Application of the Random Encounter Model in citizen science projects to monitor animal densities

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Abstract

Abundance and density are vital metrics for assessing a species' conservation status and for developing effective management strategies. Remote-sensing cameras are being used increasingly as part of citizen science projects to monitor wildlife, but current methodologies to monitor densities pose challenges when animals are not individually recognisable. We investigate the use of camera traps and the Random Encounter Model (REM) for estimating the density of West European hedgehogs (*Erinaceus europaeus*) within a citizen science framework. We evaluate the use of a simplified version of the REM in terms of the parameters' estimation (averaged versus survey-specific) and asses it's potential application as part of a large-scale, long-term citizen science project. We compare averaged REM estimates to those obtained via Spatial Capture-Recapture (SCR) using data from nocturnal spotlight surveys. There was a high degree of concordance in REM-derived density estimates from averaged parameters versus those derived from survey-specific parameters. Averaged REM density estimates were also comparable to those produced by SCR at 8 out of 9 sites; hedgehog density was 7.5 times higher in urban (32.3 km^{-2}) versus rural (4.3 km^{2}) sites. Power analyses indicated that the averaged REM approach would be able to detect a 25% change in hedgehog density in both habitats with >90% power. Furthermore, despite the high start-up costs associated with the REM method, it would be cost-effective in the long term. The averaged REM approach is a promising solution to the challenge of large-scale and long-term species monitoring. We suggest including the REM as part of a citizen science monitoring project, where participants collect data and researchers verify and implement the required analysis.

Introduction

Information about animal abundance and density, and how these are affected by biotic and/or abiotic factors, are important when developing management strategies and allocating conservation efforts (Fryxell, Sinclair and Graeme, 2014). However, the range of methods available for estimating animal density is substantial (Williams, Nichols and Conroy, 2002), such that it can be a challenge to decide which method is best for specific species in different contexts. Ideally, the chosen method should be the one best suited to answering the research question, but factors such as accuracy, precision, cost-effectiveness and suitability across different landscapes, are often key considerations (Gitzen, Millspaugh and Cooper, 2012; Hayward *et al.*, 2015). Consequently, researchers may produce estimates that are not directly comparable across space or time. This can, in turn, hamper efforts to estimate national and international population sizes, which are useful for identifying rates of decline on large spatial scales, and critical to estimating a species' overall conservation status (e.g., Schipper *et al.*, 2008, Croxall *et al.*, 2012; Magera *et al.*, 2013; Mathews *et al.*, 2018).

Finding suitable methods for large-scale, long-term monitoring of abundance is challenging. For example, distance sampling (e.g., Buckland *et al.*, 2001; Giunchi, Gaggini and Baldaccini, 2007; Durant *et al.*, 2011) and capture-recapture methods (e.g., Ruell *et al.*, 2009; Garrote *et al.*, 2011; Lampa *et al.*, 2015;) are often expensive, time-consuming, can be restricted to certain habitats or seasons (Hubert *et al.*, 2011), and may require licenced surveyors if direct capture is necessary (Prange *et al.*, 2014). Furthermore, surveying human-dominated landscapes, such as residential urban areas, is problematic due to access restrictions to private land. One solution to large scale monitoring across urban areas is to involve citizen scientists in scientific research to monitor urban wildlife (Scott *et al*., 2014, 2018; Hof and Bright, 2016; Croft, Chauvenet and Smith, 2017).

A method that circumvents many of the challenges associated with estimating abundance is the use of remote-sensing camera traps (hereafter cameras). Using cameras to estimate abundance and density from individually-identifiable species has been used successfully across many different species and habitats (see reviews in Burton *et al.*, 2015; Caravaggi *et al*., 2017), and can involve citizen scientists (e.g. Swanson *et al.*, 2015; McShea *et al.*, 2016). However, estimating density/abundance is more problematic where individual animals are not distinguishable, e.g. based on pelage or other characteristics. Consequently, Rowcliffe *et al.* (2008) proposed the Random Encounter Model (REM), whereby population density is estimated by modelling the rate of contact between animals and camera traps, without the need for individual recognition. To date, the REM has been used for a limited range of species and habitats (e.g., Rahman, Gonzalez and Aulagnier, 2017; Rowcliffe *et al.*, 2008; Rovero and Marshall, 2009; Manzo *et al.*, 2012; Zero *et al.*, 2013), and has not been validated on small mammals or used in urban landscapes. Furthermore, only a few studies have attempted to validate the accuracy and precision of the method through comparisons either with populations of known density (e.g., Rowcliffe *et al*., 2008) or with other well-established methods such as spatial capture-recapture methods (but see Anile *et al.*, 2014).

Camera traps are being used increasingly as part of citizen science projects to monitor wildlife at global, national and local scales (e.g., van der Wal *et al.*, 2016; Steenweg *et al.*, 2017; Hsing *et al.*, 2018), allowing data collection to take place in areas that would otherwise be difficult to access (Parsons *et al.*, 2018). One significant potential obstacle for the inclusion of citizen scientists in REM studies is the requirement of the camera detection zone and animal parameters to be measured. These parameters need to be extracted from the footage obtained by the camera traps as they need to be specific to each survey, and any biased measurements can affect accuracy and precision of the density estimates markedly (Rowcliffe *et al.*, 2008). Training is required to extract and measure these parameters from the footage; however, such technical tasks may not be suitable for all citizen scientists, which could impact data quality and accuracy (Newman, Buesching and Macdonald, 2003). Furthermore, time-consuming and repetitive activities could increase participant drop-out (Eveleigh *et al.*, 2014). One way around this problem is conducting pilot studies, whereby researchers estimate all required parameters for the focal species. By taking measurements from a representative sample of habitats, the averaged parameters can be used to calculate densities across other surveys, where only camera deployment would be needed. Such an approach would allow the participation of citizen scientists and reduce the pitfalls associated with the methodology.

This study aims to assess the effectiveness of the REM for estimating the density of a focal animal species within a citizen science framework and asses its potential application as part of a large-scale, long-term citizen science project across different landscapes. The West European hedgehog (*Erinaceus europaeus*) was selected as a model species, as hedgehogs are currently of conservation concern in the United Kingdom (UK) (Joint Nature Conservation Committee, 2010) where populations have declined markedly since the 1950s (Wembridge, 2011; Roos, Johnston and Noble, 2012) in both rural and urban environments (Wembridge, 2011; Williams *et al*., 2018a; b; Yarnell *et al.*, 2014). However, there is a paucity of information about hedgehog densities in different habitats because of the lack of a suitable method for estimating density on both small and large spatial scales. Specifically, we will: (1) compare hedgehog densities using the REM based upon survey-specific versus averaged parameters; (2) compare density estimates derived from the REM to those generated using Spatial Capture-Recapture (SCR) methods applied to nocturnal spotlight counts; and (3) assess the suitability of the REM for large-scale, long-term species monitoring based on costs and power to detect population changes. These findings are discussed in the context of the REM's suitability for the long-term, large-scale monitoring of wildlife within a citizen science framework.

Methods

Three rural and five urban sites across England were selected based on where researchers were currently studying hedgehogs or where hedgehog conservation officers were located (Figure 1; Table 1). One site (Brackenhurst) was surveyed in both 2017 and 2018, but these were considered temporally independent (e.g. Tinker *et al.* 2017), creating a total of nine density surveys. Populations were assumed closed, as study areas were bound by barriers that should limit hedgehog movements (e.g. major roads; Rondinini and Doncaster, 2002), and surveys were carried out over a short period of time. All data were collected under licence from Natural England; ethical approval was granted by Nottingham Trent University's Animal, Rural and Environmental Science Ethical Review Group.

Land cover of the study areas was mapped using OS Mastermap Topography Layers and high resolution (25cm) Vertical Aerial Imagery (https://digimap.edina.ac.uk/; EDINA Digimap Ordnance Survey Service, 2017). Following Benza *et al.* (2016), urban and rural sites were defined as areas with >25% and <25% of built land cover, respectively (Table S1). Built land cover was calculated as the area of buildings, roads and pavements divided by the total area of the study site. Urban sites were dominated by residential housing; rural sites consisted of mixtures of arable, pasture and amenity land, woodland and streams.

Camera trapping

Trapping effort required to obtain an adequate sample size and improve the precision of REM density estimation depends on the density and day range of the focal species (Rowcliffe *et al.,* 2008). Therefore, based on the expected hedgehog density (4-36 individuals/km^2; Dowding, 2007; Hubert *et al.,* 2011; Parrott, Etherington and Dendy, 2014) and daily movement range (0.68 km; Dowding *et al.,* 2010), 100-1000 camera nights would be needed (Rowcliffe *et al.,* 2008). To achieve this, four sets of 30 camera trap locations (CTLs) that covered the whole study area were randomly generated for each survey using Geospatial Modelling Environment (GME) (Version 0.7.4.0; Beyer, 2015). To ensure an even distribution of cameras across each study area, the minimum spacing between cameras was calculated using the inverse of the square root of the number of camera positions per week (30), divided by the size of each study area (Bartolommei, Manzo and Cozzolino, 2012; Balestrieri *et al.*, 2016). Thirty cameras (Bushnell 119537 Trophy Cam 8MP Night Vision; Bushnell Outdoor Products, Overland Park, KS, USA) were deployed within each study site simultaneously and moved to new locations four times. Cameras were moved to maximise the number of camera placements (Rowcliffe *et al.*, 2008) and ensure good coverage of the entire study area. Each camera remained in one location for at least five consecutive nights (mean = 6.2 ± 0.04 SE) before being moved.

Community engagement took place to obtain permission to place camera traps in urban gardens, targeting the houses closest to the randomly-generated CTLs. Where the householder did not grant permission, the next nearest garden to the random point was targeted until permission was obtained. When random points were located on roads or inaccessible areas, they were moved to the closest garden. Access to rural sites was obtained by contacting the landowners.

Unbaited cameras were attached to posts, fences, wooden stakes, or trees, approximately 0.2m above the ground so that passing hedgehogs would be detected. In urban areas, cameras were placed in back gardens, enclosed front gardens, school grounds, or in discreet locations in recreational parks to reduce the chances of theft. Cameras were set to work on night mode (dusk till dawn), and to record 30-second video clips with a 1-minute interval between each. The 1-minute delay was chosen to provide a balance between punctuated sampling and continuous monitoring, minimising the risk of missing independent detections whilst reducing battery wastage through multiple recordings of the same individual (Henschel and Ray, 2003; Rowcliffe *et al.*, 2008). The choice of videos over photos was made to allow researchers to extract animal speed more accurately by considering the path followed by the individual while in front of the camera, rather than measuring the distance between the first and last position recorded using photographs (Rowcliffe *et al.*, 2016). All other functions were left on the default settings. Some householders indicated that they regularly placed supplementary food in their gardens; these houses (Brighton, n = 4; Ipswich West, n = 1; Ipswich East, n = 2) were included in the analyses as they represented the *a priori* availability of food that the hedgehogs would likely encounter. Conversely, if evidence was found that food was provided as a consequence of involvement in the study, these houses (Reading, n = 3; Ipswich West, n = 3) were excluded to avoid violating the assumption of independent movement in relation to the cameras (Rowcliffe *et al.* 2008).

Camera-trapping rates were converted to density estimates (individuals km^{-2}) using independent videos only (Rowcliffe *et al.* 2008). Specifically, density (D) was estimated as:

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

where y = number of detections of the focal species, t = survey effort, v = daily movement range, and r and θ are the radius and arc of the camera trap detection zone, respectively (see Rowcliffe *et al.,* 2008). Survey effort (*t,* hours) was calculated as the number of trapping nights per site multiplied by the number of hours the cameras were active per night; the latter was calculated as the period between the earliest and latest hedgehog recording on that site. When a camera was moved or turned off by homeowners, knocked down by livestock, ran out of battery, or if memory cards or cameras malfunctioned, survey effort was reduced by subtracting the total number of affected days from the trapping effort. Camera detection parameters were obtained for each video on-site when the cameras were collected (Rowcliffe *et al*., 2011); by playing the videos on a laptop, surveyors were able to use landmarks (e.g. buildings, trees, edges, rocks) as reference points to determine the exact location of the hedgehog with respect to the camera, and to take measurements of the detection arc (θ, radians) and distance (r, metres) using a compass and tape measure (see Rowcliffe *et al.*, 2011).

Animal speed was also extracted from videos to calculate the daily movement range (v, km h^{-1}). This was calculated by multiplying travel speed (μ) by the proportion of time spent active (p), where travel speed (μ) was determined by dividing the distance travelled while in the detection zone, by the time the animal was seen on the video (see Rowcliffe *et al.*, 2016 for detailed description). The proportion of time spent active (p), and its variance, was obtained using the R package *activity* (Rowcliffe *et al.,* 2014). All videos (including non-independent videos) were included in the speed calculation at each site.

Ideally, to avoid bias, the REM parameters should be obtained for each specific survey (Rowcliffe *et al.*, 2008), but obtaining these data is difficult and time-consuming. Therefore, we compared REM density estimates for each survey based on survey-specific parameters (ssREM) and mean parameter estimates averaged across all surveys (aveREM) as in Cusack *et al*. (2015), Pfeffer *et al.*, 2017 and Rahman, Gonzalez and Aulagnier (2017). The aveREM approach is evaluated as a way to overcome the pitfalls associated with the measurement of the REM parameters and to evaluate its utility as part of a programme involving citizen scientists. The parameters that were averaged across surveys included daily movement range (v) and the camera detection parameters: angle (θ) and distance (r). Survey effort was calculated independently for each site. Variance and 95% confidence limits were estimated by non-parametric bootstrapping (Rowcliffe *et al.,* 2008). All analyses were performed in R 3.2.2 (R Core Team, 2017) using the package *remBoot* (Caravaggi *et al.*, 2016).

Spotlight surveys and Spatial Capture-Recapture models

As the true densities at each site were unknown, reference densities were calculated by analysing individual encounter history data from nocturnal spotlight surveys using spatial capture-recapture (SCR: Efford, 2004) models. SCR is an extension of traditional (non-spatial) capture-recapture that estimates population density from spatially-referenced detections by incorporating information such as movement, spatial organisation of detectors, and space use by individuals (Royle, Fuller and Sutherland, 2018). Hedgehogs were surveyed at night along pre-defined transects across publicly-accessible land (Dowding *et al.*, 2010). Transects were placed on main and secondary roads, footpaths, and across fields, so that the entire study area was surveyed. For each site, the pre-defined transects were surveyed with uniform intensity on each night. Survey effort varied from 6-20 nights per site. All hedgehogs found during the spotlight surveys were approached on foot and captured by hand, weighed (g) using an electronic balance (Salter 1035 platform scale) and sexed (Morris, 2006). Animals were classified as adults if they weighed >600g (Young *et al.*, 2006; Haigh 2011; Hubert *et al.*, 2011). Healthy adult hedgehogs (few visible parasites, no injuries and normal ball-curling anti-predator behaviour) were marked uniquely with five coloured heat-shrink tubes (10mm in length) attached to the dorsal spines using a portable soldering iron. All hedgehogs were released at the point of capture and were observed from a distance until they moved off. The locations of all individuals were recorded using a handheld GPS device (Garmin GPS 60).

For analysis, each transect was divided into 50m 'trap' sections to ensure that the effective trap size was small enough in relation to the home range size of the hedgehogs to allow detection in multiple traps, but also large enough for computational tractability relative to a continuous space model (Fuller *et al.*, 2015; Sutherland *et al.*, 2018). To create spatial encounter histories, the location of each hedgehog's capture/recaptures were transposed to the midpoint of the closest 'trap' and to a sampling occasion (defined as the whole study area being surveyed). Data from two consecutive sampling nights were pooled if the whole study area was not surveyed on a single night. The creation of 'traps' and spatial queries were performed in ArcGIS 10.3.1 (ESRI, 2015). Only adult individuals were included in the analysis.

In total, eight SCR models were fitted: the null model (no covariates) and all additive combinations of constant and session-specific density (D), sex-specific detection (p) and sex-specific space use (σ). Models were ranked according to the Akaike's Information Criterion (AIC) value (Burnham and Anderson, 2004) and fitted in R (R Core Team, 2017) using the package oSCR (version 0.42.0; Sutherland, Royle and Linden, 2016).

Bland-Altman plots, also called Tukey mean difference plots, were used to compare the densities estimated by the ssREM and aveREM, and the aveREM and the most parsimonious SCR model (Bland and Altman, 1999; Giavarina, 2015) at each site. The Bland-Altman plot is a method for quantifying the difference between two quantitative measurements by calculating the difference for each pair of values, plotting these differences against the corresponding means, and constructing limits of agreement. Limits of agreement (LoA) are calculated from the mean $(\bar{d})$ and standard deviation (s) of the differences. We expected 95% of the differences to lie within $\bar{d} \pm 1.96s$.

All figures cited in the Results are mean ± SE unless stated otherwise.

Future population monitoring using REM

The suitability of the aveREM for long-term monitoring was assessed based on its power to detect 10%, 25% and 50% changes in population density with statistical power of 0.80, 0.95 and 0.99, and on the sample size (number of CTLs) required in future surveys. Power (defined as 1-β, where β is the probability of a Type II error: Steidl, Hayes and Schauber, 1997) was calculated using two-tailed paired-sample *t*-tests. Analyses were implemented in the R package *pwr* (version 1.2-2; Champely, 2018).

The costs associated with the REM were estimated from start-up costs (equipment purchases), human resources and survey length (number of days from recruiting members of the public to the collection of the last camera traps) for urban and rural landscapes. Although only 30 cameras were used each week, equipment costs were calculated for the purchase of 40 cameras to account for damage and malfunction. Human resources were quantified in terms of the hours of labour required to conduct the survey, including community engagement, fieldwork (i.e., deployment/collection of cameras, measurements of parameters) and data analyses. Hours of labour were not available for two study areas (Hartpury and Reading). Labour costs were calculated using the 2018 minimum national UK wage (7.83£/hour; GOV.UK, n.d.) only for reference purposes.

Results

Hedgehogs were detected by camera trapping and spotlight surveys at all sites. However, the REM could not be fully implemented (i.e., no confidence intervals associated with the density estimate were generated) at one site (Sutton Bonington) due to a small sample size (only one camera recorded hedgehogs). Camera trapping surveys were associated with a trapping effort of 47,507 hours and 802 independent hedgehog videos (Table 2). Video clips of other species recorded included domestic cats *Felis catus* (n = 1058), foxes *Vulpes vulpes* (n = 550), rabbits *Oryctolagus cunniculus* (n = 549) and badgers *Meles meles* (n = 44). Spotlight surveys were associated with a trapping effort of 613 hours over 1,415 km of walked transects; 111 individual hedgehogs were captured, of which 45 (41%) were recaptured (Table 3).

There was a high degree of concordance in the density estimates derived from ssREM and aveREM (Figure 2, Figure 3). The greatest disparity was evident in Reading, with densities being much higher when estimated using ssREM than aveREM; however, the estimates were within the Limits of Agreement (Figure 3). Hedgehog densities were higher within urban (averaged REM = 32.3 km^{-2}) versus rural (4.3 km^{-2}) areas. Mean camera detection arc (θ) and distance (r) were 0.240 ± 0.038 radians and 1.97 ± 0.44 metres, respectively; and they were not significantly different across urban and rural landscapes (Mann-Whitney U test: W_θ=2196; W_r=2267.5; p-value>0.05). Mean daily movement range was 0.52 ± 0.14 km h^{-1}(Table 5), significantly higher in rural (0.63 ± 0.06) than in urban landscapes (0.46 ± 0.06; Mann-Whitney U test: W=34615; p-value <0.05).

The most parsimonious SCR model included the combination of session-specific density (D), constant detection (p) and sex-specific space use (σ) (Table S2). As with the aveREM, hedgehog densities derived using the SCR method were higher in urban versus rural locations (Figure 2; Table 4). Densities estimated by the aveREM and SCR models were comparable for each site, with both methods producing estimates with overlapping 95% CIs (Figure 2). In addition, the mean difference of the densities estimated by the two methods was within the LoA at eight sites (Figure 3). However, the aveREM was more precise than the SCR at seven out of the eight sites; the exception was Ipswich West, where a very high density with an extremely large 95% CI was estimated by the aveREM in relation to both the corresponding SCR estimate for that site, and to all other urban sites.

Power analyses

Using a paired approach, all surveys conducted in this study would have been able to detect a 25% change in hedgehog density with >90% power (Table 6). Therefore, following our study design of deploying cameras for 6 nights (± 0.04) in an area of 0.68km^2 (± 0.03), 51 and 34 CTLs would be needed in rural and urban areas, respectively, to detect a 25% change in population density with 90% power (Table 7).

Resource costs

The REM had high start-up costs, principally due to the initial purchase of cameras (£6,400; Table 8). Higher start-up costs are also required in urban (£10,630) versus rural (£8,532) areas because of the difference in labour costs: human resources required to carry out urban surveys (468 hours) were, on average, 2.3 times higher than in rural sites (200 hours) due to the need to carry out community engagement and to process a higher number of videos. However, as camera traps are reusable, any subsequent site survey would only need to cover labour costs, decreasing expenditure per site to £3,664 and £1,566 in urban and rural areas, respectively. Survey length in urban sites (46 ± 1 days) was higher than in rural sites (23 ± 5 SE) due to the need to enlist the help of householders.

Discussion

The three methods used in this study (nocturnal capture-recapture data analysed using SCR, camera trap data analysed using survey-specific parameters within a random encounter model (ssREM), and camera trap data analysed using averaged REM parameters (aveREM)) generated similar estimates of hedgehog density in both urban and rural landscapes. Our results show that using a simpler approach (aveREM) does not compromise the quality of the estimate. Furthermore, only the aveREM is potentially amenable for inclusion as part of any future citizen science national survey of hedgehogs, as nocturnal spotlight and SCR require animals to be caught, marked and re-caught, requiring training and licensing. However, the implementation of ssREM is laborious and repetitive, which could compromise data-quality and accuracy (Newman, Buesching and Macdonald, 2003), and cause participants to drop out (Eveleigh *et al.*, 2014) if citizen scientists were to be involved in the measurement of all parameters. Furthermore, all participants would need to partake in additional training which adds costs and complexity to the project. However, an aveREM approach, where citizen scientists only collect data, would circumvent these issues, while being capable of detecting population changes with a high degree of power.

Here, we suggest that the aveREM could be implemented as part of a large-scale, long-term citizen science project based on a 'contributory model' (*sensu* Shirk *et al.*, 2012) in which the project is designed by scientists, and members of the public contribute primarily with data (Supporting Information 2, Figure S1). Such an approach would help to reduce labour costs, which is one of the main limitations of large-scale monitoring studies (Lindenmayer *et al.*, 2012), and will also provide valuable outcomes for science, local communities and social-ecological systems (Table 9). Our proposed framework will require researchers to carry out a pilot study (following the methodology of this study) to obtain specific REM parameters and the corresponding ssREM densities for the focal species across a range of habitat types. Once enough REM parameter measurements have been taken (i.e., densities estimated by the ssREM and aveREM are comparable), their average can be used for other surveys, of the same focal species and on similar landscapes, as part of a citizen science monitoring programme. Under this framework, citizen scientists would be involved during the data collection (i.e., community engagement and camera trapping surveys; Table 9), which could take on average 418 and 160 hours (per survey) in urban and rural areas, respectively. However, for the long-term implementation of the project, time resources in urban areas could be reduced further (down to 268 hours) on successive repeated surveys as community engagement will not be needed (i.e., same gardens/locations will be re-sampled). The framework we suggest requires a significant commitment on the part of the citizen scientist, although a recent national survey of hedgehogs in England and Wales demonstrated that surveyors oblige, despite the large commitment (Williams *et al.*, 2018a).

The REM method is, however, associated with significant start-up costs through the purchase of camera traps, memory cards, batteries and other ancillary equipment, and also community engagement costs. While we acknowledge that the costs associated with the REM were very broadly estimated here, we suggest that future REM studies should consider more detailed cost estimations, as suggested by Gálvez *et al.*, (2016). Yet, many of these are one-off costs: by "recycling" cameras between successive survey locations, the survey cost per site is diminished. For example, hedgehogs can be surveyed from April-October inclusive (Williams *et al.*, 2018a), and given that 51 and 34 CTLs are required in urban and rural areas, respectively, to detect population changes, a set of 30 cameras deployed on average 6 nights, could allow 14 sites to be surveyed a year, and for cameras to re-used over multiple years.

The hedgehog densities estimated in this study in both urban (13.9-25.9 km^{-2}; Ipswich West excluded – see below) and rural landscapes (1.2-6.8 km-^{2}) are comparable to those from other studies in the UK and Europe. For example, Dowding (2007) and Hubert *et al.* (2011) recorded densities of 17 km^{-2} and 36.5 km^{-2} in urban sites in England and France, respectively, whilst Parrott, Etherington and Dendy (2014), Hubert *et al.* (2011) and Young *et al.* (2006) recorded densities in rural locations of 4 km^{-2}, 4.4 km^{-2} and 9 km^{-2}, respectively. Whilst this concordance is potentially reassuring, one important caveat is that because of the inherent difficulties associated with studying wild hedgehog populations, true population size in all of these studies is not known. What these data do indicate clearly, however, is that densities are much higher in urban sites that have been surveyed, likely due to favourable environmental conditions such as higher food availability including supplementary feeding (Hubert *et al.*, 2011; Pettett *et al.*, 2018) and decreased risk of predation by badgers (Young *et al.*, 2006; Trewby *et al.*, 2014; Pettett *et al.*, 2017).

Although this study focused on one species, the approach taken here could also be used for multiple species monitoring over a large number of sites (Burton *et al.*, 2015; Caravaggi *et al.* 2016). All that is required is that the parameters for each species detected are recorded. Consequently, the REM has potential for future monitoring, not only of hedgehog populations but of a wide range of other species.

Limitations and recommendations

Despite its apparent potential, the REM methodology may be associated with some constraints that need to be considered and addressed. First, based on results of this study, the REM could not be implemented at one site (Sutton Bonington) as the population was very low (only two animals were captured during nocturnal spotlight surveys), and only one camera recorded hedgehogs. However, this could be resolved by deploying cameras for longer, expanding the area of survey sites and/or increasing camera density to achieve Rowcliffe *et al.*'s (2008) recommendation of a minimum of 10 independent captures. The first two options would potentially impact the assumption that populations are closed as hedgehogs may breed throughout much of the year, with males making exploratory movements in search of females, and juvenile animals being recruited (Morris, 2006). However, if densities change during the survey, the REM will estimate densities averaged across the trend (Rowcliffe *et al.*, 2008), so these approaches are likely to be viable.

Second, our findings indicate that the density and behaviour of hedgehogs in urban areas are likely influenced by differences in housing density, as shown in urban red foxes (Harris and Rayner, 1986). For example, despite both the aveREM and SCR producing high densities with large confidence interval in Ipswich West, the aveREM produced densities two times greater than the corresponding SCR estimate. The difference between the aveREM and SCR estimates could be due to habitat structure and hedgehog behaviour as Ipswich West was a highly urbanised area, containing the greatest proportion of built-up land and the smallest proportion of gardens (Table S1), which were mainly back gardens. The preference of hedgehogs for back gardens in urban areas (Dowding *et al.*, 2010) could have made the difference in the areas surveyed by both methods more prominent in highly urbanised areas: data analysed by SCR was mainly collected on roads and front gardens, while the REM data was mainly collected in back gardens. In our study design, cameras were mainly placed in back gardens to avoid theft and damage, and this has probably affected the random placement of cameras. This limitation is likely to be encountered in any camera trapping study in urban areas. We trust that the study design used here is robust and can work across a range of rural/urban landscapes, and with different housing densities in urban areas. However, understanding landscape structure and habitat preference will allow researchers to evaluate the impact of these features when estimating densities using the REM.

Remote sensing techniques are being used increasingly as part of citizen science projects to monitor wildlife at large spatial scales. This study is the first to use the Random Encounter Model (REM) to study small mammals across a range of landscapes, and its application as part of a citizen science framework. Our results indicate that an approach based upon averaged parameters (aveREM) is a potential suitable method for estimating hedgehog density across both urban and rural habitats, and one that is capable of detecting a 25% change in population size with high statistical power. Furthermore, it is a method that could be implemented as part of a contributory citizen science project, once pilot studies have been carried out to obtain the required parameters. The use of motion-activated cameras would also enable the monitoring of multiple species in both landscapes. However, further studies on a wider range of species are required across the broad range of urban and rural habitats/landscapes to derive suitable average parameters for inclusion in any national monitoring program.

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Data accessibility

Camera trap raw data, including footage and camera deployment files, used to estimate the REM densities and encounter history spotlight data to estimate SCR densities are available from Figshare (https://figshare.com/s/18252f7b85939e6b9b72). Raw video data are not shared to protect the participants' privacy.

Supporting Information

Supporting Information 1

Table S1. Habitat composition of urban (n=5) and rural (n=4) sites.

Table S2. Spatial Capture-Recapture candidate models and specific coefficients values used to estimate densities of hedgehogs in urban and rural landscapes.

Supporting Information 2

Citizen science framework for implementing the Random Encounter Model (REM)

Figure S1: Citizen science monitoring framework based on the use of the Random Encounter Model.

Data 1: R code for all analyses.

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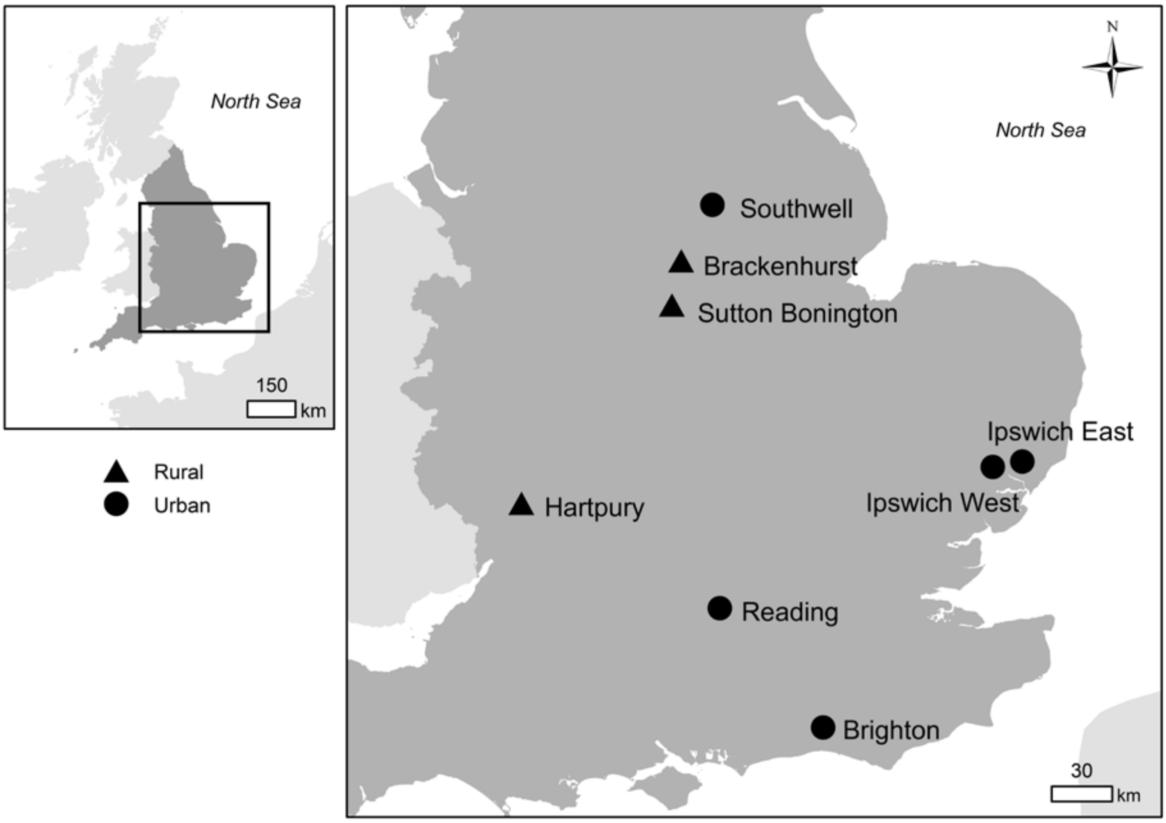

Figure 1. Location of study sites in England, UK. Rural study sites (n = 3) are represented by triangles; urban sites (n = 5) are represented by circles.

Figure 2. Hedgehog density (km^{-2}) estimates derived from averaged Random Encounter Model parameters (aveREM), site-specific Random Encounter Model parameters (ssREM), and Spatial Capture-Recapture (SCR) method in urban (n = 5) and rural (n = 4) environments. Error bars represent 95% confidence intervals.

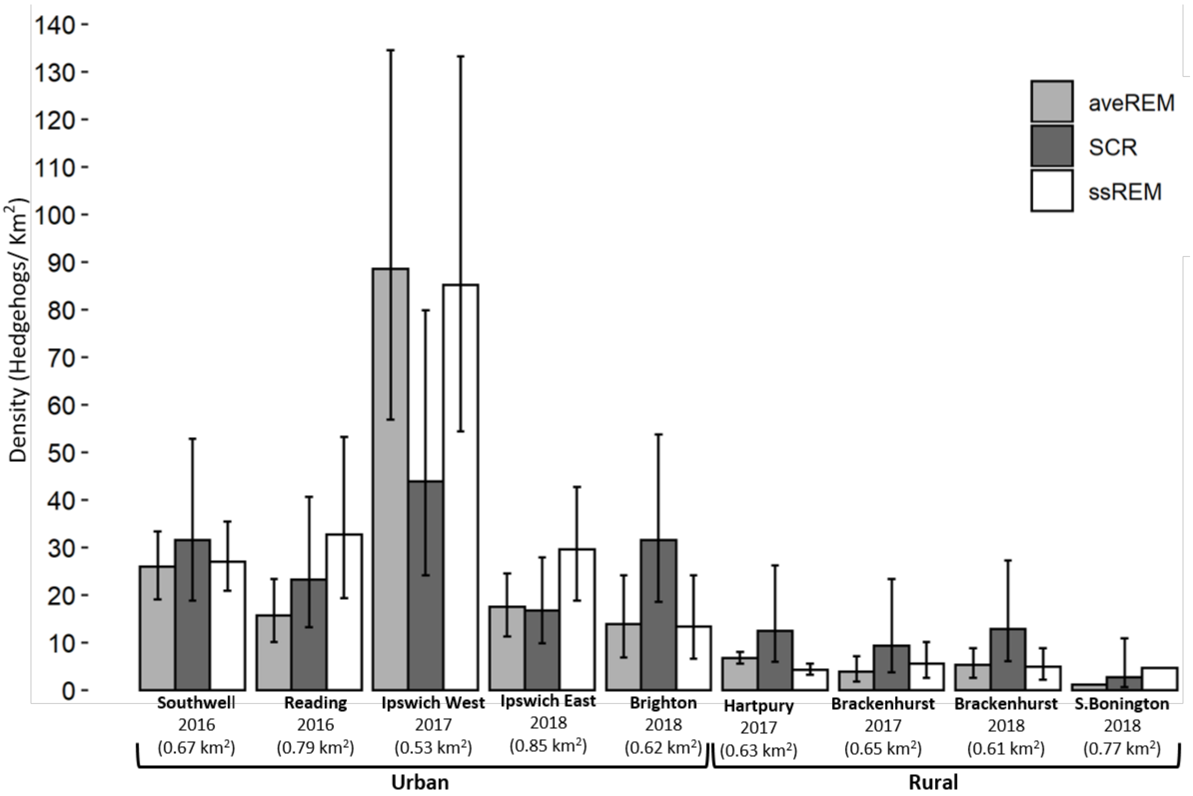

Figure 3. Bland-Altman plot of log-transformed difference [aveREM -SCR] against log-transformed mean density [(SCR+REM)/2] and limits of agreement between the SCR and averaged REM estimates of hedgehog density (km^{-2}) at each site: (a) Sutton Bonington, (b) Brackenhurst 2017, (c) Brackenhurst 2018, (d) Hartpury, (e) Ipswich East, (f) Reading, (g) Brighton, (h) Southwell and (i) Ipswich West. The dashed lines represent the log-transformed upper and lower 95% CI of agreement limits.

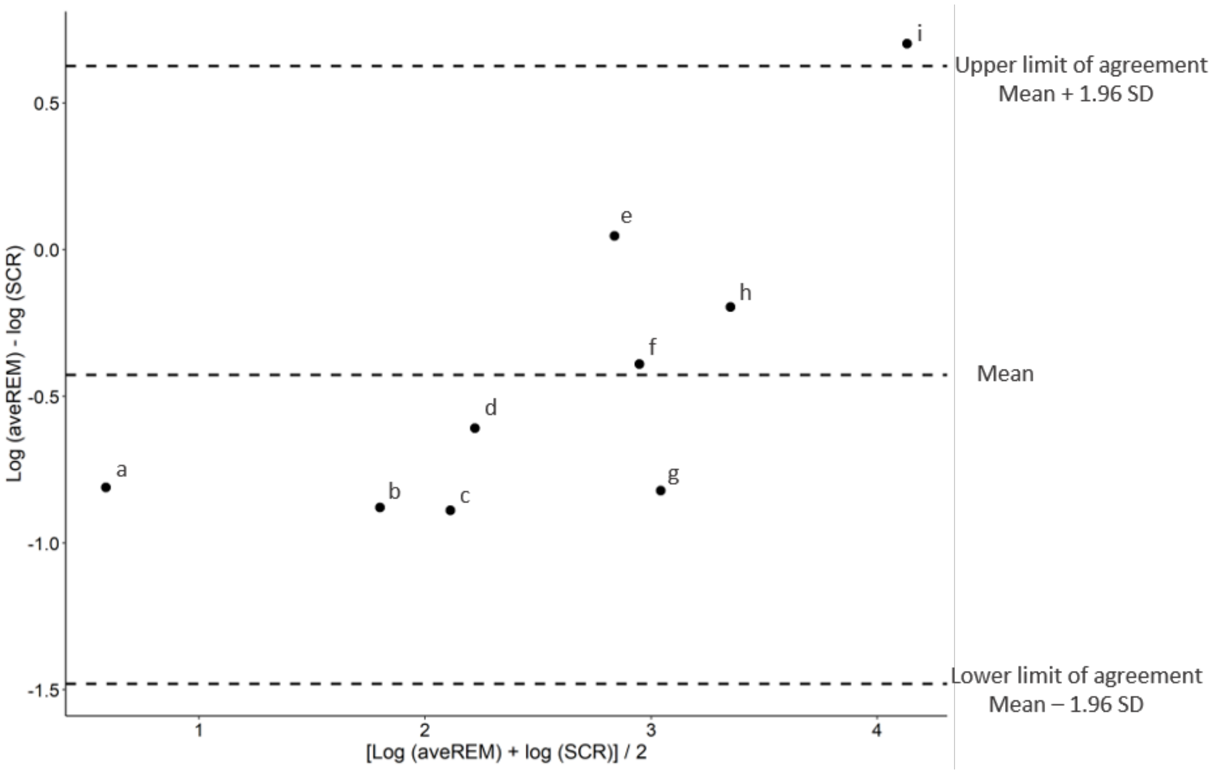

Table 1. Description of urban and rural study sites, survey timing and surveyed area.

Habitat	Urban					Rural			
Year surveyed	2016		2017	2018		2017		2018	
Survey name	Southwell	Reading	Ipswich West	Ipswich East	Brighton	Hartpury	Brackenhurst 2017	Brackenhurst 2018	Sutton Bonington
Survey period	May-June	Sept-Oct	April-May	April-May	May-June	June-July	Sept-Oct	April-May	July-August
Percentage of built-up land cover	40%	47%	56%	32%	34%	14%	12%	11%	20%
Area surveyed (km^2)	0.67	0.79	0.53	0.85	0.62	0.63	0.65	0.61	0.77
Centroid coordinates (Lat/Long)	53°04’32.40″N 0°57’53.95″W	51°25’42.50″N 0°54’42.89″W	52°03’57.88″N 1°07’59.83″E	52°04’08.52″N 1°11’28.94″E	50°51’02.45″N 0°12’10.34″W	51°54’26.89″N 2°18’34.15″W	53°03’47.63″N 0°57’22.63″W	53°03’47.63″N 0°57’22.63″W	52°49’53.09″N 1°14’51.55″W

Table 2. Summary of camera trapping surveys. CTs= camera traps

Habitat	Urban					Rural				TOTAL
Year surveyed	2016		2017	2018		2017		2018		
Survey name	Southwell	Reading	Ipswich West	Ipswich East	Brighton	Hartpury	Brackenhurst 2017	Brackenhurst 2018	Sutton Bonington	
Camera trap locations	112	120	118	118	109	120	117	59	101	974
Trapping nights	746	632	711	774	708	660	723	308	754	6016
Trapping effort (hours)	5222	6952	5688	5418	4956	3960	6507	2772	6032	47,507
% of CTs with footage of hedgehogs	32%	23%	56%	24%	14%	13%	9%	7%	1%	21%
No. videos of hedgehogs	110	89	409	77	56	22	21	12	6	802

Table 3. Summary of nocturnal spotlight surveys.

Habitat	Urban					Rural				TOTAL
Year surveyed	2016		2017	2018		2017		2018		
Survey name	Southwell	Reading	Ipswich West	Ipswich East	Brighton	Hartpury	Brackenhurst 2017	Brackenhurst 2018	Sutton Bonington	
No. survey sessions	11	8	6	15	10	10	13	17	20	90
Survey effort (hours)	40	42	42	124	37	59	27	40	202	613
Total transects length (km)	7.3	10.7	5.6	12	7.2	8.8	5.2	5	7.3	69.1
Total km walked	141	110	88	372	116	169	88	111	220	1,415
No. hedgehogs captured	20	16	14	19	19	8	5	8	2	111
% of hedgehogs recaptured	35%	6%	29%	21%	58%	63%	80%	100%	50%	41%

Table 4. Hedgehog density (individuals per km^{-2}) at urban and rural sites estimated using the averaged Random Encounter Model parameters (aveREM), survey-specific Random Encounter Model parameters (ssREM), and Spatial Capture-Recapture (SCR) method. Figures in parentheses are 95% confidence intervals.

Habitat	Urban					Rural			
Year surveyed	2016		2017	2018		2017		2018	
Survey name	Southwell	Reading	Ipswich West	Ipswich East	Brighton	Hartpury	Brackenhurst 2017	Brackenhurst 2018	Sutton Bonington
aveREM density estimate (95% CI)	25.9 (19.1-33.3)	15.7 (10.1-23.3)	88.6 (56.9-134.5)	17.5 (11.3-24.5)	13.9 (6.9-24.1)	6.8 (5.6-8.1)	3.9 (1.8-7.1)	5.3 (2.6-8.8)	1.2 *
ssREM density estimate (95% CI)	27.0 (20.9-35.5)	32.7 (19.4-53.2)	85.2 (54.4-133.3)	29.6 (18.8-42.7)	13.4 (6.6-24.1)	4.3 (3.2-5.6)	5.6 (2.6-10.1)	4.9 (2.2-8.8)	4.7 *
SCR density estimate (95% CI)	31.5 (18.8-52.9)	23.2 (13.2-40.6)	43.9 (24.1-79.9)	16.7 (9.9-27.9)	31.6 (18.6-53.7)	12.5 (5.9-26.2)	9.4 3.7-23.4)	12.9 (6.1-27.2)	2.7 (0.7-10.9)

*not enough data available to estimate 95% CI

Table 5. Summary of the independent variables required to calculate animal density from camera traps using the Random Encounter Model. Parameters from Sutton Bonington were not included in the average due to the small sample size (n=6) and its impact on the averaging the activity levels.

Habitat	Urban					Rural			Mean	SD	SE
Year surveyed	2016	2017		2018		2017		2018			
Survey name	Southwell	Reading	Ipswich West	Ipswich East	Brighton	Hartpury	Brackenhurst 2017	Brackenhurst 2018			
Average speed (μ, km/h)	0.77	0.40	0.55	0.52	0.64	1.04	0.50	0.74	0.65	0.20	0.07
Activity level (p)	0.83	0.73	0.79	0.84	0.75	0.61	1.05	1.00	0.83	0.14	0.05
Daily movement range (v, km/h)	0.64	0.29	0.43	0.44	0.48	0.63	0.53	0.74	0.52	0.14	0.05
Detection distance (r, m)	1.81	2.01	2.59	1.53	2.23	2.53	1.56	1.50	1.97	0.44	0.16
Detection arc (ɵ, radians)	0.244	0.209	0.209	0.262	0.262	0.314	0.209	0.209	0.240	0.038	0.013

Table 6. Statistical power of the averaged Random Encounter Model to detect 10%, 25% and 50% of population change between two surveys. Sample size refers to the number of camera trap locations at each site.

Habitat	Survey name	Sample size	Power to detect the stated change in density		
			10%	25%	50%
Urban	Southwell	110	0.99	1	1
	Reading	120	0.97	1	1
	Ipswich West	115	0.90	1	1
	Ipswich East	118	0.98	1	1
	Brighton	109	0.66	0.99	1
Rural	Hartpury	120	1	1	1
	Brackenhurst 2017	117	0.51	0.99	1
	Brackenhurst 2018	59	0.43	0.99	1

Table 7. Number of camera trap locations (CTLs) needed to detect 10%, 25% and 50% population change with 0.80, 0.90 and 0.95 statistical power in future surveys. Sites arranged by coefficient of variation (CV) values.

Survey	Hedgehog density (km^{-2})	CV (%)	% change in density	No of CTLs required to achieve stated level of statistical power		
				0.80	0.90	0.95
Hartpury	6.8	9	10	14	18	22
			25	4	4	5
			50	2	3	3
Southwell	25.9	14	10	34	44	55
			25	7	8	10
			50	3	4	4
Ipswich East	17.5	19	10	61	81	100
			25	11	14	17
			50	4	5	6
Reading	15.7	20	10	67	89	109
			25	12	15	19
			50	4	5	6
Ipswich West	88.6	23	10	87	116	143
			25	15	20	24
			50	5	6	7
Brackenhurst 2018	5.3	30	10	144	193	238
			25	24	32	39
			50	7	9	11
Brighton	13.9	31	10	152	202	250
			25	26	34	41
			50	8	10	12
	3.9	38	10	234	312	386

Brackenhurst 2017			25	39	51	63
			50	11	14	17

Table 8. Resources required to estimate hedgehog densities in urban and rural sites using camera trapping with the Random Encounter Model (REM) and spotlight surveys with the Spatial Capture-Recapture (SCR). Hours of labour are average values obtained from rural (n=3) and urban (n=4); associated costs are based on the national minimum UK wage (£7.83/hour) as a benchmark.

Method	Category	Description	Urban		Rural	
			Units	Cost (£)	Units	Cost (£)
REM	Equipment	Camera traps	40	6400	40	6400
		Memory cards/batteries	40	354	40	354
		Padlocks/chains	40	212	40	212
		Subtotal	£6,966		£6,966	
	Labour (hours)	Community engagement	150	1175	-----	-----
		Fieldwork	268	2098	160	1253
		Data analysis	50	392	40	313
		Subtotal	£3,664		£1,566	
		TOTAL	£10,630		£8,532	
SCR	Equipment	Spotlights	2	300	2	300
		Marking equipment set	2	418	2	418
		Subtotal	£718		£718	
	Labour (hours)	Fieldwork	184	1441	62	485
		Data analysis	30	235	25	196
		Subtotal	£1,676		£681	
		TOTAL	£2,394		£1,399	

Table 9. Summary of the expected outcomes of implementing the Random Encounter Model as part of a citizen science project and the activities required by the citizen scientists and researchers.

Outcomes for:	**Details**
Individuals	Conservation awareness
	Development of new monitoring skills
Species' ecological knowledge	Spatial and temporal large-scale data to monitor population trends, distributions and diversity of species
	Access to data from private land (i.e. urban areas)
Social-ecological system	Stewardship action and behavioural changes (i.e., enhancement of wildlife habitat in urban landscape)
Involvement of:	**Main Activities**
Citizen scientists	Community engagement (i.e., recruitment and retention of participants)
	Camera traps deployment/collection
	Data reporting
Researchers	Provision of camera trapping training
	Data analysis, interpretation and dissemination