ORIGINAL RESEARCH

Camera trap distance sampling for terrestrial mammal population monitoring: lessons learnt from a UK case study

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Abstract

Accurate and precise density estimates are crucial for effective species management and conservation. However, efficient monitoring of mammal densities over large spatial and temporal scales is challenging. In the United Kingdom, published density estimates for many mammals, including species considered to be common, are imprecise. Camera trap distance sampling (CTDS) can estimate densities of multiple species at a time and has been used successfully in a small number of studies. However, CTDS has typically been used over relatively homogeneous landscapes, often over large time scales, making monitoring changes (by repeating surveys) difficult. In this study, we deployed camera traps at 109 sites across an area of 2725 km^2 of varied habitat in North-East England, United Kingdom. The 4-month survey generated 51 447 photos of wild mammal species. Data were sufficient for us to use CTDS to estimate the densities of eight mammal species across the whole-survey area and within four specific habitats. Both survey-wide and habitat-specific density estimates largely fell within previously published density ranges and our estimates were amongst the most precise produced for these species to date. Lower precision for some species was typically due to animals being missed by the camera at certain distances, highlighting the need for careful consideration of practical and methodological decisions, such as how high to set cameras and where to left-truncate data. Although CTDS is a promising methodology for determining densities of multiple species from one survey, species-specific decisions are still required and these cannot always be generalized across species types and locations. Taking the United Kingdom as a case study, our study highlights the potential for CTDS to be used on a national scale, although the scale of the task suggests that it would need to be integrated with a citizen science approach.

Introduction

Measuring animal density and abundance is important for monitoring trends in wildlife populations and for developing effective conservation and management strategies (Fryxell et al., 2014). Yet, developing robust methods and tools to estimate population densities accurately and precisely over large spatial and temporal scales are challenging for many taxa (Morellet et al., 2007). Calculating density estimates for mammals can be particularly difficult given that many species are nocturnal and easily disturbed by observers, and many occur at low densities. Consequently, monitoring efforts often rely on indirect observations of presence, such as dung or footprints. These indirect observations can be converted into measures of animal density if conversion factors such as rates of production and decay are known; however, the accuracy and precision of this approach are often questioned (Kuehl et al., 2007; Yoxon & Yoxon, 2014).

The extent of the challenge of estimating the abundance of mammal species is evident in published estimates for mammal species in the United Kingdom. For example, a recent estimate of abundance for one of the United Kingdom's most common species, the rabbit (*Oryctolagus cuniculus*), spanned two orders of magnitude, from 2 to 255 million (Croft et al., 2017). This imprecision largely results from a lack of species records overall, and a lack of habitat-specific density estimates, which makes it difficult to scale up to a national level. The lack of data on many mammal species is not unique to the United Kingdom and academics have highlighted the need for better monitoring of terrestrial mammals worldwide, including in Europe (ENETWILD-consortium et al., 2019; van Strien et al., 2016), Africa (Brashares & Sam, 2005) and Asia (Singh & Milner-Gulland, 2011). It is clear that new monitoring approaches are needed that can be deployed over large areas to generate a substantial number of records and produce reliable density estimates.

As technologies have developed, camera traps have been increasingly used as a means of passively monitoring species (Rovero & Zimmermann, 2016). Camera traps are particularly useful for monitoring elusive species and can gather large quantities of data more quickly than many more traditional survey methods (Burton et al., 2015). Methods for abundance estimation with camera traps have been developed for species in which individuals can be identified (Head et al., 2013; Silver et al., 2004; Williams et al., 2017) and for species in which individuals cannot be identified (Chandler & Royle, 2013; Gilbert et al., 2021; Howe et al., 2017; Luo et al., 2020; Moeller et al., 2018; Nakashima et al., 2017; Rowcliffe et al., 2008). Palencia et al. (2021) showed that three of these methods [random encounter model (REM), random encounter and staying time (REST) model and camera trap distance sampling (CTDS)] could be used to estimate densities consistent with independent estimates from line transects and drive counts. Although there were no significant differences between estimates produced by the methods, Palencia et al. (2021) suggested that CTDS would be more suitable for low-density species because the number of records increases more rapidly than with other methods (which use only initial contacts as their samples). The potential to accumulate larger datasets more rapidly would be beneficial for monitoring over large spatial scales, using shorter repeated surveys to track changes in populations. As with traditional point transect distance sampling (Buckland et al., 2001), CTDS typically assumes that detection is certain at distance zero but accounts for imperfect detection of animals further away from the camera. CTDS has been used to estimate densities that are consistent with either true known densities (Cappelle et al., 2019) or previously published estimates (Corlatti et al., 2020; Harris et al., 2020; Howe et al., 2017). CTDS has also been used to estimate densities of multiple species simultaneously (Bessone et al., 2020; Cappelle et al., 2021; Palencia et al., 2021).

In many countries, the level of monitoring is inconsistent among species, resulting in limited data on some species, even when they are considered common [e.g. rabbits in the United Kingdom (Croft et al., 2017) or wild boar across parts of Europe (ENETWILD-consortium et al., 2019)]. By gathering data and estimating density for multiple species at a time, CTDS may help to address this imbalance, as well as saving time and resources by removing the need for multiple surveys of different species. To date, studies that have used the CTDS method have been carried out in landscapes with little variation in habitat and with little human influence (Bessone et al., 2020; Cappelle et al., 2019, 2021; Corlatti et al., 2020; Harris et al., 2020; Howe et al., 2017). In many regions and countries, however, the landscape is much more varied and includes habitats heavily altered by humans. The method would need to be reliable and practical to employ over landscapes such as these if it was to be used for large-scale monitoring.

In this study, we aim to generate density estimates, including habitat-specific estimates, for a range of medium-large terrestrial UK mammal species. We assess our estimates against previously published density estimates for those species. Finally, taking the United Kingdom as a case study, we discuss the opportunities, limitations and challenges of using CTDS for large-scale and long-term species monitoring.

Materials and Methods

Survey area

Data were collected in North-East England. The 2725 km^2 study area covered County Durham, plus areas of Gateshead, Sunderland and Darlington. The region's landscape is varied, with mountain, heath and bog habitat in the west, improved grassland (high productivity grassland) in the centre of the region and a variety of habitats in the east, including arable and urban (Fig. 1; habitat classes from the Land Cover Map 2015, LCM; Rowland et al., 2017). The area's human population is around 1.1 million, with population densities ranging from 0.1 ha^{-1} in the most rural areas of County Durham to 20.2 ha^{-1} in urban areas such as Sunderland (ONS, 2021). The Human Influence Index (HII) ranks human influence from 0 (no influence) to 64 (maximum influence) according to nine measures of human presence (WCS and CIESIN, 2005); average HII was 37 (range 14–64; WCS and CIESIN, 2005) across our study sites.
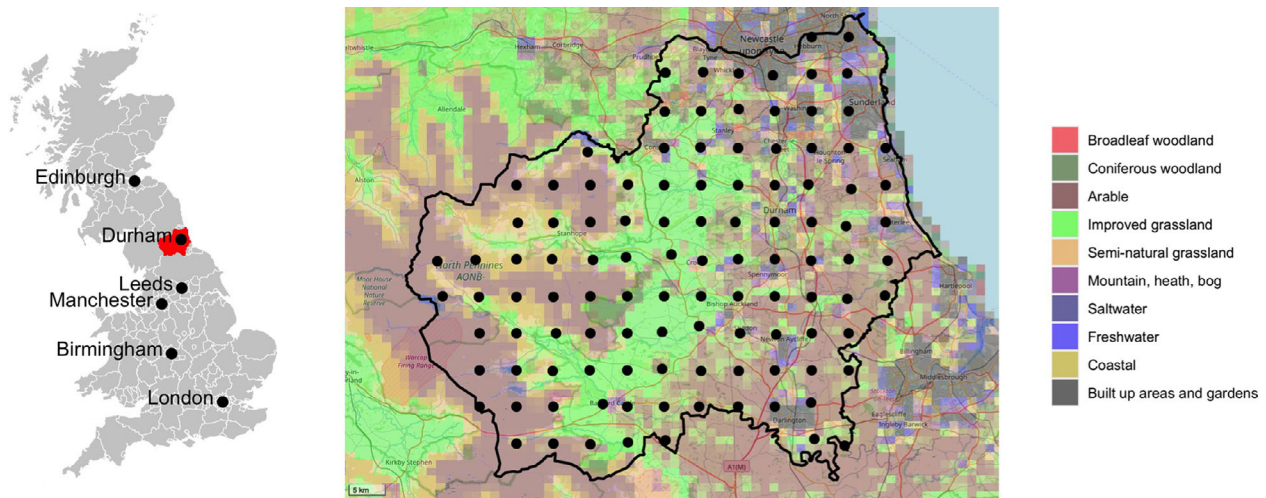
Figure 1. Left: location of survey area in the United Kingdom shown in red. Right: Map of 109 sites where camera traps were placed in County Durham. Habitat data from Land Cover Map 2015 (1 km dominant aggregate class, Rowland et al., 2017). Background map: © OpenStreetMap contributors, © CARTO licensed under CC BY-SA 2.0.

Camera trap survey

Within the study area, a grid was defined with 5 km² spacing and random geographical origin, with camera traps placed at the coordinates of the centre point of each cell in the grid. The survey took place over 109 sites (Fig. 1). Fifty Browning Strike Force BTC-5HDP cameras were rotated in a random order around these sites between June and October 2018. Orientation was randomly assigned for each camera. If cameras could not be placed in the exact predetermined location or orientation due to land access, vegetation blocking the field of view (FOV) or other reasons, then we placed them at the nearest suitable point, within the same habitat and without targeting placement to increase or decrease detection probability.

Researchers usually recommend setting cameras at the shoulder height of the target species (Meek et al., 2016) but this is obviously problematic when surveying multiple species of varying sizes. We also had issues with cameras being triggered or the FOV being partially or entirely blocked by vegetation when set at lower heights. Therefore, cameras were placed at a height of between 0.7 and 1.0 m from the ground and angled slightly downward. Cameras were set to 'rapid fire' mode, with eight photos taken in quick succession each time the camera was triggered. The delay between triggers was set to a minimum of 1 sec and the trigger speed of the camera was 0.3 sec according to manufacturers (Browning, 2017).

Availability for detection and angle measurements

CTDS requires an estimate of the availability for detection (Howe et al., 2017). We estimated the proportion of time

for which each species was available for detection by fitting a circular kernel model to radian time data, using the R package 'activity' (Rowcliffe et al., 2014) (Appendix S1). This method assumes that, at the daily peak, 100% of the population was available for detection. This assumption can be violated by any species but semi-arboreal species, in particular, will spend a proportion of their active period out of the view of camera traps. In our study, therefore, the assumption could have been violated for grey squirrels which spend a proportion of time in trees. However, our estimate for the availability of grey squirrels (0.33) was very similar to published data on the proportion of time grey squirrels spent on the ground in Italy (0.35, calculated using radio collars and observations, and taking a weighted average of the two figures published for Spring/Summer and Autumn/Winter) (Wauters et al., 2002). Consequently, we used our calculated figures for availability in our density estimations but we acknowledge that this might over-estimate availability and underestimate density for grey squirrels.

Detection is likely to decrease towards the edges of the FOV (Rowcliffe et al., 2011). However, if cameras are set to take long bursts or videos, then moving animals will still be detected at large angles; for this reason, Howe et al. (2017) used the full FOV of the camera in their CTDS density calculations. Despite this, it has been recommended that angles are measured as well as distances to check whether the sensitivity of the sensor across angles is uniform (Howe et al., 2017). These checks could be particularly important where cameras are set to take single images (Corlatti et al., 2020) or where there are unavoidable delays between triggers, such as in our study. We measured angles to image subjects and used these

data to calculate the effective detection angle (Hofmeester et al., 2017) (Appendix S1). As the effective detection angle differed from the FOV angle in almost all cases, we used this as our angle measurement for estimating density.

Distance sampling methodology

Howe et al. (2017) recommend defining snapshot moments to discretize the number of times an animal could be detected, and suggested values between 0.25 and 3 sec are likely to be useful. Corlatti et al. (2020) suggested using the minimum interval between captures as the value for the interval between snapshot moments when cameras are set to take single photos. Although we set our cameras to record in bursts of eight photos, there was an unavoidable delay of at least 0.3 sec between photos within a burst, and 1 sec between triggers (figures according to manufacturers; Browning, 2017). Therefore, we wished to set the snapshot interval to the average minimum interval between captures. However, as the figures reported in manufacturer's handbooks are not always accurate (Corlatti et al., 2020), we calculated the average of intervals between photos for periods of time when the camera was being constantly triggered during set up. We used this (0.8 sec) as our snapshot moment interval.

During camera set up, reference photos were taken with distance markers placed at 2-m intervals up to 10 m along the centre and down the sides of the FOV. Distance intervals were further decreased to 1-m intervals following data collection by using the overlaid grid tool in Adobe Photoshop (for details, see Caravaggi et al., 2016). As precise distances were more difficult to determine further away from the camera, animals at distances over 8 m were assigned to either an 8–10 m or 10+ m category. We measured distances of animals in all images. Images were screened and tagged in DigiKam (www.digikam. org).

As data in the 10+ m category accounted for <5% of overall data for each species, we right-truncated at 10 m for all species (Buckland et al., 2001). Distance sampling methodology assumes that detection is certain at zero distance; however, in CTDS, this assumption could be violated by animals passing underneath the camera or through the FOV before the camera is triggered (Howe et al., 2017). For each species, we worked on the assumption that detectability was highest in the distance category with the most captures per unit area and we left-truncated at the left boundary of that category. Exceptions to this rule were made in cases where: (1) data distribution was determined to be due to the presence of trails rather than animals being missed by the camera; (2) left truncation resulted in data being present in fewer

than five distance categories, causing poor model fit and inaccurate estimates of effective detection distance (required to calculate density estimates; Hofmeester et al., 2017); or (3) species showed attraction to the cameras. In all cases where we made exceptions to the left-truncation rule, sensitivity to left-truncation was checked by calculating densities at different left-truncation scenarios. In addition, for roe deer that showed attraction to cameras mostly at night, we calculated density estimates using daytime-only captures (defined as between sunrise and sunset). For this, we adjusted the total sampling time and calculated a measure of availability for detection using the same method as above, but setting the bounds of the model to be the sunrise/sunset times of the middle day of the survey period. We did not left-truncate these data.

We calculated survey-wide density estimates for species where >80 photos (and >10 photo sequences) were obtained. We used the Land Cover Map 2015 (1 km dominant aggregate habitat class; Rowland et al., 2017) to assign a habitat to each site where a camera trap was positioned. Habitat-specific density estimates were calculated if (after truncation): (1) the species had >80 photos in the habitat; (2) there were >10 sites in that habitat and (3) data were present in five or more distance categories. To calculate density, we followed the methods of Howe et al. (2017) and used the model selection process proposed by Howe et al. (2019) (Appendix S2). We also explored the effect on density estimates and confidence intervals of variance in the effective detection angle and snapshot moment. All analyses used R version 4.1.2 (R Core Team, 2021), with final models and density estimates calculated using the 'Distance' package (Miller et al., 2019). We compare our density estimates to those published by the national mammal society in the United Kingdom (Mathews et al., 2018), and in a paper by Croft et al. (2017) who gathered data on mammal occurrence and abundances from across the United Kingdom and used a systematic modelling approach to produce national and habitat-specific density estimates.

Results

We were able to place cameras at the exact random point at 48/109 sites. Of the cameras which were displaced, the average displacement from the point was 0.30 km (range 0.02–1.76). Small displacements (<0.1 km) were most commonly due to moving a camera to place it on a post or structure (e.g. at the edge of a field). Large displacements (>0.5 km) were mostly due to a lack of access permissions. A small number of displacements (5) were due to points falling on buildings or roads. Displacements occurred across a range of habitats but, most commonly,

Table 1. Species-specific information, including density estimates per km² [95% CI] calculated across the whole-study area, ordered by species body size.

Species		Sites captured	Number of photos	Availability for detection	Effective detection angle	Truncation left, right (m)	Density per km² [95% CI]	C.V.	Mathews et al. (2018) Density per km² [95% CI]	Croft et al. (2017) Density per km² estimate range
Roe deer (Capreolus capreolus)		31	2742	0.39	0.77	1, 10	5.67 [2.67–10.52]	0.38	1.09 [0.89–1.22]	3.22–25.70
Badger (Meles meles)		14	459	0.30	0.56	2, 10	1.32 [0.84–4.22]	0.40	2.31 [1.61–4.18]	0.42–5.08
Red fox (Vulpes vulpes)		45	1397	0.43	0.59	2, 10	5.97 [1.37–21.15]	0.39	1.47 [0.43–2.66]	0.38–2.10
Brown hare (Lepus europaeus)		28	3635	0.53	0.56	1, 10	5.97 [2.86–12.89]	0.43	2.39 [1.76–8.21]	0.58–16.48
Rabbit (Oryctolagus cuniculus)		66	30 725	0.48	0.55	2, 10	101.83 [51.63–186.65]	0.39	148.46	9.70–1192.00
Hedgehog (Erinaceus europaeus)		26	2034	0.13	0.60	1, 10	23.31 [7.39–45.33]	0.46	2.15	3.42–56.06
Grey squirrel (Sciurus carolinensis)		25	4181	0.33	0.59	1, 10	7.64 [3.73–13.03]	0.30	11.13 [5.52–15.63]	8.27–77.60
Stoat (Mustela erminea)		17	163	0.55	0.51	0, 10	0.22 [0.07–0.44]	0.55	2.09	–

For each species, we give: number of sites species was captured at; total number of photos (i.e. observations); proportion of time available for detection; effective detection angle; density per km² with 95% CI estimated from bootstrap; estimated coefficient of variation (C.V.) from bootstrap; density estimates (per km²) with 95% CI where provided in Mathews et al. (2018; calculated by taking abundance published and dividing by area of Great Britain); density estimate (per km²) range published in Croft et al. (2017). Animal silhouettes by Anthony Caravaggi and Claus Rebler, licensed under CC BY-NC-SA 3.0.
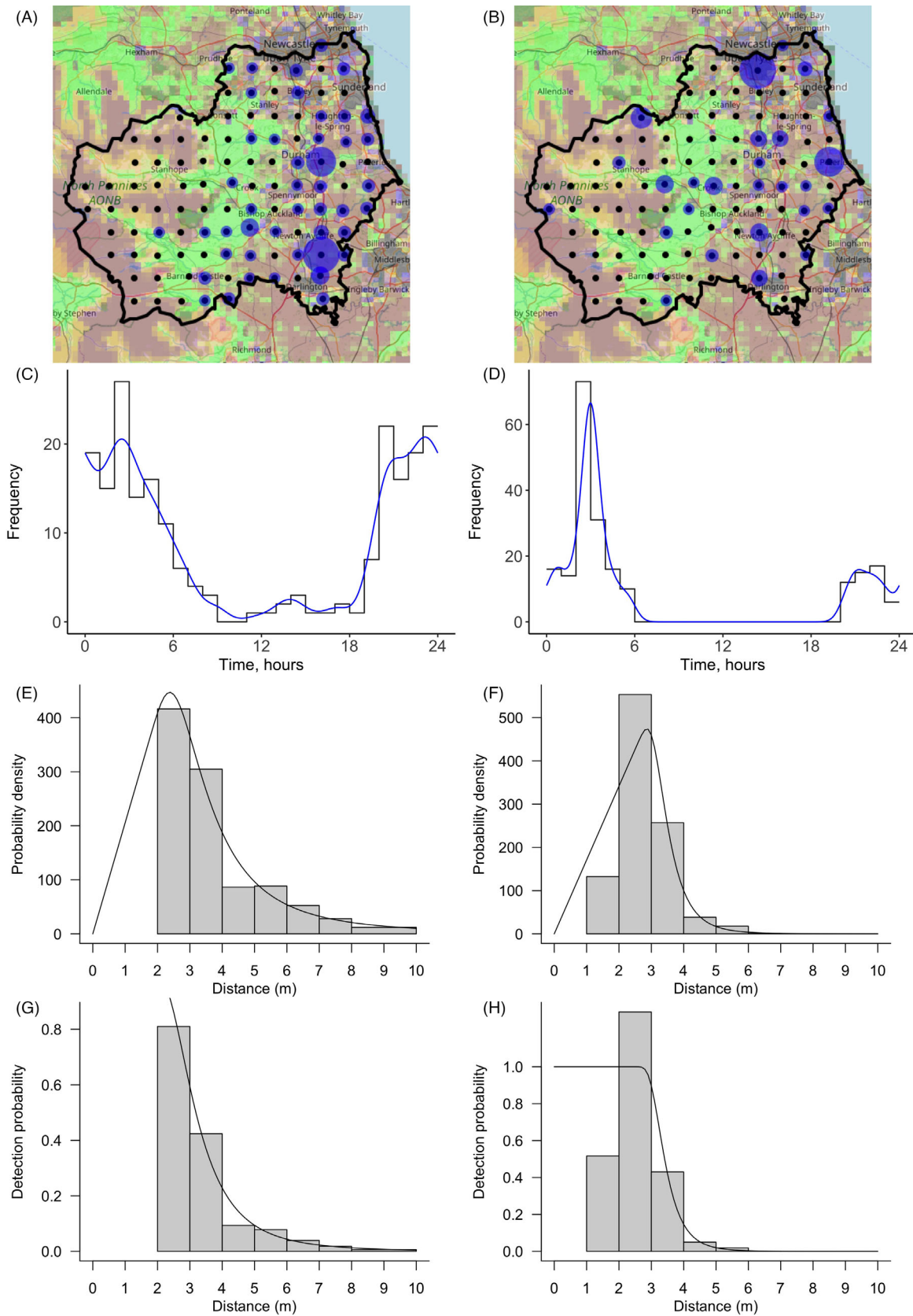
Figure 2. Example species distribution maps (A and B), activity schedules (C and D), probability density (E and F) and detection probability curves (G and H) for red fox (*Vulpes*; left) and hedgehog (*Erinaceus europaeus*; right). Species maps show locations of all cameras (black circles) with locations of captures for the species (blue circles) scaled to the number of captures. Colours on map represent habitat data from Land Cover Map 2015 (1 km dominant aggregate class, Rowland et al., 2017) key for colours can be found in Figure 1. Background map: © OpenStreetMap contributors licensed under CC BY-SA 2.0. Activity schedules show circular kernel models fitted to radian time data of relative frequency of independent captures over the 24 h period. The probability density graphs show the probability density of observed distances and detection probability graphs show detection probability as a function of distance from unadjusted hazard-rate point transect models.

were in improved grassland. More information on camera displacements is in Table S1.

Despite efforts to set cameras away from livestock and to reduce triggers from vegetation, these problems occurred at 41 sites; cameras were stolen from a further two sites. Wherever we were able, cameras were redeployed at these sites either immediately or as soon as possible after the previous deployment. We included data from all deployments in our analyses. Cameras at 18 sites were deployed for fewer than 14 days (range 4–13), owing to interference by livestock and/or saturated memory cards, with no possibilities for further deployments (or the same issue occurring on multiple deployments). Cameras with shorter deployments were in the LCM habitat classes: mountain, heath and bog (5); semi-natural grassland (4); improved grassland (4); arable (3) and built-up areas and gardens (2).

Overall effort totalled 1785 camera days. In total, the survey generated 435 024 images and 51 447 photos contained a wild mammal. We focussed our analyses on eight mammal species for which data were adequate to calculate density estimates at a survey-wide level (Table 1). The number of sites at which these species were detected ranged from 14 (badger) to 66 (rabbit). At 15 sites, none of the eight species were captured. Sites where species were detected varied between species, but the majority of captures were in the east of the survey area in grassland/arable/urban habitats, with fewer captures in the mountain/heath/bog habitats in the west (Fig. 2; Figures S3–S8). Activity schedules (Fig. 2; Figures S3–S8) and associated availability for detection (Table 1) were in line with expectations for the species studied, with strictly nocturnal species such as hedgehogs having lower availability for detection (0.13) than diurnal or crepuscular species such as brown hare (0.53; Table 1). Effective detection angles for all species were within the range 0.51–0.60 radians with the exception of roe deer, the largest of the focal species, which was 0.77 (the same as the FOV angle determined by manual testing; Table 1). All effective detection angles were smaller than the FOV angle in the manufacturer's guide (0.96; Browning, 2017).

We left-truncated at the distance category with the largest number of captures per unit area for red fox, brown hare, rabbit, grey squirrel and stoat (Table 1). For three species (badger, hedgehog and roe deer), following this rule was not appropriate and we made exceptions

(Appendix S3). For these species, the point of left-truncation made only a small difference to the badger density estimate, but large differences for the roe deer and hedgehog density estimates (Table S2). Roe deer density estimates for the whole-study area and habitat-specific estimates using daytime only captures were slightly lower than estimates calculated with all data but confidence intervals still overlapped (Tables 1 and 2; Table S3).

The unadjusted hazard rate model was selected as the model of best fit for all species (following model selection criteria in Howe et al., 2019). Density estimates ranged from 0.22 per km^2 for stoat to 101.83 per km^2 for rabbit (Table 1). Coefficients of variation were all between 0.30 and 0.46, except for stoat, which had CV = 0.55 (Table 1). Density estimates were similar to estimates previously published by Mathews et al. (2018) and Croft et al. (2017), with almost all of our density estimates (except hedgehog and roe deer) falling within their published ranges and/or *vice versa* (Table 1). We also explored variation in the effective detection angle and snapshot moment and found that, because variance in these measures was very small (relative to the variance arising from spatial heterogeneity in captures), the effect of these sources of variance on density estimates and confidence intervals was also very small (Table S4).

Across the whole survey, cameras were placed within seven different habitat classes. Of these, four were represented at 10 or more sites and habitat-specific densities could be estimated. Data were adequate to produce at least one habitat-specific density estimate for each species, but not all species had sufficient data to support a density estimate for every habitat (Table 2). We used the same truncation distances for each species as in the survey-wide estimates (Table 1), but calculated habitat-specific availability for detection and effective detection angle measures (Table S5). The unadjusted hazard rate model was selected for all estimates, except for roe deer in arable habitat, for which the unadjusted half-normal model was selected.

The habitat-specific density estimates produced in our study largely fall within the ranges predicted for those habitats by Croft et al. (2017) (Table S5). Habitat-specific density estimates were often similar to survey-wide density estimates (i.e. falling within or close to the confidence

Table 2. Density estimates per km² [95% CI] calculated across the whole-study area and for four different habitats.

Species	Whole-study area (109)	Arable (29)	Built-up areas and gardens (16)	Improved grassland (38)	Mountain, heath, bog (13)
Roe deer (Capreolus capreolus)	5.67 [2.67–10.52]	12.42 [3.89–32.28]	**	4.34 [3.33–49.99]	*
Badger (Meles meles)	1.32 [0.84–4.22]	2.01 [0.78–5.82]		1.81 [0.17–2.87]	
Red fox (Vulpes vulpes)	5.97 [1.37–21.15]	19.26 [3.60–28.97]	2.55 [0.40–13.19]	0.49 [0.35–1.83]	
Brown hare (Lepus europaeus)	5.97 [2.86–12.89]	10.94 [2.88–34.83]		7.40 [2.60–14.06]	
Rabbit (Oryctolagus cuniculus)	101.83 [51.63–186.65]		112.19 [7.74–334.96]	99.39 [45.60–164.71]	26.37 [8.92–51.75]
Hedgehog (Erinaceus europaeus)	23.31 [7.39–45.33]	2.86 [0.76–7.67]	**	6.59 [1.40–13.03]	*
Grey squirrel (Sciurus carolinensis)	7.64 [3.73–13.03]	8.76 [0.72–19.79]	3.88 [0.79–8.76]	10.83 [3.51–26.37]	
Stoat (Mustela erminea)	0.22 [0.07–0.44]	*		0.55 [0.15–2.74]	*

Number of sites a camera was positioned at for each habitat shown in brackets in header. Cells marked with an Asterix indicate the species was captured in this habitat, however data were not sufficient to calculate density estimates; either due to not enough photos captured (*) or data being present in less than five distance categories (**). Blank cells indicate this species was not captured in this habitat during this survey. Animal silhouettes by Anthony Caravaggi and Claus Rebler, licensed under CC BY-NC-SA 3.0.

interval range of survey-wide estimates), but with some notable differences (Table 2). Density estimates calculated for arable habitat were higher than survey-wide estimates for all species except hedgehog, for which the arable density estimate was 10 times lower. For improved grassland, the density estimate was also much lower than survey-wide estimates for hedgehog and fox. Badger, brown hare, grey squirrel and stoat all had higher density estimates in improved grassland than the survey-wide estimates. For mountain, heath and bog habitat, there were sufficient data to estimate density for rabbit only. This density estimate was around a quarter of the survey-wide estimate.

Discussion

We used CTDS to estimate survey-wide and habitat-specific densities for a range of UK mammal species across a varied landscape. The study was rapid, relative to previous studies of multiple species over large spatial scales, and the lessons learned should have much wider implications for using CTDS on a large scale for country-wide mammal monitoring. Here, we discuss our findings with respect to three issues: (1) the calculated density estimates and how they compare to previous published estimates; (2) practical and methodological issues that need careful consideration in future and (3) implications of the study for country-wide mammal monitoring.

Accuracy and precision of density estimates

Five of our eight species had density estimates which fell within the confidence intervals of the estimates in Mathews et al. (2018), and/or *vice versa*, and all but two of our density estimates fell within the ranges predicted by Croft et al. (2017). Our estimates are for North-East England only and, therefore, some differences to national estimates are expected. Estimates for three species (hedgehog, roe deer and stoat) differed considerably from national estimates. For hedgehog, this could be due to the distribution of data (with few captures at both small and large distances) causing poor model fit and inaccurate density estimates. We estimated high densities of roe deer relative to national estimates; this result is expected because, although roe deer are widely distributed throughout the United Kingdom, North-East England (where our study was based) has a higher abundance than other areas, such as central and southeast England (Crawley et al., 2020). For stoats, our density estimate was lower than that of Mathews et al. (2018), but they noted that their estimate was unreliable due to a lack of data (and hence no CI could be produced). Croft et al. (2017) were similarly unable to produce an estimate for stoat density, because of this lack of data.

Our study is the first CTDS survey to produce density estimates for both the whole-survey area and specific habitats within that area. The ability to produce these habitat-specific density estimates will be beneficial for conservation management, and will help to address data gaps. It is also useful for scaling up density estimates, as shown by Croft et al. (2017) who used habitat-specific density estimates to generate UK-wide density estimates. The confidence intervals surrounding our habitat-specific estimates are large in some cases (Table 2). However, considering the lack of data, and the published ranges of the current best density estimates for UK mammal species, our estimates are still amongst the most precise produced for these species to date.

Practical and methodological issues

The ability to use CTDS to generate density estimates across multiple species and habitats from one survey is encouraging, suggesting the method could be deployed on large scales for species monitoring. However, for countries such as the United Kingdom where the landscape is heterogenous and includes human-altered habitats, there are practical limitations to consider. CTDS requires camera traps to be set at pre-determined (usually systematically random) points. In most surveys, the potential to deploy all cameras at pre-selected points is constrained. However, in our study, 56% of our cameras were displaced, some over quite large (>1 km) distances. Whilst Howe et al. (2017) states that small displacements should not bias estimates, if cameras are displaced to be put on trees or other features that species (e.g. grey squirrels who spend time in trees) may be attracted to then those species could be captured more frequently at smaller distances which has implications for density estimation. Furthermore, it is unclear what the effect of larger displacements (usually caused by land access issues) would be on density estimates. Whilst we made sure that displaced cameras were still within the same habitat, previous studies have shown that even within the same habitat, small-scale factors—such as the presence of log-/trail features—can result in large differences in capture rates (Kolowski et al., 2021; Kolowski & Forrester, 2017). This could be problematic for any large-scale camera trap survey (particularly in heterogenous landscapes) that use CTDS or any other method that requires cameras to be set at pre-determined random locations. Alternative designs might be required to mitigate against displacements, such as deploying multiple cameras at each site (Kolowski et al., 2021). Ultimately, however, covariation between land access and animal abundance is always likely to constrain the accuracy of wildlife surveys.

Camera traps surveys are often vulnerable to camera theft, vegetation triggering cameras and livestock

damaging cameras (Jumeau et al., 2017; Meek et al., 2019; Nichols et al., 2017; Swanson et al., 2015). The heterogenous landscape of our study appeared to exacerbate this issue, with almost half of our cameras being affected and ~85% of photos resulting from vegetation/livestock triggers. This necessitated multiple and, in some cases, shorter deployments. Whilst multiple deployments were an inconvenience, we do not believe they biased density estimates; however, shorter deployments could influence survey-wide density estimates if shorter deployments occur more frequently in certain habitats. Relative to their frequency in the overall survey, improved grassland and semi-natural grassland had more short deployments. As some of the density estimates for improved grassland were different from the survey-wide estimates, shorter deployments in that habitat could have biased survey-wide estimates. Future surveys in heterogenous landscapes must factor in ample extra time for redeployments due to practical challenges.

As well as these practical issues, CTDS also presents methodological challenges. These include the species-specific decisions that must be made and which need careful consideration, owing to their strong influence on density estimates. Perhaps the most challenging factor to consider is left-truncation. Left-truncation can be problematic if used inappropriately, because the loss of data results in extrapolation of the slope of the probability detection function at distance zero, which is then used to estimate density. Nevertheless, left-truncation is commonly used in CTDS when animals are likely moving underneath the camera, causing fewer than expected detections at small distances (Bessone et al., 2020; Cappelle et al., 2019, 2021; Howe et al., 2017; Palencia et al., 2021). In a large multi-species study, it would be beneficial to have one method for deciding when and by how much to left-truncate; hence, we trialled a rule across all species, left-truncating at the start of the distance category with the most captures per unit area surveyed. Whilst this rule worked for most species, it was inappropriate for three species: badgers, for which the lack of detections at short distances was more likely due to trails at a larger distance; hedgehogs, for which a lack of spread in the data caused problems when truncating and roe deer, which showed attraction to cameras. These cases all demanded species-specific decisions about left-truncation distances (Appendix S3).

Other aspects of CTDS that must be considered on a species-by-species basis include identifying which species may be reacting to cameras, as this may lead to more detections than expected at distance zero. Multiple ways of dealing with this have been proposed, including left-truncation (Cappelle et al., 2019) and removing images where animals show a reaction to the camera (Bessone et al., 2020). In our study, we used left-truncation for roe deer as this species appeared to be attracted to cameras. However, because roe deer were mainly reacting to cameras at night (Fig. S2), presumably due to the infrared flash (Henrich et al., 2020) we also produced estimates using daytime-only captures (Table S3) as an alternative to left-truncation. We found similar density estimates and estimates of variance produced by the two methods (restricting data to daytime captures only, or left truncating at 1 m), suggesting that either could be appropriate for dealing with reactivity to cameras. Future studies using CTDS should consider sample size and causes of reactivity to determine which method is most appropriate.

Semi-arboreal species pose particular problems for density estimation. For these, calculating availability for detection using the method outlined by Rowcliffe et al. (2014) may be inappropriate. This is because the assumption of 100% detection at times of peak activity may be especially problematic for species that spend time active out of the view of cameras. In our study, the proportion of time available for detection for grey squirrels (a semi-arboreal species) was highly similar to the figure calculated by Wauters et al. (2002) for proportion of time grey squirrels spent on the ground in Italy. Whilst this provides some reassurance, it would be preferable to have observational data on time on the ground for the period and location being studied.

To survey species of varying size, and to reduce vegetation-induced camera triggers, we set cameras higher than would be advised for many species in our study (Meek et al., 2016). Smaller-bodied animals may have been captured at a larger range of distances and angles if cameras were deployed at lower heights height (e.g. Marcus Rowcliffe et al., 2011). In turn, this might have obviated the need for some of the decisions around left-truncation, whilst rendering valid the full FOV. There is, of course, a trade-off between ideal placements for animals of different sizes and this identifies one of the limitations of community-wide (or multispecies) monitoring by this method. For effective multispecies monitoring using CTDS, deployments at different heights might be necessary to survey different components of the community.

CTDS for country-wide mammal monitoring

To carry out effective conservation and management for species, and to meet national obligations for species monitoring (United Nations Environment Programme, 2018), large-scale monitoring in many countries needs to be improved. However, monitoring on a national level is inherently costly and approaches need to be cost-effective and practical to employ. CTDS offers a way to monitor

multiple species concurrently, over large spatial scales, and uses a methodology (distance sampling) benefitting from existing resources and software. As highlighted by Schaus et al. (2020), the start-up cost of any camera trapping survey is high; however, cameras can be rotated around sites to reduce costs and can be used in repeated surveys for many years. CTDS is also less demanding of time than many other methods (e.g. line transects); our study was conducted over a large area, and calculated density estimates for multiple species, but was conducted by a single researcher. CTDS thus offers a promising solution to improve terrestrial mammal monitoring efforts in the United Kingdom and other countries.

There are multiple ways CTDS could be deployed on a national scale. If it would be beneficial to obtain regional densities (perhaps for local species management purposes) then setting up a grid of cameras across the country at the same resolution as in our study (5 km^2) might be most appropriate. Alternatively, it might be beneficial to have a stratified sampling approach to obtain habitat-specific density estimates, including for rare but important habitats. Either way, in order to achieve such large-scale monitoring, it is likely that support from citizen scientists would be required. Citizen scientists play a large and important role in ecological data collection in many countries, including the United Kingdom (Pocock et al., 2015). Citizen science projects already enlist volunteers to deploy camera traps (Hsing et al., 2018; Lasky et al., 2021; Locke et al., 2019; McShea et al., 2016). Such projects could collect data appropriate for CTDS by allocating sites to participants and training them to follow the methodology to calibrate cameras. Although the expertise of citizen scientists is sometimes questioned (Kosmala et al., 2016), many projects exist that require citizen scientists to follow strict protocols; for example, the UK's Breeding Bird Survey run by the British Trust for Ornithology (Harris et al., 2021). Importantly, we note that accurate hedgehog densities using the Random Encounter Model were estimated with data collected by citizen scientists who deployed camera traps following a calibration methodology similar to that in CTDS (Schaus et al., 2020).

Conclusion

Despite the methodological and practical limitations we discuss, CTDS provides a promising method to achieve large-scale monitoring for many species. Further investigation of certain aspects of the methodology (such as left-truncation) is needed, and a 'one size fits all' approach for multiple species at a time may not be possible, especially for smaller species. However, we show that with careful consideration of these factors, realistic density estimates can be calculated for multiple species, including species for which density measures have previously proven difficult to obtain. The United Kingdom is one case study of where the lack of data on wild mammal species highlights the need for improved species monitoring on a national scale. Employing CTDS on a national scale for species monitoring would be inherently costly, but costs could be reduced by enlisting existing citizen science networks and projects. The benefits of employing such a scheme would be significant, given the increasing anthropogenic pressures facing species worldwide and the current gaps in our data and knowledge, which limit our ability to predict how species will respond.

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Supporting Information

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

Appendix S1. Further details on how availability for detection, effective detection angle and the snapshot moment interval were calculated.

Appendix S2. Further details on density calculation using camera trap distance sampling and the model selection process.

Appendix S3. Further details and explanations of left truncation decisions for different species.

Figure S1. Detection probability as a function of distance (top) and probability density of observed distances (bottom) for hedgehog (*Erinaceus europaeus*) under two different left-truncation scenarios.

Figure S2. Percentage of captures in each distance category for roe deer (*Capreolus capreolus*) in the daytime (left) and the night-time (right).

Figure S3. Species distribution map (top-left), activity schedule (top-right), probability density (bottom-left) and detection probability (bottom-right) graphs for roe deer (*Capreolus capreolus*).

Figure S4. Species distribution map (top-left), activity schedule (top-right), probability density (bottom-left) and detection probability (bottom-right) graphs for badger (*Meles meles*).

Figure S5. Species distribution map (top-left), activity schedule (top-right), probabilitydensity (bottom-left) and detection probability (bottom-right) graphs for brown-hare (Lepus europaeus).

Figure S6. Species distribution map (top-left), activity schedule (top-right), probability density (bottom-left) and detection probability (bottom-right) graphs for rabbit (*Oryctolagus cuniculus*).

Figure S7. Species distribution map (top-left), activity schedule (top-right), probability density (bottom-left) and detection probability (bottom-right) graphs for grey squirrel (*Sciurus carolinensis*).

Figure S8. Species distribution map (top-left), activity schedule (top-right), probability density (bottom-left) and detection probability (bottom-right) graphs for stoat (*Mustela erminea*).

Table S1. Details of camera trap placements including information on which camera traps were displaced from the pre-determined random point and the reason for the displacement.

Table S2. Densities [95% CI] calculated across the whole-study area under different left-truncation scenarios for species where truncation decisions were questioned due to: data not being consistent with understanding of species (badger); poor model fit (hedgehog); or animals being attracted to cameras (roe deer).

Table S3. Density estimates [95% CI] and other species/habitat-specific information for roe deer using daytime capture data only.

Table S4. Densities [95% CI] calculated across the whole-study area including estimates presented in the paper (standard) and lower and upper estimates which incorporate variation from effective detection angle and snapshot moment calculations.

Table S5. Habitat-specific density estimates [95% CI] and other species/habitat-specific information.