deploying cameras near dens sites or trails, or avoiding habitat deemed less favourable. I attempted to overcome this in all of the camera surveys by adhering to a grid of randomised locations, which was broadly achievable. In theory, given sufficient spatial sampling

across the focal species' habitat range, heterogeneity in encounter rates should not bias density unless areas representing activity extremes are over sampled by chance. In **Chapter 2** I presented a method of identifying trap rate outliers which indicated the potentially biased placement of one of the cameras near a badger sett. This approach can be applied to any density analysis methods that have trap rate as a parameter to help improve the accuracy of the results. Although truly random camera placement is rarely easy to achieve, we found that we were able to position most cameras at distances from their predetermined locations which were <20% of the between-camera distance. More substantial deviations were experienced where the habitat was dominated by pasture, as observed in **Chapters 2, 4 and 5**, where cameras were frequently sited at field boundaries. This sampling design could result in bias if badgers preferentially use or avoid boundaries, leading to inflated or underestimated density estimates, respectively. However, the alignment of our estimates with those of SMR (**Chapter 2**), which is less sensitive to non-random animal movement, suggests the REM and CT-DS were not substantially biased by the tendency to place cameras at boundaries. Supporting this conclusion, recent exploratory analyses, which utilised badger telemetry data from two of the sites examined in **Chapter 2**, found that badgers do not generally show preferential movement along habitat boundaries, except after culling, where a slight preference for using boundaries was observed (Brown, 2024, MSc thesis), and during the spring mating season (February), when a strong preference for using habitat boundaries was detected (Eng, 2022, MSc thesis). The latter form of seasonal variation was found to bias REM density estimates by up to 45.2% (95% CI 21.3% – 69.1%), though these analyses would benefit from replication at additional sites to confirm this result. Our surveys, which were conducted between May – November, are unlikely to have been biased by such seasonal differences in badger movement but, where possible, the integration of spatial information on the habitat use of the target species is likely to improve the accuracy of the REM and CT-DS estimates, particularly if realised camera placement is not entirely random.

Where camera traps elicit a behavioural response from animals, the resulting non-random animal movement can also bias model parameter estimates (Delisle *et al.*, 2023). I explored the impact of reactive behaviours on density estimates in **Chapter 2**, finding that CT-DS was highly sensitive to the exclusion of reactive sequences, which halved the estimated density in the most-affected survey. While the REM has a standardised method for controlling bias from reactive behaviours, a number of different approaches are suggested for dealing with this in CT-DS analyses, and the most appropriate method likely depends on the observed behaviour type (Delisle *et al.*, 2023). I explored this further in **Chapter 4**, using the categorisation of reactive behaviours to guide the method of bias mitigation. Since reactive behaviours were recorded in every camera survey and

all of the species studied in this thesis (Fig. 4.2), it is clearly important to take steps to mitigate bias from such behaviour, which is standardised in the REM but necessitates categorising behavioural types for CT-DS.

6.3. Assessing precision and suitability for animal management

The ability to detect population trends for effective wildlife management relies on precise abundance estimates, with a threshold of coefficient of variation (CV) $\leq 20\%$ conventionally used as a benchmark of precision (Pollock *et al.*, 1990; Williams *et al.*, 2002). However, a recent systematic review of methods of abundance estimation for individually unidentifiable species found that such precision is difficult to achieve (Morin *et al.*, 2022). The results presented in **Chapter 2** are consistent with this pattern, as density estimates for SMR, the REM and CT-DS all had wide confidence intervals, with all CV values exceeding 20%. This was particularly true of low-density populations and where variability in trap rate was high (e.g. site A; survey 1), or where resighting data were limited (e.g. Site D; survey 5). Likewise, in **Chapter 4**, the least precise estimates (red foxes) also had the lowest estimated density and highest variability in trap rate. These results caution against the use of the REM and CT-DS for low-density populations and highlight the importance of considering the spatial distribution of the target species when planning surveys.

For low-density populations or where animal's spatial distribution is clustered, precision can be improved by increasing camera trapping effort (Morin *et al.*, 2022). Whilst the high CV values reported in **Chapter 2** generated recommendations against using the REM and CT-DS for low-density populations, in **Chapter 4**, I found that precise estimates were achievable using both methods with increased survey effort. Based on a relatively low-density badger population in Woodchester Park, a survey comprising 100 camera traps deployed for 42 days (REM), or 56 days (CT-DS), was sufficient for obtaining density estimates with CV values of $\leq 20\%$. Shorter deployment durations of 21 days (REM) and 28 days (CT-DS) were possible with 140 cameras. Furthermore, in **Chapter 5**, I found that REM estimates with CV of 16% were attainable using 100 cameras deployed for an average of 51.2 days, for a badger population living at a relatively low density of 1.39 badgers per km² (95% CI 1.0 – 1.9 badgers per km²; REM). As such, in contrast to Guerrasio *et al.* (2022), these results suggest that the REM and CT-DS are suitable for informing the management of low-density wildlife populations but emphasise the importance of appropriate survey design and sufficient effort to achieve precise results.

6.4. Requisite effort for camera surveys

Obtaining reliable abundance estimates is challenging when time and resources are limited. The biggest constraint of camera-based approaches is often the initial equipment costs, followed by the

time investment necessary for camera deployment and image processing (Schaus *et al.*, 2020). Practitioners must determine the optimal sample size to obtain sufficiently accurate and precise results, but such decisions are complicated by lack of empirical guidance and discrepancies in the literature. In **Chapter 2**, following Rowcliffe *et al.* (2008), I estimated the necessary number of camera traps based on the expected badger density and day range, exceeding the recommended minimum of 40 placements at each site. However, the imprecise results, where in some cases the CV of density estimates exceeded 60%, indicated insufficient sampling effort, despite conditions of relatively high badger density. To explore this phenomenon further, in **Chapter 4**, I evaluated the minimum effort required to obtain precise density estimates by subsampling data from an intensive camera survey at Woodchester Park, Gloucestershire. Additionally, in **Chapter 5**, I used power analysis to assess the necessary sample size for detecting long-term population trends.

In **Chapter 4**, I found that camera surveys required a minimum of 100 camera placements and deployment times of at least 42 days (REM) or 56 days (CT-DS) to achieve the desired level of precision in a relatively low-density badger population. This is consistent with several modelling studies which recommend at least 100 camera placements, particularly under circumstances of high trap-rate variability (Rowcliffe *et al.*, 2008; Cappelle *et al.*, 2021). Previous studies suggest that increasing the number of camera placements has a more substantial impact on precision than increasing deployment durations (Rowcliffe *et al.*, 2008), and the results in **Chapter 4** agree with this (Fig. 4.9). Since it is also advisable to limit sampling durations to meet the assumption of population closure, survey designs with denser camera grids, using more cameras for a shorter duration, are likely to generate estimates which are more precise and therefore more informative for wildlife management. While the results in this thesis offer practical guidance for practitioners planning camera surveys, they may not be valid in other density scenarios. For example, what survey effort might be required for populations living at very low densities, such as those of conservation concern? And if the study species is highly abundant, would fewer than 100 cameras suffice? Given the density ranges reported in **Chapter 4**, from 0.5 red foxes per km² (95% CI 0.4 – 0.8 red foxes per km²) to 45.5 muntjac per km² (95% CI 35.1 – 59.1 muntjac per km²; REM), our data present an appropriate means of answering these questions in future analyses.

In **Chapter 5** I used power analysis to assess whether our survey designs (in terms of the number of camera traps, given our deployment durations) were sufficient for detecting increases in badger density using the REM and CT-DS over four years of population monitoring. The results suggest that the sample sizes used in our surveys (100 cameras deployed for 51.2 days at site A and 34 cameras deployed for 50.1 days at site B) were sufficient to detect increases in density with 80% power if surveys were spaced 24 months apart, assuming an annual population growth rate of 25%.

If surveys were conducted 12 months apart, more cameras were required at site A to detect comparable changes (158 cameras using the REM or 301 cameras with CT-DS). If the annual growth rate was 5%, neither survey has a sufficient number of cameras to detect increases in density, even with surveys spaced 36 months apart. However, as the population density increases each year post-cull, the power to detect a given percentage change will increase too. In the early phase of logistic growth, absolute change in population density is likely to be small and hard to detect, and the same would be true in the late phase when the population is close to carrying capacity. However, in the middle, when the population grows relatively rapidly, absolute changes in population size would be larger and therefore easier to detect. Population declines, on the other hand, are not constrained by biology, so may be easier to detect than population increases. As such, when using these camera-based methods for monitoring populations of endangered species, where detecting both population increases and decreases is important, more frequent surveys would still be advisable. Our findings highlight the importance of adequate planning for camera surveys and demonstrate how tools such as power analysis can be used to predict whether survey designs will be sufficient to achieve the desired outcomes.

6.5. Choosing the optimal method

The last few decades have seen the development of a number of invasive and non-invasive tools for estimating animal density using camera traps, though comparison between methods is limited. The REM and CT-DS lend themselves to being tested against each other due to their compatible sampling designs, and several shared assumptions and model parameters (Palencia *et al.*, 2021). In this section I compare the performance of the three camera-based methods applied in this thesis, focussing on accuracy, precision and ease of implementation, and also evaluate the cost and survey requirements of the REM and CT-DS specifically.

Methods which do not rely upon recognising individual animals have an apparent advantage over capture-recapture tools such as SMR as they obviate the need for trapping and marking, which can be stressful for the target species and challenging to implement at scale. Additionally, the resighting requirements necessary to ensure robust results are often difficult to achieve with camera trap surveys, as evidenced by the results in **Chapter 2**. On average, in our SMR analyses 56% of the images of marked animals could be identified. This value fell to 25% in the worst affected survey, and our simulations suggested this limitation may have resulted in the density being underestimated by 15%. Difficulty identifying whether badgers were marked or unmarked in camera trap images was often the result of overexposed images (Fig. 2.6), which can occur when the proximity of animals or habitat features in the field of view are too close to the camera or the camera's exposure settings are calibrated for subjects at greater distance. Despite attempts to adjust exposure during image

processing, very few fur clips were distinguishable in overexposed images. Overexposure is less problematic for the REM and CT-DS, providing it does not affect the ability to identify species or locate animals reliably in images (e.g. Fig. 2.6), thereby maximising data usage with these methods.

The alignment of density estimates across the three camera-based methods in **Chapter 2**, and with reference density estimates in **Chapter 4**, supports the accuracy of both the REM and CT-DS for estimating the density of unmarked animals. However, an inconsistency was reported in **Chapter 4**, where the REM point estimate for badgers was almost half that of the CT-DS estimate, although there was some overlap of the confidence intervals (Table 4.2). The CT-DS density estimate was also closer to the MNA density estimate, as discussed in detail earlier in this discussion (Chapter 6.2).

Inspection of the density estimates obtained in **Chapter 2** (Table 6.1) shows that CT-DS models tended to be closer to the reference SMR density estimates, but this was dependent on the inclusion of reactive sequences. Since reactivity can generate substantially biased results using both methods (Delisle *et al.*, 2023), the standardised method for controlling such bias presented by the REM could be advantageous over CT-DS. Reviewing the density estimates in **Chapters 2, 3, and 4**, highlights the tendency for CT-DS to generate higher estimates than the REM, particularly when bias from reactive sequences is not controlled, a trend which was observed in eight of the 12 sampled populations (Table 6.1). However, when reactivity to camera traps was accounted for in CT-DS, there was general consistency across the two methods and a large degree of overlap between the confidence intervals. In **Chapter 5**, I report that the REM density estimates were consistent across a range of survey effort, whereas CT-DS tended to be biased high when survey effort declined.

Comparing the precision of the density estimates obtained in **Chapters 2, 4 and 5**, indicates that SMR (as implemented in this study, using random camera placements designed for REM and CT-DS) tended to be the least precise approach, while the REM marginally outperformed CT-DS in most cases (Table 6.1). However, since SMR does not demand random camera placement, it is likely that the precision of our SMR density estimates could have been improved by deploying an additional array of cameras at badger setts to obtain more images of marked individuals. When examining the effect of sampling effort on the precision of density estimates, the results in **Chapter 4** suggest that CT-DS was consistently less precise than the REM, and the difference in precision was more pronounced when the survey effort was <4,000 camera trap-days (Fig. 4.9). Compared to the REM, CT-DS consistently overestimated density when survey effort was low, and shorter deployment durations were necessary to reach a CV of 20%, although both methods required 100 camera placements to achieve this. These results suggest that precise density estimates can be obtained with

both methods given reasonable survey effort, but fewer resources may be necessary for the REM, highlighting its advantage over CT-DS.

Table 6.1 Summary of spatial mark-resight (SMR), the random encounter model (REM), and camera trap distance sampling (CT-DS) density estimates presented in this thesis, showing the associated 95% confidence intervals (CI) and coefficient of variation (CV).

Thesis chapter	Site (survey)	Species	Method	Density (individuals/km ²) [95% CI]	CV
2	A (1)	Badger	REM	4.9 [1.5 – 16.1]	0.67
			CT-DS (react. incl.)	6.2 [1.4 – 27.3]	0.86
			CT-DS (react. excl.)	6.0 [1.4 – 26.4]	0.86
	B (2)		REM	20.2 [11.8 – 34.4]	0.28
			CT-DS (react. incl.)	19.8 [11.4 – 34.1]	0.28
			CT-DS (react. excl.)	13.8 [7.6 – 25.1]	0.31
	B (3)		REM	11.7 [6.3 – 22.0]	0.33
			CT-DS (react. incl.)	14.5 [9.4 – 22.4]	0.22
			CT-DS (react. excl.)	13.1 [8.7 – 19.8]	0.21
	C (4)		SMR	16.8 [10.4 – 27.1]	0.25
			REM	12.1 [7.7 – 18.9]	0.23
			CT-DS (react. incl.)	14.0 [8.9 – 22.0]	0.23
			CT-DS (react. excl.)	12.5 [7.8 – 20.0]	0.24
	D (5)		SMR	11.8 [6.6 – 21.0]	0.30
			REM	14.5 [9.1 – 23.1]	0.24
			CT-DS (react. incl.)	18.1 [9.1 – 36.2]	0.36
			CT-DS (react. excl.)	8.9 [4.6 – 17.2]	0.34
	E (6)		SMR	17.6 [6.8 – 45.3]	0.51
			REM	1.4 [0.6 – 3.0]	0.42
			CT-DS (react. incl.)	2.3 [0.9 – 5.7]	0.49
			CT-DS (react. excl.)	1.6 [0.6 – 4.5]	0.54
4	Woodchester Park	Badger	REM	3.6 [2.6 – 4.9]	0.16
			CT-DS (react. excl.)	6.0 [4.5 – 8.9]	0.17
		Muntjac	REM	45.5 [35.1 – 59.1]	0.13
			CT-DS (react. excl.)	48.0 [36.7 – 66.9]	0.15
		Red fox	REM	0.5 [0.4 – 0.8]	0.22
			CT-DS (react. excl.)	0.5 [0.3 – 0.8]	0.24
		Roe deer	REM	16.4 [12.1 – 22.3]	0.16
			CT-DS (react. excl.)	15.1 [9.4 – 37.7]	0.44
5	A	Badger	REM	1.39 [1.01 – 1.91]	0.16
			CT-DS (react. excl.)	1.13 [0.64 – 1.70]	0.27
	B		REM	2.86 [1.55 – 5.27]	0.32
			CT-DS (react. excl.)	4.72 [2.08 – 8.23]	0.35

In **Chapter 5**, I explored if the REM and CT-DS could detect statistically significant ($p \leq 0.05$) increases in badger density with sufficient power ($\geq 80\%$) given our study designs. There were no substantial differences between the two methods, with the REM marginally outperforming CT-DS at site A and the opposite trend at site B. However, at site A, where both the year one densities and the absolute increase in density were comparable, the REM required substantially fewer cameras to detect population increases. For example, to detect a 25% increase in badger density between two consecutive surveys with 80% power, given the same average survey duration (51.2 days), the REM required 256 cameras while CT-DS required 448. Considering the cost of the equipment and resources required to process images from these additional cameras, the REM far outperforms CT-DS in this scenario. For example, based on the figures presented in Table 5.7, the first year of a survey using 256 cameras would cost an estimated £88,000, while using 448 cameras would almost double the cost to £160,000.

Regarding ease of implementation, the methods required the same procedures and fieldwork skills. Camera traps are relatively straightforward to operate, making it feasible to train volunteers and citizen scientists to support surveys (Schaus *et al.*, 2020). In terms of data analysis, similar statistical knowledge and coding abilities are required by both methods. At present, a fully automated pipeline does not exist for either method, but Zampetti *et al.* (2024) highlight the particular suitability of CT-DS for an unsupervised framework with integration of machine learning tools for species classification.

To summarise the comparison of the REM and CT-DS, our results suggest that both methods are suitable for obtaining accurate estimates of unmarked animals, though the discrepancy between the estimated badger densities in **Chapter 4** warrants further analysis. The REM was consistently more precise than CT-DS, and accuracy was robust to declining survey effort. Though there were no substantial differences in data processing requirements, the REM may facilitate precise density estimation with fewer camera traps and higher power, potentially reducing the cost of camera surveys compared to CT-DS.

6.6. Utilising camera trap data to inform wildlife management decisions

Information obtained from camera traps has many scientific uses beyond abundance estimation, such as inference of species presence, richness, and distribution. The collection of ancillary data, including time and temperature, coupled with the development of statistical tools has enabled acquisition of information that can help understand species' ecological requirements and guide management practices. Camera traps are also becoming increasingly popular for studying animal

behaviour and for monitoring behavioural changes in response to environmental triggers (Caravaggi *et al.*, 2020).

In **Chapter 4**, data from camera traps was used to assess the management priorities for four species at Woodchester Park, Gloucestershire. Using heat maps to visually depict the spatial distribution of species, I found that each had a distinct pattern of habitat use. For example, both deer species tended to avoid the central region of the park, which was characterised by open pasture and a busy public footpath, and the areas in which muntjac and roe deer were most frequently detected did not overlap with each other. Despite population control, the two deer species were highly abundant, with the density of non-native muntjac exceeding the native roe deer by a ratio of approximately 3:1. The distinct patterns of habitat use could support suggestions that that muntjac exert interspecific competition on roe deer (Zini *et al.*, 2023). If the reported densities of these two species are high relative to carrying capacity, grazing pressure could have a profound impact on the vegetation and woodland composition of Woodchester Park. More substantial management interventions may therefore be necessary, particularly as the park is designated as a Site of Special Scientific Interest.

Unsurprisingly, in comparison with the two deer species, the abundance of badgers and, in particular, red foxes were relatively low at Woodchester Park. While culling of these species is not permitted in the park itself, removal likely occurs on nearby farms, highlighting the potentially wide-reaching impacts of culling. Though there are no published earlier density estimates for foxes in Woodchester Park, the badger population has been intensively studied since 1976 (Cheeseman, 1987), providing long-term abundance trends. Our results represent the lowest published density estimate for badgers in the study area to date. Such low numbers of badgers and foxes could lead to disruption of the species composition in Woodchester Park. Though the broader ecological consequence of controlling predators is highly debated (Roos *et al.*, 2018), badger removal has been found to be associated with an increase in hedgehogs (Trewby *et al.*, 2014) and foxes (Trewby *et al.*, 2008), and a recent meta-analysis concluded that predation by foxes can limit the numbers of ground-nesting birds (Roos *et al.*, 2018). Notably, some hedgehogs were recorded on our camera traps at Woodchester Park (Fig. 4.3), which have not been recorded for a number of years at this site (Ruth Cox, *pers. comms*). A range of other mammalian predators, including stoats and polecat/ferrets, were also detected (Fig. 4.3), which may support the ‘mesopredator release’ hypothesis (Rogers & Caro, 1998). Data from continued population monitoring in 2024, which do not form part of the analysis in this thesis, will help to understand if the structure of the community is changing.

Activity level is a key component of the REM and CT-DS models, and measuring it is valuable for many studies of animal behaviour and ecology. For example, activity patterns can indicate how species respond to anthropogenic pressures such as urbanisation and human disturbance, facilitating appropriate conservation strategies (Lindsay & Macdonald, 1985; Lovell *et al.*, 2022; Chen *et al.*, 2023). Comparing the activity patterns obtained for foxes and badgers in **Chapter 4** with those from comparable analyses on data from a heavily urbanised London park (Lovell *et al.*, 2022), both species in our study had reduced activity during the middle of the night which was not evident in the populations studied in London. This could be due to the impact of human disturbance in urban habitats or an abundance of food in the predominantly wooded landscape of Woodchester Park, reducing the need for continuous foraging. Both species were also culled in close proximity to Woodchester Park which could have influenced activity patterns. Ham *et al.* (2019) found that badger culling was associated with a decline in activity level, hypothesised to be due either to the removal of particularly ‘bold’ individuals which might emerge early (Lindsay & Macdonald, 1985) or to better access to food when competitor numbers are reduced. While our results in **Chapter 5** present a snapshot of badger activity following repeated widespread culling, continued assessment in future surveys over the next three years will make it possible to use data from camera traps to assess whether badger activity changes as populations recover post-cull.

Animal movement speed, which is important for the REM parameterisation, can be derived from camera trap data if distances are estimated reliably. Short-term measurements can be used to infer longer-term estimates of day range by summing activity across the daily activity cycle (Rowcliffe *et al.*, 2016). Changes to these metrics may reflect behavioural adaptations. For example, Ham *et al.* (2019) found that after culling, surviving badgers moved faster and had larger home ranges. In **Chapter 5**, I report that the average movement speed and day range of badgers in post-cull sites was higher than corresponding measurements derived from populations unaffected by culling in **Chapter 2** (Miles *et al.*, 2024). As for our activity-level hypotheses, a controlled study would be necessary to confirm the validity of this trend, but our results are nonetheless interesting and future surveys at these sites will make it possible to assess if behavioural changes in response to population control can be detected using camera trap data.

6.7. Could the REM and CT-DS be integrated into bTB management policy?

This thesis explores the suitability of the REM and CT-DS within wildlife management frameworks, specifically within the context of badger vaccination for bTB control. I show that, given sufficient survey effort, these camera-based methods can deliver accurate and precise estimates of badger density that would enable population monitoring and detection of population abundance trends. Here I compare these camera-based approaches with alternative abundance methods, discuss the

practical considerations of integrating the REM and CT-DS within national bTB control policy, and draw attention to the potential limitations of using these methods for this purpose.

Although this research applied the REM and CT-DS to small-scale projects, both techniques are adaptable for broader, landscape-level studies, as evidenced by their use in monitoring wild boar populations across Europe to assess pathogen transmission risks, where study sites ranged from 16km² to 730km² (Acevedo *et al.*, 2022; ENETWILD-consortium *et al.*, 2023). The scale of a survey is not explicitly modelled in the REM or CT-DS and therefore, unlike spatial methods, camera spacing does not need to consider the target species home range. Utilising 100 camera traps and designs similar to previous studies, which spaced cameras 1km to 2km apart (e.g. Palencia *et al.*, 2021; Mason *et al.*, 2022; Palencia *et al.*, 2022; Henrich *et al.*, 2023), it would be possible to cover an area of 81 km² to 171km², comparable to the scale of the East Sussex badger vaccination trial (DEFRA, 2021b). In **Chapter 5** I show that increasing the camera spacing to such vales would not substantially increase the cost of the survey (Fig. 5.3). However, working at this scale would likely incur additional costs for mileage, as vehicles would be required to deploy camera traps, which are not included in the calculations for figure 5.3.

While abundance estimation with the REM or CT-DS is more complex and resource intensive than the simple capture-recapture method employed by Benton *et al.* (2020), camera-based approaches may be more suitable for estimating vaccination coverage in post-culling landscapes where recapture rates could be low. Furthermore, the potential inclusion of 'trap shy' individuals in our camera-trapped samples may better represent the wider population, overcoming the limitations of approximating the 'trappable' population expressed by Benton *et al.* (2020). This is also true of non-invasive genetic capture-recapture analyses (Smith *et al.*, 2020), which have been used to estimate badger abundance at a national scale (Judge *et al.*, 2017). The foundation of this method in robust capture-recapture frameworks is appealing, particularly as the costs of genotyping have decreased substantially in recent years (Park & Kim, 2016), though the sampling process remains resource intensive (Wilson *et al.*, 2003). An evaluation of the cost and practicality of implementing genetic tools at scale would be beneficial in this context. Camera surveys may demand comparatively less fieldwork than capture-recapture methods, although, as highlighted in **Chapter 5**, the time required to process images is a major constraint to scaling these methods for national implementation. However, work in this area is progressing quickly (Vélez *et al.*, 2023). Restricting density analyses to badgers, and utilising artificial intelligence software to classify species, would substantially reduce the cost of the camera-based methods presented in this thesis. Where resources allow, the additional benefit of using camera traps is the potential for simultaneous density

estimation of multiple species (Fig. 4.3), facilitating a broader study of the impact of badger management on ecosystem dynamics.

A recurring challenge in our analyses, common to many ecological studies, was how to accurately estimate the area vaccinated. When area is not directly defined, density models approach this calculation statistically. For example, in SMR the area sampled is inferred from the spatial detection process and the movement of marked individuals. Methods which do not rely on individual recognition, such as the REM and CT-DS, calculate the area studied by summing the effective detection area of camera traps. However, when using these methods to estimate vaccination coverage, it is also necessary to determine the area vaccinated, which is distinct from the area sampled by camera traps. This is particularly relevant to small-scale projects, such as those detailed in **Chapters 3 and 5**, where the study sites ranged from 1.8 km² to 5.1km², similar to the scale of many current badger vaccination projects. In **Chapter 3**, I presented a method of estimating the area vaccinated utilising Dirichlet tessellations to delineate the effective ‘footprint’ of vaccinating badgers on the farms targeted for vaccination. Dirichlet tessellations use the location of badger setts to delineate territory boundaries (Doncaster & Woodroffe, 1993), taking advantage of information which is recorded during preliminary site surveys prior to badger vaccination. Additionally, in our study, we used knowledge of physical boundaries to badger movement, such as large water bodies or urban infrastructure, to help refine territory boundaries. This approach is straightforward and easy to implement with basic GIS skills and suitable for scaling up across larger areas, as highlighted by Doncaster and Woodroffe (1993). Boundaries can also be augmented with information from telemetry data or bait marking if available (Doncaster & Woodroffe, 1993).

I chose not to use the same Dirichlet tessellations approach used in **Chapter 2** at post-cull sites in **Chapter 5**, as comparable knowledge of territory structure was lacking for the post-cull sites. Instead, published estimates of territory sizes, inferred from data obtained during the Randomised Badger Culling Trial (RBCT; Woodroffe *et al.*, 2006a; Bielby *et al.*, 2014), were used to approximate the territory sizes of badgers in setts on land which was vaccinated. However, there are several shortcomings of this method. Firstly, social group territory sizes can vary substantially with habitat and resource availability (Kruuk & Parish, 1982; Judge *et al.*, 2017), so estimates from different environments may not be representative of our study sites. Secondly, there was no way of identifying with certainty which social groups and setts vaccinated badgers originated from. Since badgers in post-culling landscapes are more likely to trespass into the territories of neighbouring social groups (Ham *et al.*, 2019), it is possible that badgers inhabiting setts located beyond the boundaries of our study sites were trapped and vaccinated, and therefore our approximations will have underestimated the area vaccinated. For this particular project, detailed knowledge of local badger home ranges may

have been beneficial. However, when considering the use of camera-based approaches for estimating vaccination coverage on a larger scale, attempting to delineate social group home ranges is likely to be unnecessary. The areas targeted by future studies examining vaccination coverage should be large enough to encompass numerous home ranges and far exceed the average social group home-range size, thereby minimising the edge effects that may have influenced our results.

In **Chapter 5**, I explored application of the REM and CT-DS to monitoring the recovery of badger populations after culling. The results suggest that, in post-cull scenarios, where the rate of population recovery is slow, small changes in population size may be difficult to detect with camera surveys spaced 12 months apart. Surveys spaced 24 or 26 months apart would be necessary for this purpose. However, population declines, which are not constrained by biological and ecological processes, may be more pronounced and easier to detect. As such, the government could use this approach to monitor the effectiveness of badger culling operations, where population declines of 70% may be detectable and annual assessments could be conducted.

6.8. Implications for bTB eradication policy

The results of this thesis have important implications for the UK's bTB eradication policies. In England, badger culling is expected to be gradually phased out in favour of badger vaccination (DEFRA, 2020, 2024d). However, with few post-cull vaccination studies to date, the contribution of this strategy to bTB eradication remains uncertain. Byrne *et al.* (2021) emphasise the need for “robust, reproducible, and cost-effective metrics of badger population size at local and national level” to assess the effectiveness of badger vaccination in controlling bTB. Our results support the use of camera traps for this purpose and address a key question regarding the feasibility of this approach by estimating the coverage achieved in culled and uncultured areas. Additionally, this thesis provides guidance for policymakers on the necessary effort and cost of long-term population monitoring and estimating vaccination coverage with camera traps.

Although vaccination is a well evidenced method for controlling zoonoses, concern has been expressed within the farming community that such an approach would be ineffective in the control of bTB as too few badgers would be trapped and vaccinated to make it worthwhile (Chivers *et al.*, 2022; Woodroffe *et al.*, 2024). Yet there is little evidence to support this assumption. In **Chapter 3** I found that, across five vaccination operations, vaccination coverage consistently surpassed 30% (range 30.1% – 109.1%; using badger territories to estimate the area vaccinated), a threshold identified with statistical modelling to be necessary for local elimination of bTB in badger populations in the Republic of Ireland, when implemented alongside cattle control measures (Aznar *et al.*, 2018). I also found that high vaccine coverage was apparently attainable post-cull under some density

scenarios, as detailed in **Chapter 5**, although the results were highly imprecise, making inference of coverage challenging. Nonetheless, these results are encouraging, suggesting that badger vaccination is practical and can achieve coverages which may be sufficient for reducing *M. bovis* transmission among badgers and, hence, from badgers to cattle.

The imprecision of the results in **Chapter 5** suggests that estimating coverage as a snapshot in the first- or second-year post-cull is unlikely to be sufficient for understanding the effectiveness of a post-cull badger vaccination strategy. The badger population is expected to increase with time post-cull, which means a given proportional change in population size should become detectable with greater statistical power over time. Additionally, trappability (the percentage of all individuals known to be alive in the population that are captured; Tuytens *et al.*, 1999) is expected to increase with time post-cull as badgers face more competition for resources and may be more attracted to bait, and non-trap-shy cubs are introduced to the population. Consequently, estimates of vaccination coverage should become more precise over time as the population size – and the number of badgers vaccinated – grows, leading to more precise density estimates. However, monitoring population size early in a post-cull scenario remains important, as it provides a baseline for understanding how vaccination coverage changes over time. Continued population monitoring for several years may therefore be necessary. Our power analyses support this conclusion, as detecting changes in density with sufficient power necessitated surveys conducted 36 months apart under annual population growth rate scenarios of $\geq 10\%$. Assessing vaccination coverage over larger geographic scales than considered in **Chapter 5** (up to 5km²) would also help to address uncertainty in the results. Stochastic variation would be reduced if both the number of badgers vaccinated and the population within the area vaccinated increased (e.g. by studying a larger area), thus improving the precision of the estimated proportion vaccinated. Both density estimation methods explored in this thesis are scalable, and the precision of the results could be improved further with the use of more camera placements. Longer-term studies over areas larger than considered in **Chapter 5** are therefore recommended, such as a vaccination trial on the scale of the RBCT.

Interestingly, no cubs were captured during vaccination operations at sites A or B, as described in **Chapter 5**, which were examined in the first- and second-years post-cull, respectively. Typically, cubs make up 27% of the population (Rogers *et al.*, 1997), though birth rate is likely to be low immediately after culling (Cheeseman, 1993). Because numbers were small in the present study, it is difficult to be confident in the conclusions, however, the small number of cubs captured invites speculation as to whether vaccinating badgers soon after culling is the most effective strategy. Vaccination only works on susceptible individuals, and young cubs are less likely to have been exposed to *M. bovis* (Woodroffe *et al.*, 2006b), and so more likely to be susceptible to infection.

Vaccinating cubs before they have the opportunity to disperse may also help reduce the risk of disease transmission to the wider population (Gaughran *et al.*, 2019). At the very least, this pattern suggests future studies should focus on larger areas to explore this observation further, such as the entire area selected for vaccine delivery in **Chapter 5**.

Our results provide valuable information for policymakers deciding optimal approaches for estimating badger density within the framework of bTB policy. A recent strategy update for bTB policy in England included an expression of intention for a national badger survey (DEFRA, 2024d). This survey could follow the structure of the most recent national badger survey, which estimated mean social group size using capture-recapture analyses of genotyped badger hair and combined this with sett survey data to estimate badger densities across England and Wales (Judge *et al.*, 2017). It also presents an opportunity to incorporate camera traps, by carrying out methods such as the REM and CT-DS alongside sett surveys and capture-recapture analyses to provide an independent estimate of badger density. Our analysis in **Chapter 4** suggests that surveys should use a minimum of 100 cameras for this purpose, and short deployment times of three or four weeks are possible if there are at least 140 camera placements. As large variability in badger density is expected across the country (Judge *et al.*, 2017), our results should serve as minimum guidance for practitioners. Cost will likely play a critical role in deciding which method to implement. The results in **Chapter 5** suggest that obtaining badger density estimates with camera traps is expected to cost a similar amount to delivering badger vaccination, depending on the frequency of surveys, the use of volunteer assistance and the integration of artificial intelligence. This analysis provides policymakers with valuable insights into the projected cost of scaling these methods, enabling comparison with alternative strategies.

6.9. Wider application of the REM and CT-DS

This thesis explores the application the REM and CT-DS to a variety of terrestrial mammals, including badgers, muntjac, red foxes, and roe deer, in areas with medium to high population densities. Other studies have utilised these methods for a range of species in different habitats, with various behavioural characteristics and ecological traits. Most commonly the REM and CT-DS have been applied to ungulates (including Grevey's zebra *Equus grevyi*, Zero *et al.*, 2013; Moose *Alces alces*, Pfeffer *et al.*, 2018; red deer *Cervus elaphus* and wild boar *Sus scrofa*, Palencia *et al.*, 2022), as well as a number of carnivora (including African lions *Panthera leo*, Cusack *et al.*, 2015b; Leopards *Panthera pardus*, Cappelle *et al.*, 2021; and Asiatic black bears *Ursus thibetanus*, Miura *et al.*, 2022), and lagomorphs (including brown hares *Lepus europaeus*, rabbits *Oryctolagus cuniculus*, Mason *et al.*, 2022; and Iberian hares *Lepus granatensis*, Palencia *et al.*, 2022). While CT-DS has been successfully applied to aboral species (such as western chimpanzees *Pan troglodytes verus*, Cappelle *et al.*, 2021;

and grey squirrels *Sciurus carolinensis*, Mason *et al.*, 2022), the use of the REM for such species is less common (but see Balestrieri *et al.*, 2016). This section examines which species and habitats are likely to be most suitable for these models.

The REM and CT-DS are valuable for monitoring individually unidentifiable species, but methods such as photographic mark-resight may be more appropriate where species are individually identifiable, particularly if the population density is expected to be very low. For example, African lions, which occur at densities as low as 1.2 (95% CI 0.72–1.99) individuals per 100km² in Botswana, are easiest to monitor when cameras are placed strategically to maximise encounter rates (Rich *et al.*, 2019). Since African lions can be identified from their natural markings (ear nicks, manes, whisker spot patterns, and scars; Rich *et al.*, 2019), photographic mark-recapture is likely to be more suitable in this context as it does not demand random camera placement.

Behavioural characteristics of the focal species, including habitat use and social cohesion, may influence the choice of density method. Aggregated use of space can lead to biased and highly variable trap rates, affecting the accuracy and precision of the REM and CT-DS models, though several approaches exist to mitigate such bias. A study of African lions in the Serengeti found that population density was consistently overestimated due to the tendency for lions to gather beneath trees for shade during the day, thus congregating near camera traps (Cusack *et al.*, 2015b). This bias was countered by restricting data to nighttime periods, when lions moved more freely around the habitat. Similarly, Garrote *et al.* (2021) found that inflated population density estimates of Iberian lynx *Lynx pardinus* could be corrected by compensating for the rate at which lynx used tracks, where camera-traps were positioned. Gregarious species also tend to generate aggregated trap rates, and therefore less precise density estimates. Though the REM and CT-DS can be adapted for non-independent detections by treating the group as the unit of measure and multiplying density estimates by the average group size (Rowcliffe *et al.*, 2008), simulations suggest that the results are least biased when applied to non-gregarious species (Hayashi & Iijima, 2022).

In habitats where animals – or their signs – are easily visible, count surveys, such as line transects, standard distance sampling techniques, and aerial surveys, may be easier. The REM and CT-DS are of particular value in forested areas, where animals can be difficult to find and random camera placement is easy to adhere to, and mountainous regions that are difficult to access repeatedly (Kavcic *et al.*, 2021). Adaptation of the REM for use with acoustic detectors also makes this method widely applicable to species in both marine and terrestrial environments (e.g. birds, bats, and cetaceans; Lucas *et al.*, 2015).

6.10. Practical guidance for conducting camera trap surveys

Our research contributes practical recommendations for optimising camera trap surveys. Knowledge of the necessary survey effort for obtaining precise density estimates and detecting population trends, analysed in **Chapter 4** and discussed in detail previously in this discussion (Chapter 6.4), is particularly valuable. Since it is not uncommon for some cameras to malfunction, or to be disturbed or stolen, an over-cautious approach is recommended, aiming for a minimum of 100 camera placements, +10%, to mitigate any potential losses. Our cost-effort analysis in **Chapter 5**, which considered the entire process, from planning and preparing surveys to deploying cameras and analysing images, can serve as a template for estimating the resource requirements for similar surveys.

As discussed in **Chapters 2 and 4**, one of the biggest challenges encountered with fieldwork was the interference of livestock with cameras (Fig. 2.7). The loss of data from surveys in Cornwall (**Chapters 2 and 3**), where livestock interference was highest, likely contributed to the low precision of the results. When using data from camera images to estimate animal speed and the dimensions of the detection zone, it is important not to overlook movements to the camera's field of view which may affect the accuracy of distance estimates on which these parameters depend. To reduce the impact of such disturbances, cameras should be checked and recalibrated regularly, particularly if livestock are present. I found that calibrating deployments at the beginning, midway point and upon collection was sufficient for a seven-week survey, where cattle and sheep were present (**Chapter 5**).

6.11. Conclusions

This research contributes to the understanding of how camera traps can be used to estimate the density of unmarked animals to inform management decisions. I have tested the reliability of the REM and CT-DS, two methods which are growing in application, across a range of mammal species and density scenarios and applied them in a novel context: estimating badger density and vaccination coverage to assess bTB management strategies. I compared the accuracy and precision of both models and explored how to mitigate potential sources of bias. By integrating population monitoring with badger vaccination, I showed that a sufficient proportion of the population can be vaccinated, even where density is relatively low, consistent with the hypothesis that badger vaccination is a feasible strategy for bTB control. However, in a post-culling landscape, long-term population monitoring may be necessary to reliably estimate vaccine coverage and to understand the likely implications of a post-culling badger vaccination strategy. I show that acceptable precision can be obtained with reasonable survey effort and provide recommendations for survey designs needed to achieve this. I also present a detailed analysis of the resource requirements of using camera-based approaches for estimating animal density and the likely financial cost of scaling these methods for

3545 integration within national bTB policy. Whilst many of the results are discussed in the context of bTB
3546 control, they are broadly applicable to animal management and conservation policies. Overall, the
3547 findings support the use of camera-based approaches for informing management decisions, whilst
3548 highlighting the importance of robust survey design to achieve reliable results.

7. References

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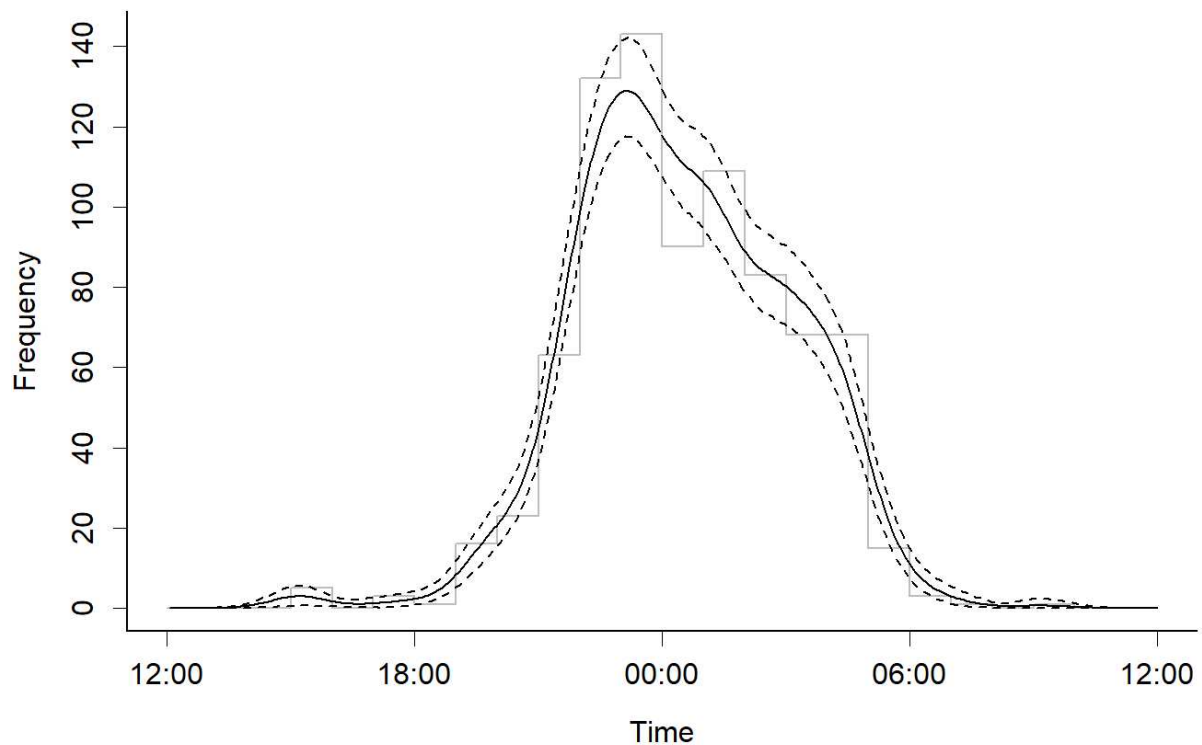
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Appendix 1: Supplementary information for Chapter 2

Figure S1 Activity pattern of badgers, characterised by fitting circular kernel models to radian time distributions of camera trap records from four sites in Cornwall where badgers were cage trapped, vaccinated and uniquely marked for spatial mark-resight analyses. Badgers were largely nocturnal, with comparatively few records between 12:00 and 18:00.



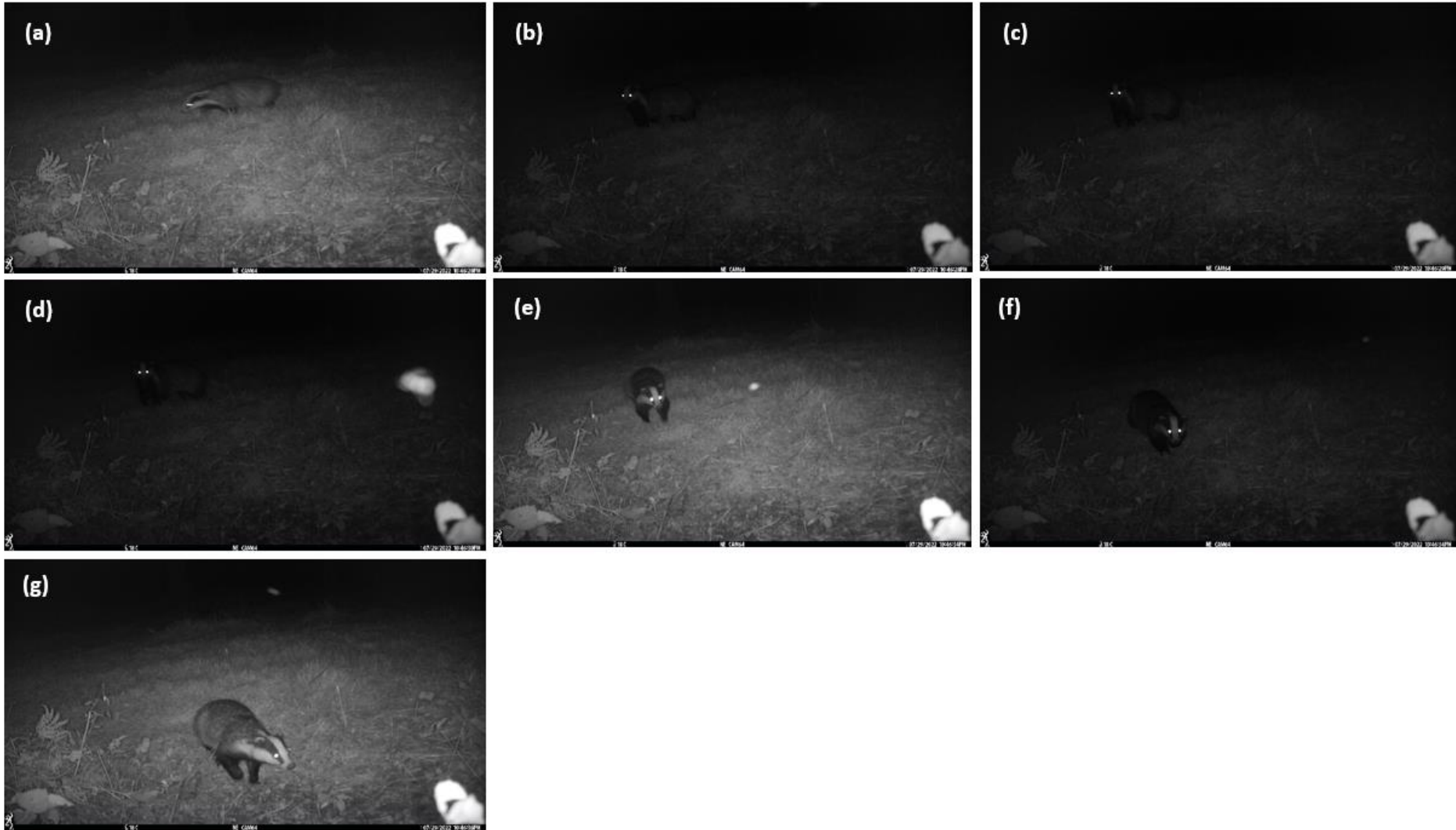
4362 **Appendix 2: Supplementary information for Chapter 4**

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4364 **Figure S2** Sequences illustrating ‘attraction’ to camera traps occurring after the first encounter for badger (a – g), muntjac (h – ae) and roe deer (af – bo).

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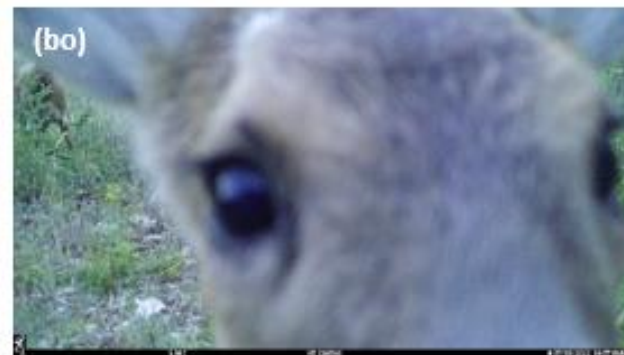
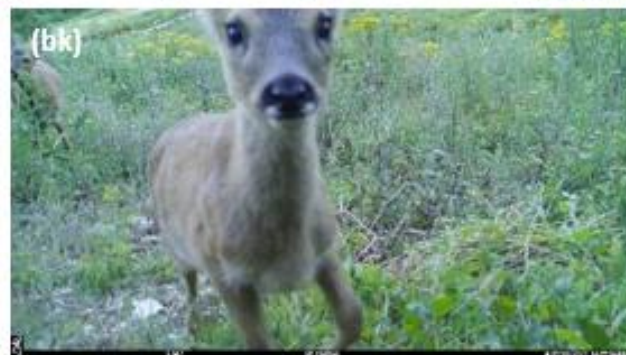




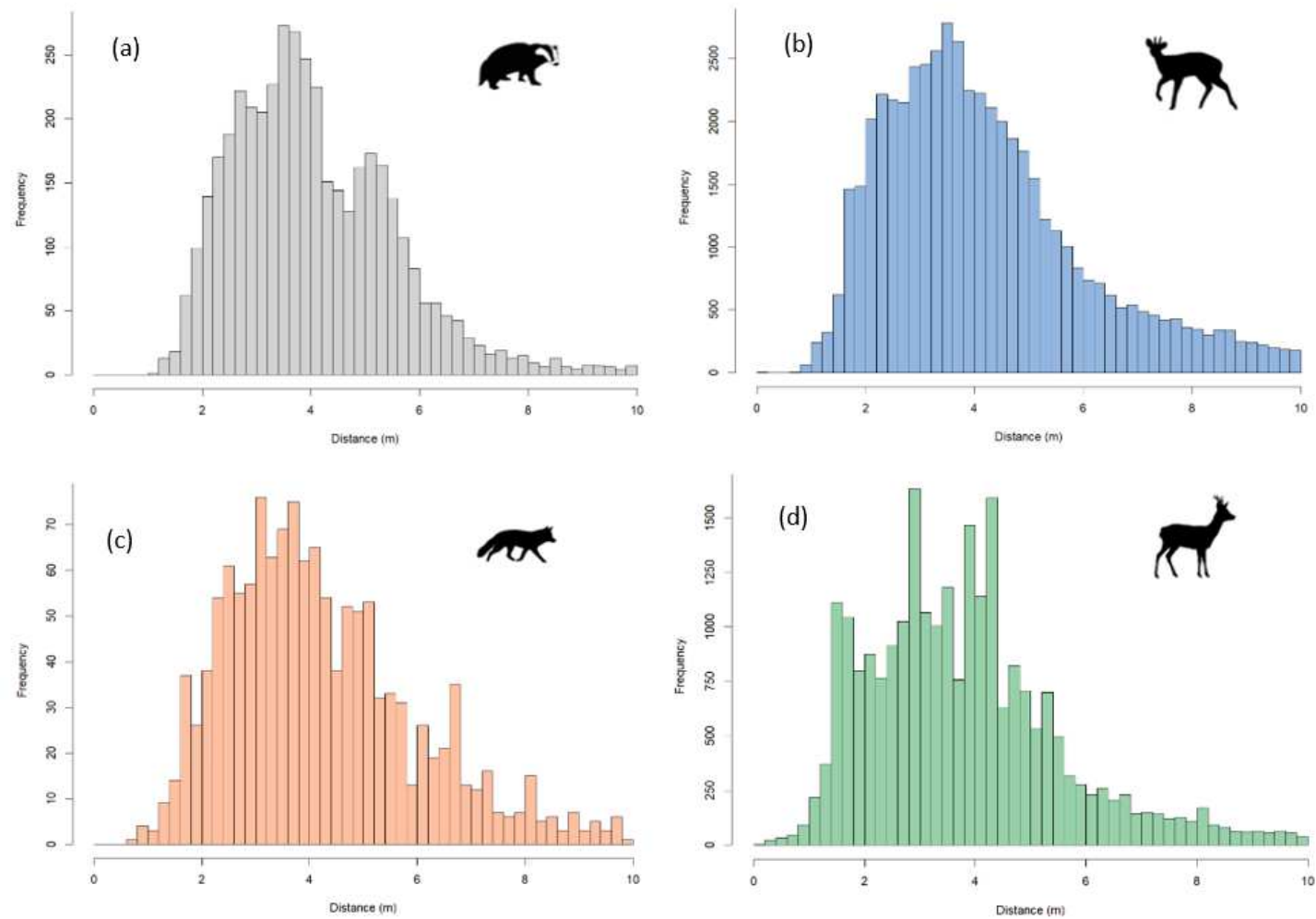
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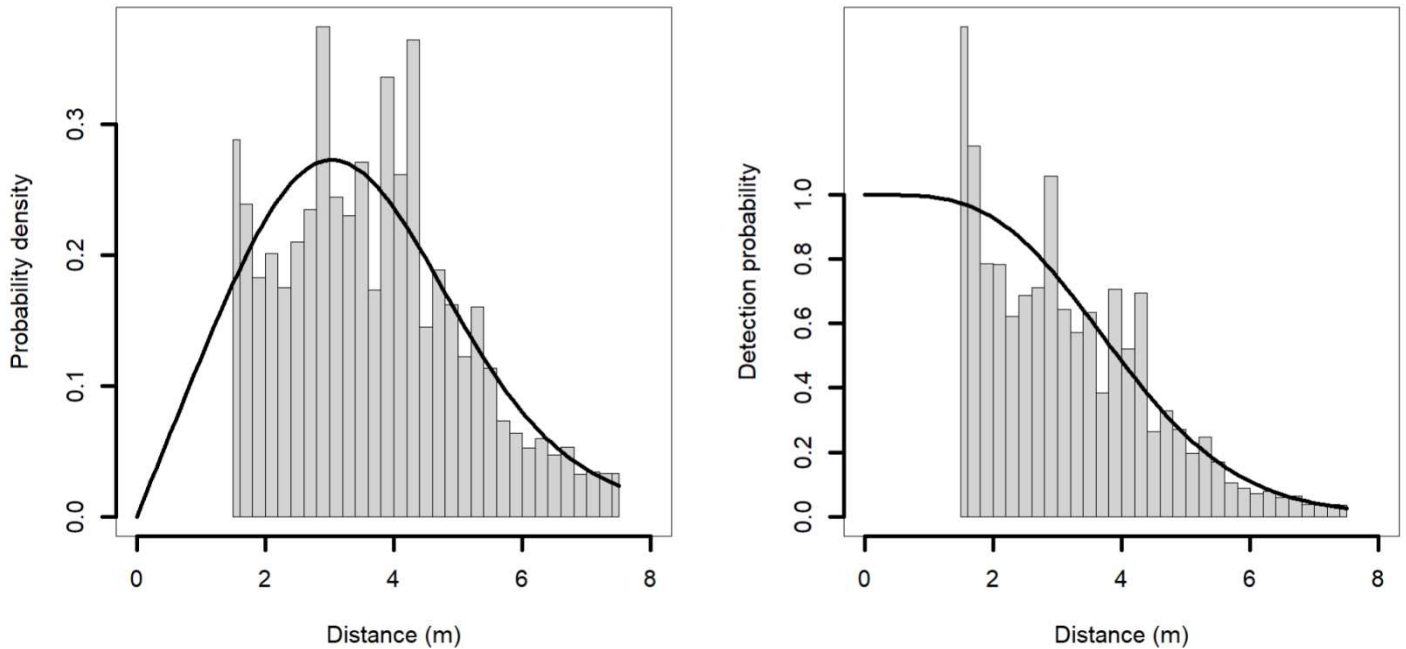
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4372 **Figure S3** Frequency distributions of animal distances from camera traps at Woodchester Park, shown for badgers (a), muntjac (b), red foxes (c), and roe
4373 deer (d). Species silhouettes were sourced from Anthony Caravaggi, Gabriela Palomo-Munoz (licence CC BY-NC-SA 3.0; [https://creativecommons.org/](https://creativecommons.org/licenses/by-nc-sa/3.0/)
4374 [licenses/by-nc-sa/3.0/](https://creativecommons.org/licenses/by-nc-sa/3.0/)) and Ferran Sayol (licence CC0 1.0).



4375 **Figure S4** Probability density (left) and detection probability (right) curves for the chosen camera trap
 4376 distance sampling model for roe deer. As detection probability is assumed to decline with distance
 4377 from the camera, 'spikes' were identified where this pattern was not followed (between 2.8m and
 4378 4.2m). The detection probability graph shows detection probability (black line) as a function of
 4379 distance using the half-normal point transect model with two adjustment terms. The bars of the
 4380 detection probability histogram are resized to visualise the fit of the model, rather than representing
 4381 true detection probability. This rescaling aligns the bars with the shape of the detection function,
 4382 explaining why some bars exceed a value of 1.



4383 **Table S5** Density model parameters for the random encounter model (REM) and camera trap
4384 distance sampling (CT-DS) estimated using the full data or each specified time interval (defined in
4385 Table 4.1), presenting the mean and standard error (in square brackets). Estimates chosen for the
4386 final density models are marked with an asterisk.

4387

	Time interval 1	Time interval 2	Time interval 3	Full data
Model parameters				
Shared				
Activity level	0.28 [0.02]	0.33 [0.02]	0.32 [0.02]	0.30 [0.01] *
Effective detection angle (radians)	-	-	-	0.66 [0.02] *
REM				
Trap rate (contacts/camera/day)	0.09 [0.02] *	0.10 [0.02] *	0.08 [0.01] *	-
Speed (m/s)	0.21 [0.02]	0.25 [0.02]	0.21 [0.02]	0.22 [0.02] *
Effective detection radius (m)	-	-	-	5.50 [0.10] *
CT-DS				
Truncation distances (left, right; m)	1.5, 7.5 *	2.0, 6.8 *	2.0, 8.0 *	-
Probability of detection	0.41 *	0.43 *	0.33 *	-

Appendix 3: Supplementary information for Chapter 5

Table S6 Data from the Randomised Badger Culling Trial of the estimated home range sizes of badger social groups within 500m of culling operations that took place within the past two years (from Bielby *et al.*, 2014). Home range areas were estimated using the Dirichlet tessellations method detailed in Woodroffe *et al.* (2009b). We used the average home range size to estimate circular home ranges around badger setts (Table 5.2, method 2).

Triplet	Social group	Home range size (ha)	Years since culled
B	B2A	120.3	0
B	B2AM	148.6	0
B	B2AQ	290.0	0
B	B2G	168.5	0
B	B2AD	124.5	1
B	B2AE	219.0	1
B	B2AP	306.6	1
B	B2AS	192.4	1
B	B2AU	111.5	1
B	B2C	156.9	1
B	B2D	192.0	1
C	C3AL	56.1	1
C	C3AM	179.6	1
C	C3B	277.9	1
A	A3L	175.4	2
B	B2B	202.8	2
C	C3J	278.9	2
E	E3AD	134.0	2
E	E3AF	129.0	2
E	E3AM	171.4	2
E	E3BG	168.1	2
E	E3BH	171.9	2
E	E3BN	76.0	2
E	E3H	298.8	2
F	F1W	288.8	2

4397 **Table S7** Summary of the parameters used for power analyses. Projected badger densities are shown for four years under three population recovery rate
 4398 scenarios. Badger density was estimated using the random encounter model (REM) and camera trap distance sampling (CT-DS). Sample size was estimated
 4399 as the mean sample size of the of the density components weighted by their contribution to the overall error of density estimates.

Site	Density method	Sample size	Pooled standard deviation	Paired years	Year one density (badgers/km ²)	Projected density given stated % annual increase (badgers/km ²)			Effect size given stated population increase		
						5%	10%	25%	5%	10%	25%
A	REM	187.5	2.4	1-2	1.39	1.46	1.53	1.74	0.03	0.06	0.15
				1-3		1.53	1.68	2.17	0.06	0.12	0.32
				1-4		1.61	1.85	2.71	0.09	0.19	0.55
A	CT-DS	161.4	2.5	1-2	1.13	1.19	1.24	1.41	0.02	0.05	0.11
				1-3		1.25	1.37	1.77	0.05	0.09	0.25
				1-4		1.31	1.50	2.21	0.07	0.15	0.43
B	REM	70.8	2.6	1-2	2.86	3.00	3.15	3.57	0.06	0.11	0.27
				1-3		3.15	3.46	4.47	0.11	0.23	0.62
				1-4		3.31	3.81	5.59	0.17	0.36	1.05
B	CT-DS	37.8	2.1	1-2	4.72	4.96	5.19	5.90	0.11	0.22	0.56
				1-3		5.20	5.71	7.38	0.23	0.47	1.26
				1-4		5.46	6.28	9.22	0.35	0.74	2.14

4400

Appendix 4: Details of published manuscripts using data from this thesis

Evaluating camera-based methods for estimating badger (*Meles meles*) density: implications for wildlife management (Chapter 2)

Received: 11 October 2023 | Accepted: 3 August 2024

DOI: 10.1002/2688-8319.12378

RESEARCH ARTICLE



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

Verity Miles^{1,2} | Rosie Woodroffe² | Christl A. Donnelly^{1,3,4} |
Peter N. M. Brotherton⁵ | Cally Ham² | Kelly Astley² | Joana Aurélio^{2,6} |
Marcus Rowcliffe²

¹School of Public Health, Imperial College London, London, UK; ²Zoological Society of London, Institute of Zoology, London, UK; ³Department of Statistics, University of Oxford, Oxford, UK; ⁴Pandemic Sciences Institute, University of Oxford, Oxford, UK; ⁵Natural England, Peterborough, UK and ⁶Faculdade de Ciências da Universidade de Lisboa, Lisbon, Portugal

Correspondence

Verity Miles

Email: v.miles20@imperial.ac.uk

Funding information

Natural England; Cornwall Wildlife Trust; National Trust; Zoological Society of London; People's Trust for Endangered Species; Imperial College London; Department for Environment, Food and Rural Affairs, UK Government; Natural Environment Research Council, Grant/Award Number: NE/S007415/1; Participating Landholders; Garfield Weston Foundation

Handling Editor: Jenny Macpherson

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

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Ecol Solut Evid. 2024;5:e12378.
<https://doi.org/10.1002/2688-8319.12378>

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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 km² (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.

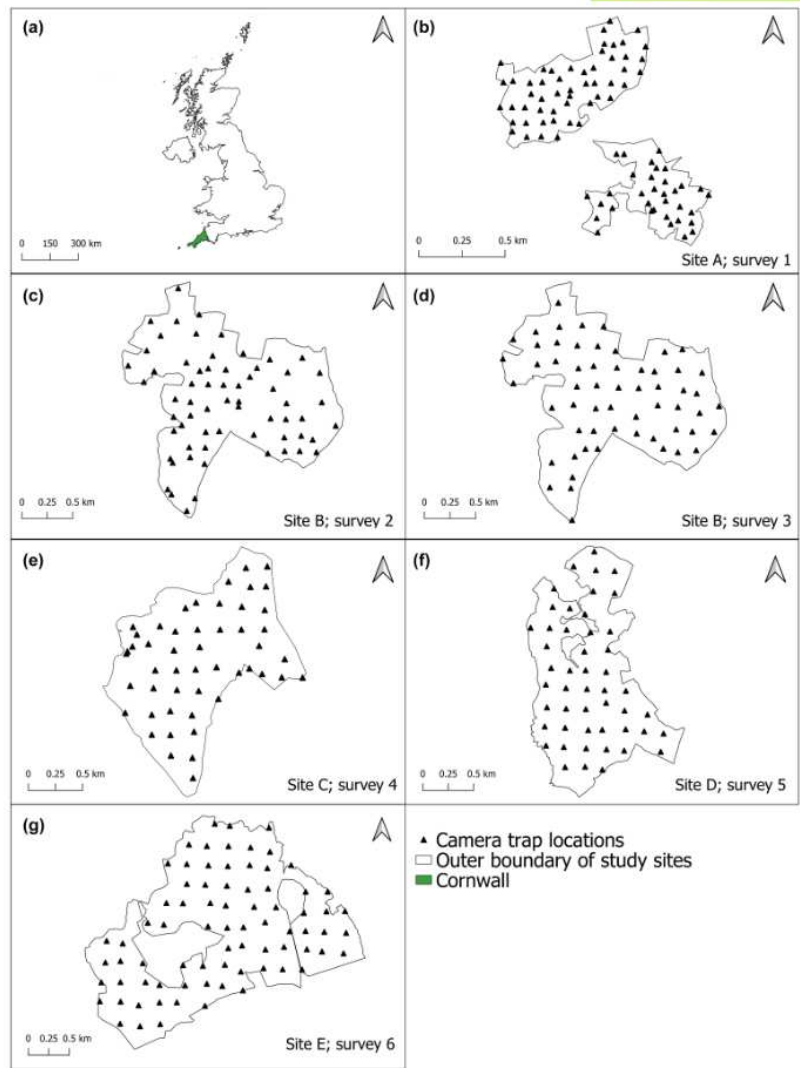


FIGURE 1 (a) Location of the five sites in Cornwall, UK and (b–g) layout of the camera grids deployed for each survey.

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)

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

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 24 h/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:

$$H = t / T \quad (2)$$

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:

$$e = \frac{\theta H}{2\pi T} \quad (3)$$

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

$$D = \frac{y}{\pi w^2 e p a} \quad (4)$$

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%

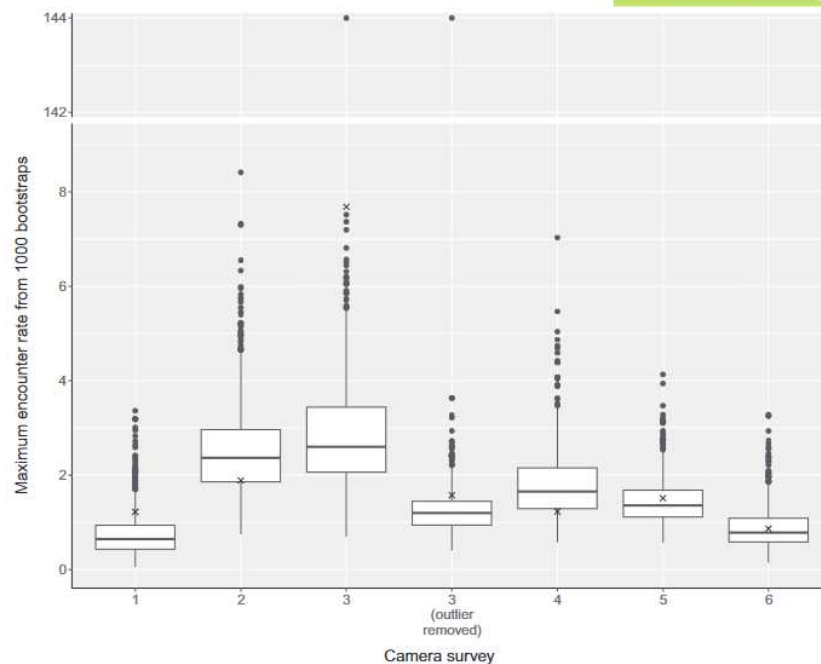


FIGURE 4 Boxplot showing the median (thick horizontal lines), interquartile range (boxes) and 2.5th and 97.5th centiles (vertical lines) of maximum encounter rates from seven data sets using 1000 samples from a negative binomial distribution fitted to the data, with sample sizes equal to the number of 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 km²), with an estimated density of 9.8 individuals per km² 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 km² 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

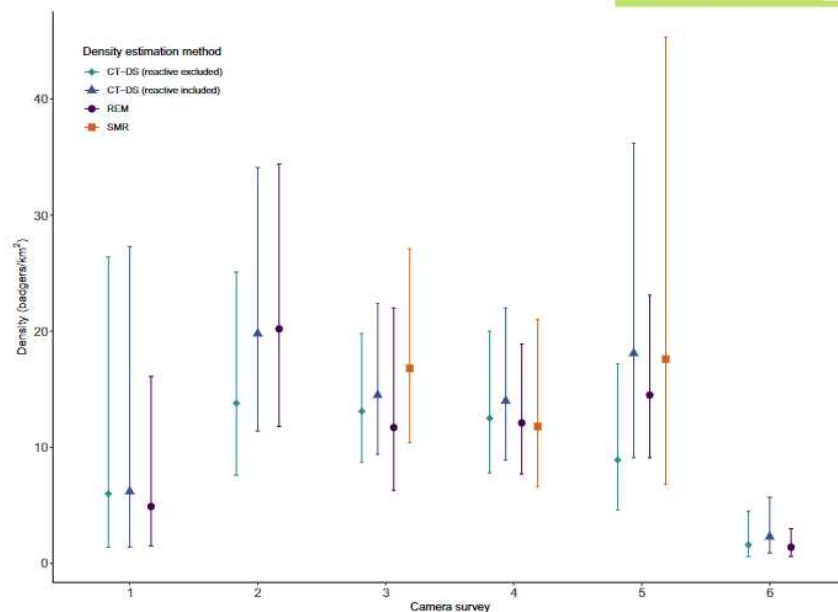


FIGURE 5 Badger densities per km² and associated 95% confidence intervals estimated from six camera surveys at five sites, using three camera trap-based methods (SMR analysis was only possible for three of the surveys).

TABLE 4 Estimated animal density per km², 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 km², detection probabilities for marking and sighting occasions of 0.09 and 0.04, respectively, and a spatial scale parameter (α) 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 km², 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 km², 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 km² (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.

ACKNOWLEDGEMENTS

This research was funded by the Natural Environment Research Council, Natural England and Imperial College London, as part of the Science and Solutions for a Changing Planet Doctoral Training

Programme, grant number NE/S007415/1. The Cornwall Badger Project was funded by Defra, the National Trust, the Garfield Weston Foundation, the People's Trust for Endangered Species, private donors to Cornwall Wildlife Trust, the Zoological Society of London, and some Participating Landholders. The Institute of Zoology is supported by Research England. For assistance with field-work, many thanks to Natalie Durrant, Sarah Ferry, Anisha Tennant, Sarah Hayes, Ruth McCabe, and Nicholas Steyn. Finally, we thank Matthew Penn for his work developing Sherlock which made image tagging more efficient.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/2688-8319.12378>.

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).

ORCID

Verity Miles  <https://orcid.org/0009-0003-7064-5488>

Rosie Woodroffe  <https://orcid.org/0000-0003-2104-3133>

Christl A. Donnelly  <https://orcid.org/0000-0002-0195-2463>

Peter N. M. Brotherton  <https://orcid.org/0000-0003-4341-9664>

Cally Ham  <https://orcid.org/0000-0002-9281-038X>

Kelly Astley  <https://orcid.org/0000-0003-4057-8491>

Joana Aurélio  <https://orcid.org/0009-0003-4249-5291>

Marcus Rowcliffe  <https://orcid.org/0000-0002-4286-6887>

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How to cite this article: Miles, V., Woodroffe, R., Donnelly, C. A., Brotherton, P. N. M., Ham, C., Astley, K., Aurélio, J., & Rowcliffe, M. (2024). Evaluating camera-based methods for estimating badger (*Meles meles*) density: Implications for wildlife management. *Ecological Solutions and Evidence*, 5, e12378. <https://doi.org/10.1002/2688-8319.12378>

Sherlock—A flexible, low-resource tool for processing camera-trapping images (using data from Chapter 2)

Penn, M. J., Miles, V., Astley, K. L., Ham, C., Woodroffe, R., Rowcliffe, M., & Donnelly, C. A.
Methods in Ecology and Evolution, 15, 91–102. (2024)

Abstract

1. The use of camera traps to study wildlife has increased markedly in the last two decades. Camera surveys typically produce large data sets which require processing to isolate images containing the species of interest. This is time consuming and costly, particularly if there are many empty images that can result from false triggers. Computer vision technology can assist with data processing, but existing artificial intelligence algorithms are limited by the requirement of a training data set, which itself can be challenging to acquire. Furthermore, deep-learning methods often require powerful hardware and proficient coding skills.
2. We present Sherlock, a novel algorithm that can reduce the time required to process camera trap data by removing a large number of unwanted images. The code is adaptable, simple to use and requires minimal processing power.
3. We tested Sherlock on 240,596 camera trap images collected from 46 cameras placed in a range of habitats on farms in Cornwall, United Kingdom, and set the parameters to find European badgers (*Meles meles*). The algorithm correctly classified 91.9% of badger images and removed 49.3% of the unwanted ‘empty’ images. When testing model parameters, we found that faster processing times were achieved by reducing both the number of sampled pixels and ‘bouncing’ attempts (the number of paths explored to identify a disturbance), with minimal implications for model sensitivity and specificity. When Sherlock was tested on two sites which contained no livestock in their images, its performance greatly improved, and it removed 92.3% of the empty images.
4. Although further refinements may improve its performance, Sherlock is currently an accessible, simple and useful tool for processing camera trap data.

Farmer-led badger vaccination in Cornwall: Epidemiological patterns and social perspectives (using data from Chapters 2 and 3)

Woodroffe, R., Astley, K., Barnecut, R., Brotherton, P. N. M., Donnelly, C. A., Grub, H. M. J., Ham, C., Howe, C., Jones, C., Marriott, C., Miles, V., Rowcliffe, M., Shelley, T., & Truscott, K. *People and Nature*, 6, 1960–1973. (2024)

Abstract

1. In the United Kingdom, the management of bovine tuberculosis (bTB) challenges the coexistence of people and wildlife. Control of this cattle disease is hindered by transmission of its causative agent, *Mycobacterium bovis*, between cattle and badgers *Meles meles*.
2. Badger culling has formed an element of bTB control policy for decades, but current government policy envisions expanding badger vaccination. Farming leaders are sceptical, citing concerns that badger vaccination would be impractical and potentially ineffective.
3. We report on a 4-year badger vaccination initiative in an 11 km² area which, atypically, was initiated by local farmers, delivered by scientists and conservationists, and co-funded by all three. Participating landholders cited controversies around culling and a desire to support neighbours as their primary reasons for adopting vaccination.
4. The number of badgers vaccinated per km² (5.6 km⁻² in 2019) exceeded the number culled on nearby land (2.9 km⁻² in 2019), and the estimated proportion vaccinated (74%, 95% confidence interval [CI] 40%–137%) exceeded the 30% threshold predicted by models to be necessary to control *M. bovis*. Farmers were content with how vaccination was delivered and felt that it built trust with wildlife professionals.
5. The percentage of badgers testing positive for *M. bovis* declined from 16.0% (95% CI 4.5%–36.1%) at the start of vaccination to 0% (95% CI 0%–9.7%) in the final year. With neither replication nor unvaccinated controls, this small-scale case study does not demonstrate a causal link between badger vaccination and bTB epidemiology, but it does suggest that larger-scale evaluation of badger vaccination would be warranted.
6. Farmers reported that their enthusiasm for badger vaccination had increased after participating for 4 years. They considered vaccination to have been effective, and good value for money, and wished to continue with it.
7. *Synthesis and applications:* Although small-scale, this case study suggests that badger vaccination can be a technically effective and socially acceptable component of bTB control. A wider rollout of badger vaccination is more likely if it is led by the farming community, rather than by conservationists or government, and is combined with scientific monitoring.

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Appendix 5: A selection of camera trap images

Figure S8 A selection of interesting camera trap photos obtained during these studies: (a) buzzard, *Buteo buteo*; (b) mallard, *Anas platyrhynchos*; (c) tawny owl, *Strix aluco*; (d) hedgehog, *Erinaceus europaeus*; (e) red foxes, *Vulpes vulpes*; (f) roe deer, *Capreolus capreolus*; (g) red fox; (h) badger, *Meles meles*, tattooed and fitted with a GPS collar; (i) an unusual record of a pine marten, *Martes martes*, in West Cornwall

