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Statistical Development of Animal Density Estimation Using Random Encounter Modelling

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Camera trapping is widely used in ecological studies to estimate animal density, although these studies are largely restricted to animals that can be identified to the individual level. The Random Encounter Model, developed by Rowcliffe et al. (2008), estimates animal density from camera trap data without the need to identify animals. Although the REM can provide reliable density estimates, it lacks the potential to account for the multiple sources of variance in the modelling process. The density estimator in REM is a ratio, and since the variance of a ratio estimator is intractable we examine and compare the finite sample performance of many approaches for obtaining confidence intervals via simulation studies. We also propose an integrated Random Encounter Model (iREM) as a parametric alternative, which is flexible and can incorporate covariates and random effects. A data example from Whipsnade Wild Animal Park (WWAP), Bedfordshire, south England is used to demonstrate the application of these methods.

Key Words: abundance estimation, Random Encounter Model, unmarked species

1 Introduction

Camera trapping can be used to monitor wildlife and obtain information on behaviour, activity patterns (Ridout and Linkie, 2009; Bridges and Noss, 2011), species interactions (Barrull et al., 2014), and to determine population density (Rowcliffe et al., 2008; Chandler et al., 2013; Howe et al., 2017). In camera trapping, fixed cameras, triggered by infra-red sensors (McCallum, 2013), are used to take photos and/or videos of animals or other objects passing in front of them. If individuals are recognizable, animal abundance can be estimated using methods that combine camera trapping with spatially explicit capture-recapture models (Royle and Young, 2008; Efford et al., 2009). In the absence of individual identification of animals, relative abundance indices such as detection rates are used as an indirect measure of animal density (Carbone et al., 2001; O'Brien et al., 2003). These methods, however, lack a functional relationship between the camera index and animal density (Jennelle et al., 2002), and have been criticized for their simplistic approaches and implicit assumption that detectability is constant across areas, time and species (Burton et al., 2015). Rowcliffe et al. (2008) formulated the random encounter model (REM), which provides estimates of true animal density, accounting for imperfect detection without the need for individual identification. The REM assumes that animals move randomly and independently of each other (Rowcliffe et al., 2013), and uses functional relationships between encounter rates, the dimensions of the camera's sector-shaped detection zone, and the speed of animal movement to estimate the density.

Here, we extend the REM and develop methods that will be broadly applicable to many species, particularly unmarked species, for density estimation from camera trap data. We show, in Section 1.1, that the REM estimator can be derived as a maximum likelihood estimator, assuming that encounters between animals and camera traps follow a Poisson model. This formulation is flexible, allowing for covariates such as habitat type to be incorporated in the model, the extension of the REM from a fixed estimate of animal speed, and for estimation of the variance of the estimated animal density. We also show that the REM can be modified to account for animals moving in groups.

The REM is a ratio estimator, where the numerator and denominator are both stochastic in nature (Chaudhary and Stearns, 1996; Van Kempen and Van Vliet, 2000). We examine and compare the performance of several techniques to find approximate confidence intervals for animal density in this case. These methods are described in Section 2.

In Section 3, we propose an extension of the REM, termed the integrated random encounter model (iREM), which combines the REM for encounters with separate speed data. The iREM builds on the maximum likelihood formulation of REM. Rather than using a fixed estimate of animal speed of movement as the REM does, the iREM jointly models the encounters between animals and camera trap and animal speed of movement data. The iREM utilizes an integrated population modelling approach, which is widely used to account for overlapping information, and the sampling variability in multiple data sets (Newman et al., 2014), and which allows for the accurate treatment of precision and correlation in the estimators (Besbeas et al., 2002; McCrea and Morgan, 2014).

In Section 4, we use simulations to evaluate bias in estimated animal density based on the REM and the iREM, and compare the performance of several approximate confidence interval methods. In Section 5, the methods are applied to estimate the density of three species from Whipsnade Wild Animal Park (WWAP), Bedfordshire, UK.

1.1 Random Encounter Model (REM)

In this section, we describe how the REM leads to a method of moments estimator of animal density (Rowcliffe et al., 2008). In the REM, animals moving in random directions at constant speed V are assumed to be detected (encountered) whenever they enter a sector-shaped detection zone of radius r and angle θ ($< \pi/2$) that represents the area "seen" by the camera. The values of r and θ are assumed to be fixed and known constants.

Let Y denote the number of animals detected by a camera trap during a time period of length t, and let $\mathbb{E}(Y) = \lambda$. Rowcliffe et al. (2008) show that under the REM

$$\lambda = \frac{2+\theta}{\pi} rtV\rho, \tag{1.1}$$

where ρ is the density of animals. Rearranging (1.1) and replacing λ by the mean number of camera trap detections, $\bar{Y}$, leads to a moment estimator of ρ, assuming that V is known. In practice, the speed of movement V, and hence the distance travelled, is likely to vary between animals and over time for individuals, and in these circumstances Hutchinson and Waser (2007) state that in (1.1) V should be replaced by the expected speed, which we denote by μ. To test the REM, Rowcliffe et al. (2008) collected separate data on animal speed to obtain an independent estimate of μ. Suppose we have observed m speed observations $V = \{V_1, V_2, ..., V_m\}$, with sample mean $\bar{V}$. Then the method of moments estimator of animal density based on (1.1) is

$$\hat{\rho} = \frac{\bar{Y}}{K\bar{V}}, \quad \text{where } K = (2+\theta)rt/\pi. \tag{1.2}$$

1.1.1 Maximum Likelihood Framework for REM

The REM estimator (1.2) can also be derived by assuming that the number of encounters in a given time period, referred to as counts, follows a Poisson model. Specifically, let us assume that Y_{ij}, the number of animals seen on camera i on day j, where $i = 1, 2, ..., c$ indexes camera traps, $j = 1, 2, ..., n$ indexes camera trap days, follows a Poisson model with expected count λ, and that the Y_{ij}'s are independent, that is, all animals are captured independently of each other and independently at each trap. Since $\lambda = K\bar{V}\rho$, then the maximum likelihood estimator of ρ is given by (1.2), if $\bar{V}$ is treated as a known constant.

Throughout this research, we assume that each count Y_{ij} records the number of encounters at a single camera for a fixed period of $t_{ij} = 1$ day. In practice, camera traps are often left running for longer periods of time, and there is a choice of how, or indeed whether, to split the total recording period into smaller units for analysis. An advantage of splitting into smaller time units is that it allows the possibility of extending the model to incorporate time-varying covariates, such as mean day-time temperature. In the absence of such covariates, if encounters at each camera occur as a Poisson process, the choice of splitting does not affect the maximum likelihood estimator of ρ provided that the $\mathbb{E}(Y)$ is multiplied by the length of the resulting recording period, t_{ij} (see Supplementary Material S1.1), and indeed this approach can accommodate varying recording periods for different cameras, as usually occurs in practice.

1.1.2 REM estimator for animals moving in groups

Rowcliffe et al. (2008) suggested that (1.2) should be modified for animals that move in groups, by estimating the density of groups, ρ_G say, based on the number of groups encountered and multiplying this by an estimate of expected group size, η, to give an estimate of individual animal density, ρ. If $\overline{Y}$ denotes the mean number of groups encountered, the right hand size of (1.2) gives an estimate of the density of groups, $\hat{\rho_G}$. Provided the centre of each detected group lies inside the detection zone and the numbers of individuals in these groups can be counted, the sample mean of these counts gives an estimator of expected group size, $\hat{\eta}$ (Buckland et al., 2001), and $\hat{\rho} = \hat{\rho}_G \times \hat{\eta}$.

2 Confidence Intervals for Animal Density

Rowcliffe et al. (2008) estimated the variance of detection rate by bootstrapping counts from the camera locations with replacement and taking the variance of a large number of resampled density estimates. They suggested estimating the variance of density by combining the variances of detection rate, animal speed and other model parameters using the delta method. Here, we further explore the delta method for integrating variances, and present additional methods of forming approximate confidence intervals for animal density that account for the variability in $\bar{V}$.

Large-sample confidence interval for ρ. To account for the sampling variability in the estimated mean speed, the delta method may be applied to approximate the variance of the REM estimator (1.2), treating both $\bar{Y}$ and $\bar{V}$ as random variables. Here, $\mathrm{cov}(\bar{V}, \bar{Y}) = 0$ because the counts and speed data used by Rowcliffe et al. (2008) to test the REM were collected from separate sources and, therefore, are considered to be independent. The delta method gives

$$\mathrm{var}(\hat{\rho}) = \left(\frac{\bar{Y}}{K\bar{V}}\right)^2 \left[\frac{\mathrm{var}(\bar{Y})}{\bar{Y}^2} + \frac{\mathrm{var}(\bar{V})}{\bar{V}^2}\right]. \tag{2.1}$$

The variances on the right side of (2.1) can be estimated either 1) nonparametrically, as $\mathrm{var}(\bar{Y}) = S_Y^2/n$ and $\mathrm{var}(\bar{V}) = S_V^2/m$, where S_Y^2 and S_V^2 are the sample variances of the counts and speed, respectively, and where m is the number of speed observations and n is the number of camera trap days; or 2) parametrically, if for example, a Poisson distribution is assumed for the counts, we would estimate $\mathrm{var}(\bar{Y}) = \hat{\lambda}/n$.

Because the delta method uses a linear approximation, confidence intervals for ρ can be easily calculated if $(\bar{V}, \bar{Y})$ is assumed to be bivariate normally distributed. This leads to approximate $100(1-\alpha)\%$ confidence limits of the form

$$\{\hat{\rho}_L, \hat{\rho}_U\} = \hat{\rho} \pm z_{\alpha/2} \times \mathrm{SE}\left(\hat{\rho}\right), \tag{2.2}$$

where $z_{\alpha/2}$ denotes the upper $\alpha/2$ quantile of the standard normal distribution. These intervals are symmetric about $\hat{\rho}$ and are always finite (Franz, 2007). While the assumption of a bivariate normal distribution is reasonable in the case of large samples, it is unlikely that the distribution of a ratio will follow a well-behaved distribution in general. And, even if samples are large, the distribution of $\hat{\rho}$ is likely to be positively skewed if the coefficient of variation of the denominator of $\hat{\rho}$ is high (O'Brien et al., 1994). Also, the approximation will fail when the denominator is close to zero (Gleser and Hwang, 1987).

Large-sample confidence interval for $\log(\rho)$. Alternatively, we could work on the log-scale to obtain $100(1-\alpha)\%$ log-normal confidence limits for $\log\rho$ that can be back-transformed to obtain an asymmetric interval for ρ. Log-normal confidence intervals offer potentially improved coverage, particularly for small sample sizes, by allowing for asymmetric shape of the sampling distribution of $\hat{\rho}$ (Buckland et al., 2001). In this case, the delta method gives

$$\mathrm{var}(\log\,\hat{\rho}) = \frac{\mathrm{var}(\bar{Y})}{\bar{Y}^2} + \frac{\mathrm{var}(\bar{V})}{\bar{V}^2}. \tag{2.3}$$

Again, the variances $\mathrm{var}(\bar{Y})$ and $\mathrm{var}(\bar{V})$ in (2.3) can be estimated based on parametric models, or nonparametrically. Approximate $100(1-\alpha)\%$ confidence limits for ρ are

$$\{\hat{\rho}_L, \hat{\rho}_U\} = \exp\left(\log(\hat{\rho}) \pm z_{\alpha/2} \times \mathrm{SE}\left\{\log(\hat{\rho})\right\}\right). \tag{2.4}$$

Fieller's Theorem. An alternative to the delta method for calculating confidence intervals for a ratio has been described by Fieller (Fieller, 1944, 1954). Fieller's method takes into account the skewness of the ratio estimator (Briggs et al., 1999), and is again based on the assumption that $\bar{Y}$ and $\bar{V}$ follow a bivariate normal distribution. The variate $\bar{Y}-\rho K\bar{V}$ in (1.2) is then approximately normally distributed with zero mean and variance $\mathrm{var}(\bar{Y})+\rho^2K^2\mathrm{var}(\bar{V})$. If the variances of $\bar{Y}$ and $\bar{V}$ are estimated nonparametrically, as in (2.1), the pivotal quantity is

$$T_0 = \frac{\bar{Y}-\rho K\bar{V}}{S_Y^2/n+\rho^2K^2S_V^2/m}, \tag{2.5}$$

which follows approximately a t-distribution with degrees of freedom corresponding to those of the estimated variance. The degrees of freedom are estimated using Satterthwaite's approximation method (Satterthwaite, 1946; Sherman et al., 2011).

A confidence interval for ρ is obtained as the set of ρ values for which the null hypothesis $\mathrm{H}_0 : \bar{Y}-\rho K\bar{V}=0$ is not rejected at the $(1-\alpha)$ level, denoted by t_q. Hence, we obtain the confidence interval

$$\frac{\left(\bar{Y}/K\bar{V}\right) \pm \left\{\left[-\left(\bar{Y}/K\bar{V}\right)\right]^2 - \left(1-t_qS_V^2/m\bar{V}^2\right)\left[\left(\bar{Y}/K\bar{V}\right)^2 - t_qS_Y^2/K^2n\bar{V}^2\right]\right\}^{1/2}}{\left(1-t_qS_V^2/m\bar{V}^2\right)} \tag{2.6}$$

(see Supplementary Material S2). In order to have two real roots, Sherman et al. (2011) stated that $a>0$. If the denominator is significantly different from zero (i.e., $m\bar{V}^2/S_V^2 > t_q$), we obtain finite confidence intervals. In addition, Fieller's confidence interval may be the complement of a finite interval ($b^2-4ac>0,\ a<0$) or the whole real line ($b^2-4ac<0,\ a<0$) (Dufour, 1997; Sherman et al., 2011). We use the `ttestratio` function in the `R` package `mratios` to calculate (2.6) (R Core Team, 2017).

Nonparametric Bootstrap. An alternative approach involves sampling from the data with replacement to provide approximate confidence intervals for $\hat{\rho}$. Nonparametric bootstrap makes no assumptions about the distribution for the data (Zhou et al., 2019).

We use the percentile and bias-corrected percentile bootstrap methods, which are suitable for estimating confidence interval of ratio estimators (Briggs et al., 1999; Chaudhary and Stearns, 1996). The bootstrap procedures are given in Supplementary Material S3.

3 The Integrated Random Encounter Model (iREM)

Here, we propose an integrated random encounter model (iREM) for estimating animal density. The iREM is an alternative to the REM, which accounts for multiple sources of variance in the data in a single framework. Integrated models of this type allow for improved precision of parameter estimates and reduced correlation (Besbeas et al., 2002; McCrea and Morgan, 2014) as well as allowing estimation of parameters that are otherwise inestimable (Cole and McCrea, 2016).

Suppose we observed m independent and identically distributed animal speed observations, V_l ($l = 1, 2, ..., m$), with probability density function $f(V_l \mid \mu,\ \nu)$, where μ is expected animal speed, and ν represents any additional parameters of the speed distribution. If the counts, Y_{ij}, for camera trap $i = 1, 2, ..., c$ and camera trap day $j = 1, 2, ..., n$, have probability mass function $h(Y_{ij} \mid \rho,\ \mu,\ \tau)$, where ρ and μ are animal density and expected speed, respectively defined in equation (1.1) and where τ represents any additional parameters of the count distribution, the joint log-likelihood is

$$\ell(\rho, \mu, \tau, \nu) = \sum_{i=1}^{c} \sum_{j=1}^{n} \log\, h(Y_{ij} \mid \rho,\ \mu,\ \tau) + \sum_{l=1}^{m} \log\, f(V_l \mid \mu,\ \nu), \tag{3.1}$$

assuming that encounters between animals and cameras are independent, and that the counts and speed data are independent. This method allows the variability of parameter estimates to be estimated using standard methods, such as the inverse of the negative Hessian matrix (Morgan, 2008). The function $h(\cdot)$ in (3.1) can also be reparameterised as $h(Y_{ij} \mid \lambda,\ \tau)$ (see Supplementary Material S4). This approach allows each component of (3.1) to be maximized separately, where the first component is maximized at $(\hat{\lambda}, \hat{\tau})$ and second component at $(\hat{\mu}, \hat{\nu})$. This approach is attractive as it involves smaller-dimensional optimization problems. The estimator of ρ from maximizing (3.1) with $h(Y_{ij} \mid \lambda,\ \tau)$ is

$$\hat{\rho} = \frac{\hat{\lambda}}{K\hat{\mu}}. \tag{3.2}$$

Using the delta method, the variance of (3.2), on the log-scale, can be estimated as

$$\text{var}(\log\,\hat{\rho}) = \frac{\text{var}(\hat{\lambda})}{\hat{\lambda}^2} + \frac{\text{var}(\hat{\mu})}{\hat{\mu}^2}, \tag{3.3}$$

where $\text{var}(\hat{\lambda})$ and $\text{var}(\hat{\mu})$ are estimated using the inverse of the negative Hessian matrix.

The iREM estimator (3.2) and REM estimator (1.2) will coincide whenever the following conditions hold: 1) the maximum likelihood estimator of λ is $\hat{\lambda} = \bar{Y}$, and 2) the maximum likelihood estimator of μ is $\hat{\mu} = \bar{V}$. The first condition is true when the counts follow a Poisson (λ) distribution (as shown in Section 1.1.1) or a negative binomial (NB) distribution with a likelihood

$$L(Y_{ij};\lambda,\ \kappa) = \prod_{i=1}^{c}\prod_{j=1}^{n} \frac{\Gamma(\kappa + Y_{ij})}{\Gamma(Y_{ij}+1)\Gamma(\kappa)} \left(\frac{\kappa}{\lambda+\kappa}\right)^{\kappa} \left(\frac{\lambda}{\lambda+\kappa}\right)^{Y_{ij}}, \tag{3.4}$$

which has NB-2 form (Hilbe, 2011). This parametrization is in terms of the mean λ and auxiliary parameter κ, where the variance is $\text{var}(Y_{ij}) = \lambda + (1/\kappa)\lambda^2$ and $1/\kappa$ is the dispersion parameter. This form allows non-integer values of $1/\kappa$. The second condition, $\hat{\mu} = \bar{V}$, is true if animals are constantly moving during the trapping period and their speeds are assumed to follow a gamma distribution, or if some species stopped altogether and zero speeds of movement are recorded, as in Rowcliffe et al. (2008), and a zero-adjusted gamma distribution (ZAGA) is assumed for speed of movement (see Supplementary Material S1 and S6, and S7 for proof of the first and second conditions, respectively).

3.1 Adding animal group size data

We can extend (3.1) to include data for animals that move in groups. Using counts of randomly sampled groups, one can estimate average group size and hence the density of individuals. Suppose that group size, s_j ($j = 1, ..., S$), is assumed to follow some discrete distribution whose support is the set of positive integers. The joint log-likelihood is

$$\ell(\rho,\tau,\mu,\nu,\phi) = \sum_{i=1}^{c}\sum_{j=1}^{n} \log h(Y_{ij} \mid \rho,\ \mu,\ \tau) + \sum_{l=1}^{m} \log f(V_l \mid \mu,\ \nu) + \sum_{j=1}^{S} \log k\left(s_j \mid \phi\right), \tag{3.5}$$

assuming that group sizes are small and counts of the number of individuals can be made (Buckland et al., 2001). In (3.5), $k(\cdot)$ is the probability mass function of the group size data and ϕ represents the unconditional mean of the discrete distribution. Here, we consider a zero-truncated Poisson model (ZTP) for the group size data, with expected mean $\eta = \phi / \left(1 - e^{-\phi}\right)$. Similar to (3.1), it is possible to reparameterize $h(\cdot)$ in (3.5) in terms of λ, where the first component is maximized at $(\hat{\lambda}, \hat{\tau})$, the second component at $(\hat{\mu}, \hat{\nu})$ and the third component at $(\hat{\phi})$ (see Supplementary Material S4.1).

3.2 Adding covariates and random effects

We might wish to add habitat type or random effects to iREM for several reasons. For example, if animals spend more time in some habitats than others or are restricted to partially overlapping home ranges, a habitat-specific covariate accounts for the variability in abundance. The REM requires that camera traps be placed randomly in the study area, with respect to animal movement. Therefore, a camera random effect could be incorporated in the model to account for any unobserved variability.

We could model animal density as a function of a linear model via the log link function such that the expected encounter rate becomes:

$$\boldsymbol{\lambda} = \left(\frac{2+\theta}{\pi}\mu r t\right) \exp(\mathbf{X}\boldsymbol{\beta}), \tag{3.6}$$

where $\boldsymbol{\beta}_{H\times 1}$ is a vector of regression parameters and β_1 is the constant term; and $\mathbf{X}_{n\times H}$ is a matrix of $H-1$ covariates, where $x_{1j} = 1$ is the first explanatory variable. Here, we consider habitat covariates and refer to this model as iREM with habitat. Generally, estimates of the regression parameters, $\boldsymbol{\beta}$, cannot be obtained analytically, so numerical methods must be employed to approximate these estimates (Green, 1984). Once these are obtained, the mean animal density over all habitats, ρ_{mean}, is computed as

$$\rho_{mean} = \sum_{k=1}^{H} \frac{A_k \exp(\beta_k)}{A_T} = \frac{\sum_{k=1}^{H} A_k \rho_k}{A_T}, \tag{3.7}$$

where A_k $(k = 1, 2, ..., H)$ is the area of habitat k in the surveyed area; and $A_T =$

$A_1 + A_2 + ... + A_H$ is the total area. Estimating average density in this way works only for categorical covariates. Our motivating example did not use continuous covariates, but we briefly note here that estimating average density in this case would require values of the covariates to be known across all grid cells of the sampling area (Miller et al., 2013). We use the `optim` function in the R software with BFGS optimisation method (R Core Team, 2017), to obtain estimates of β_k. The variance of ρ_{mean} can be estimated directly if the variances of ρ_k or β_k are known (Supplementary Material S5).

As with the covariate model (3.6), the camera random effects can be included via a log-linear link on the expected encounter rate:

$$\boldsymbol{\lambda}_{ij} = \left(\frac{2+\theta}{\pi}\mu r t\right) \exp\{\log(\rho) + b_i\}, \tag{3.8}$$

where $\boldsymbol{\lambda}_{ij}$ are the expected counts for the jth ($j = 1, 2, ..., n$) day on the ith ($i = 1, 2, ..., c$) camera, ρ is the density and b_i is a vector of camera random effects, which are assumed to be independently normally distributed with variance σ_b^2. We use Gauss-Hermite quadrature to approximate the marginal likelihood of the counts (Winkelmann, 2008). Assuming the counts Y_{ij} and speed observations V_l are independent, and that animals encounter camera traps independently of each other, the joint log-likelihood is

$$\ell(\mu, \nu, \sigma_b) \approx \sum_{i=1}^{c} \log \sum_{q=1}^{Q} \prod_{j=1}^{n_i} \frac{w_q h_{ij}(\sqrt{2}\sigma_b x_q)}{\sqrt{\pi}} + \sum_{l=1}^{m} \log f(V_l \mid \mu,\ \nu), \tag{3.9}$$

where $h_{ij}(\sqrt{2}\sigma_b x_q) = h(y_{ij} \mid b_i = \sqrt{2}\sigma_b x_q;\ \rho,\ \mu)$ is the conditional density function of the counts evaluated at b_i, w_q are weights, x_q are evaluation points, and Q is the number of quadrature points. This model is referred to as the iREM with random effect. One could also combine models (3.6) and (3.8) to determine the effect on animal density. We refer to this model as the iREM with habitat and random effect.

4 Simulation Study

We evaluate the performance of the REM estimator and iREM estimator using simulation studies. We generate scenarios in which the true animal density and expected animal speed are plausible ecologically for our motivating Whipsnade Wild Animal Park (WWAP) data set, described in Section 5. Confidence intervals of the density are estimated using the relevant methods discussed in Section 2.

4.1 Evaluation of the REM and iREM Estimators

Several researchers such as Briggs et al. (1999), Dinh and Zhou (2006) and Polsky et al. (1997), have compared different methods of forming confidence intervals for ratios through simulation studies. We examine the coverage properties and interval widths of the relevant methods described in Sections 2 and 3 of calculating confidence intervals for ρ.

We simulate speed observations from a ZAGA model and counts from a negative binomial REM with auxiliary parameter $\kappa = 2$. We set the parameter values to be similar to those estimated from the WWAP data. Specifically, the expected speed was set to $\mu = 0.71$ (km day^{-1}) and variance $\text{var}(V) = 1.275$, with probability of zero response $\omega = 0.30$; and $r = 0.012$ km, $\theta = 0.175$ radians and $t = 1$ day throughout (Rowcliffe et al., 2008). We fit the REM, a Poisson iREM or negative binomial iREM to these data.

The performance of the interval estimation methods were evaluated for two scenarios: 1) fixed and small sample sizes of camera trapping days (n) and speed observations (m), and 2) varying sample sizes for fixed parameters. We repeated the simulations 1000 times, which gives reasonable estimates of coverage without being overly computer-intensive, and with 1000 nonparametric replications in the bootstrap methods following recommendations by Carpenter and Bithell (2000). The confidence intervals from the bootstrap methods were computed by resampling both the counts and speeds. The criteria used to evaluate the performance of the relevant methods for computing confidence intervals for the REM or iREM estimators are the estimated coverage probability. That is, the proportion of samples in each simulation experiment where the true animal density fell within the estimated confidence interval, and the mean interval length.

Table 1 gives the estimated coverage probability of the different confidence interval methods based on the REM and iREM estimators. Recall that the REM and iREM estimators will coincide under certain conditions and, whether we assume a Poisson or NB model for the counts, the maximum likelihood estimator of the expected encounter rate is the sample mean (see Section 3 above). For scenario 1 (fixed sample sizes), the coverage probability of the estimated 95% large-sample confidence interval for animal density based on the REM estimator was estimated between 90% and 92% across different true values for ρ, indicating poor coverage. However, on the log-scale, the estimated confidence probabilities were closer to the nominal value. The log-scale method also gave the shortest mean interval width compared with all methods, except for the large-sample interval for $\hat{\rho}$, but as noted, that method had poor coverage. A similar performance of coverage probability was achieved by Fieller's method, but with considerably wider mean interval widths than the other methods. In addition, there were incidences of infinite confidence intervals from Fieller's method but these were low (ranging from 0% to 0.3% and increasing with density). For the bootstrap methods, the bias-corrected method generally performs better than the percentile method, as is expected, since it adjusts for the bias and skewness of the sampling distribution of $\hat{\rho}$. The coverage probabilities of the estimated 95% large-sample and log-scale confidence intervals from using the iREM estimator were similar on average to the REM estimator, but the mean interval widths were generally larger.

Increasing sampling effort (scenario 2) resulted in finite confidence intervals from Fieller's method for all experiments, but the log-scale and bias-corrected bootstrap methods gave better coverage probabilities than Fieller's method, particularly for small ρ. Although the log-scale method gave better coverage on average than the other methods, with differences from nominal coverage shrinking to zero quickly with increasing sample sizes, the mean interval widths were wider. In general, there is little to choose between the methods for large sample sizes based on the REM estimator. The coverage probability of the estimated 95% large-sample and log-scale confidence interval when using the iREM estimator is slightly better than that from the REM, particularly for large ρ (Table 1).

4.2 Evaluation of Camera Random Effect on Animal Density

We also investigate the importance of accounting for the unobserved variability from camera random effects that may affect $\hat{\rho}$. We simulate counts from a negative binomial with auxiliary parameter $\kappa = 2$ and expected counts λ_{ij} defined in (3.8), and we fit a Poisson or negative binomial iREM with random effect and a Poisson or negative binomial iREM. We set animal density, $\rho = 75$ (km^2), expected speed, $\mu = 0.71$ (km day^{-1}) and $\sigma_b = 0.10$ or $\sigma_b = 0.60$. The number of camera traps is set to 10, and for simplicity we assume each camera is functioning for the same number of days. We set the number of counts and speed observations $n = m = 25$ or $n = m = 100$, and the number of quadrature points $Q = 20$, following recommendations by Cole et al. (2003) and simulation studies (see Supplementary Material S8). Animal speed data is simulated from a ZAGA model, and we a fit a ZAGA model to these speed observations repeating each experiment 100 times and taking the average of the parameter estimates and their estimated standard errors, standard deviation (Sd), root mean square error (RMSE) and the percentage bias of the estimators. When camera random effect is small, the difference in estimated animal density between the iREM with random effect and the iREM is marginal (Table 2). Also, for both methods the bias in animal density is negligible (less than 4% of the true population density, on average for small sample sizes, and less than 2% for larger sample sizes). Increasing the camera random effect results in a large difference in estimated animal density between the two methods, and the bias is substantial for the iREM. As sample sizes increase, the precision in estimated σ_b improves.

5 Application to Whipsnade Wild Animal Park (WWAP) Data

The data used to test the REM and iREM estimators is a small data set from Whipsnade Wild Animal Park (WWAP), Bedfordshire, UK (Rowcliffe et al., 2008). The WWAP survey was conducted over a 6 week period from 13 June - 24 July, 2005 for a total of $n = 42$ camera trap days. The park houses several free-ranging species and Rowcliffe et al. (2008) considered four of these species. For the purposes of analyses we consider only three of these species that had observed zero speeds in the data: 1) wallaby, 2) water deer and 3) mara. The park was divided into four areas of contrasting habitat. The first two areas are open grasslands with scattered scrub: 1) *Downs* with a steep scarp slope; 2) *Institute Paddock* (*IP*) with gentle slopes; 3) *Old Farm* (*OF*), which is an area of rough grassland and thicket on largely level but highly broken ground; and 4) *Central Park* (*CP*), which is an area of mixed lawns, roads, buildings and enclosures housing large animals with scattered trees. To investigate how well the method works a census, counting the number of animals, was carried at the end of the trapping period between 09:30 and 14:00. Since the census was taken over a specific time period, and animals moved among habitats there were observed zero census count in some habitats for some species, even though cameras recorded all species in all habitats.

The REM estimator of animal density requires estimates of average speed of movement and average group size, if animals are found in pairs or family groups. Rowcliffe et al. (2008) used day range as an approximate estimator of speed. Rowcliffe et al. (2008) arbitrarily selected 10 individuals following each individual for 30 minutes recording the distance moved as the sum of all straight-line movements. A total of 10 focal watches were conducted between 08:00 and 18:00 (in order to control for any variation in movement patterns over the day) and day range for each species was calculated as the mean across all focal watches for that species. During these focal watches it was observed that some animals did not move during the period they were watched, hence, a zero speed was recorded. Average group sizes were estimated by systematically recording the numbers of individuals in groups encountered along transects through the study area. Since the speeds and counts were collected from separate sources, they are considered independent. Table S9.1 in Supplementary Material S9 provides a summary of the WWAP data.

5.1 The REM and iREM Estimators

In this section, we fit the REM and iREM to WWAP data, providing estimates of density in heterogeneous habitats and the overall mean density of each species over habitats.

Rowcliffe et al. (2008) estimated animal density in each habitat separately, but we can estimate these densities simultaneously using the maximum likelihood formulation of REM, obtaining confidence intervals from using the large-sample or nonparamteric bootstrap methods. Here, we estimate ρ in each habitat separately as in Rowcliffe et al. (2008) using the REM, and confidence interval estimates of $\hat{\rho}$ are computed using the large-sample method for $\log(\rho)$ and nonparametric bootstrap (1000 resamples) by resampling both the speeds and the counts from the REM estimator. For the iREM estimator, large-sample confidence interval estimates are computed from the estimated standard errors of $\hat{\boldsymbol{\beta}}$. We assume average group size and speed to be constant over all habitats. Table 3 compares estimates of animal density in each habitat and mean animal density with the census density for the three species.

For wallaby, the difference between the estimated mean animal density and census density is less than 28%, and the estimated mean animal density from the census (including estimated animal density from the census in each habitat) is captured within an approximate 95% confidence interval from all confidence interval methods. In all cases, except for estimated mean animal density, the log-scale method gave the shortest interval widths based on the REM estimator. For water deer, the difference in estimated animal density and mean density from the census is 59% but the mean density from the census is captured within an approximate 95% confidence interval from all methods. Habitat-specific density estimates for water deer differed dramatically (more than three-fold) from census values in some cases, however, it must be remembered that animals were free to move between habitats. The camera-based estimates effectively integrate across any such movements, whereas the census occurred at a single point in time, which may not have been representative of the longer survey period. In terms of which is the best method for estimating variability of the density of the water deer based on the REM, we would recommend the log-scale method as it gave the shortest interval widths for all estimates.

The estimated mean animal density of mara is very different from that of the mean census density (Table 3), and the density from the census is not captured within an approximate 95% confidence interval calculated using any of the three methods (log-scale, bias-corrected or percentile bootstrap). This result coincides with estimates from Rowcliffe et al. (2008) who showed that the REM performed well in extracting absolute densities from encounter rate data, and the estimated densities for all species, except mara, did not differ significantly from the census results. The problem with the mara estimates is a result of poor survey design. The mara like to inhabit open areas, and during the WWAP survey the mara were mostly seen in Central Park, which is an open area most frequented by people. So in order to avoid crowding camera traps with too many human photographs, camera traps were located away from these crowded areas, and where the mara did not graze frequently. Hence, limited capture data were recorded, leading to the severe underestimation of the density. The percentile bootstrap method has the shortest confidence interval widths for estimated density in Downs and IP, while the log-scale gave the shortest confidence widths for estimated animal density for the other habitats and the estimated mean animal density.

With regards to estimated standard errors from the large-sample and bootstrap methods based on the REM, the bootstrap standard error estimates are considerably larger. But, one could easily compare these on the log-scale and see clear similarities between the two methods since both methods are attempting to capture the variability that comes from using an estimate of the mean speed (see Table S9.2 in Supplementary Material S9).

The REM and iREM gave a similar performance as in our simulation example, where estimated large-sample interval widths from the iREM are larger than those estimated from the REM. As shown in Section 4.1, the iREM performed slightly better than the REM, particularly for large ρ and large sample sizes. At WWAP, there were large numbers of camera records and large census densities recorded for wallaby and water deer (see Table S9.1).

We also show the implications of using Fieller's method in practice when certain conditions (see Section 2) are not met. Table S9.3 in Supplementary Material S9 presents the results from Fieller's method. Fieller's method gave infinite (unbounded, UB) confidence intervals for wallaby. Franz (2007) state that to avoid this situation a necessary and sufficient condition must be satisfied: the $(1-\alpha)$ confidence interval of the denominator

$(K\bar{V})$ must not contain zero. If this condition is not met, then its confidence interval allows values arbitrarily close to zero and the confidence sets are unbounded. Fieller's method also provides negative confidence limits for some species. Since the distribution of $\hat{\rho}$ is positively skewed this indicates poor coverage (Buckland et al., 1993). The cases where negative confidence intervals are estimated arise when the data are rather limited; in this case, the numbers of mara recorded by camera traps were 3, 1, 2, and 3 in the Downs, IP, OF and CP, respectively (see Table S9.1 in Supplementary Material S9).

5.2 Model Comparison

Here, we apply the iREM, the iREM with habitat, the iREM with random effect and the iREM with habitat and random effect to the WWAP data set. Models are compared in Table 4 using AIC. Animal density from the census is compared with estimated animal density of the three species from the four iREM models. Estimated standard error from the Hessian matrix is given in parentheses. We also give the parameter estimates from the best model based on AIC in Table 5. The results (Table 4) show that the best method for the wallaby and water deer is the iREM with habitat and camera random effect. For the wallaby, the difference in estimated animal density from the iREM with habitat and random effect decreased by at least 90% compared with the simpler iREM method. For the water deer, estimated animal density from the iREM with habitat and random effect was closer to the census density than the estimate from the iREM with habitat alone. Model comparison based on ΔAIC indicates that the iREM with random effect is the best model for mara, even though the other models provide estimates of animal density that are slightly closer to the census density. Except for the mara, the estimated camera random effects $\hat{\sigma}_b < 1$.

6 Discussion and Conclusions

In this research, we have developed new approaches for estimating animal density from camera trap data. The random encounter model developed by Rowcliffe et al. (2008) for animal density estimation is a ratio estimator, which is simple and easy to use. We showed that this estimator can be derived using maximum likelihood estimation, by assuming the counts follow a Poisson distribution. To determine the precision of the ratio, we examined five different methods for calculating confidence intervals, five of which are relevant for the REM moments estimator. These methods include: large-sample confidence interval for animal density (delta), log-scale, bias-corrected bootstrap, percentile bootstrap and Fieller's method. Our simulation example shows that these five different methods for calculating confidence intervals can produce different confidence intervals. We found that confidence intervals derived from using the log-scale method were more dependably accurate than those constructed from the other methods. In particular, the log-scale method gave shorter interval widths, on average, compared with the other methods, except for the delta method for small sampling effort. This result is also evident in the real data analysis, and is substantiated by Buckland et al. (2001).

Fieller's method can produce reasonably accurate coverage, but it gave the widest confidence interval width for all experiments, and in some cases, failed to produce finite confidence intervals. These results are also obtained in the real data analysis, particularly for the wallaby data where confidence intervals were unbounded. The delta method performed the poorest in terms of coverage, but it gave the shortest confidence interval width, on average. For Fieller's method (Franz, 2007) and the delta method (O'Brien et al., 1994) mis-coverage would occur for small sample sizes as the distribution of the ratio is unlikely to follow a well-behaved distribution (a result seen in our simulation example for sample sizes < 200). Furthermore, it is not guaranteed for ratios that the delta method or Fieller's method would give exact confidence intervals when sample sizes are large since the denominator of the ratio may not be significantly different from zero (Franz, 2007). This is evident in our simulation example from Fieller's method when animal density and sample sizes are large.

Of the bootstrap methods, no clear patterns emerged in terms of rank of ordering of performance in coverage and confidence interval width. The bias-corrected method was designed to adjust for the bias and skew of the sampling distribution (Puth et al., 2015) but also to give similar performance where the percentile method does relatively well as shown by our simulation example, and thus can be favoured. As regards which method to adopt, we recommend the log-scale method as the method we would choose for estimating variability of animal density from the REM estimator. The log-scale method is designed to give better coverage than the other methods by allowing for the asymmetric shape of the sampling distribution of the density (Buckland et al., 2001).

As an alternative to the REM estimator, one could use the integrated Random Encounter Model (iREM) to obtain estimates of animal density and its variance. Both the REM and the iREM are simple and easy to use if the density of animals in a study area is required or if one also wishes to account for the variability in animal density in heterogeneous habitats. We have shown that it is not essential to use the integrated log-likelihood to obtain the variance of animal density in these cases, as the counts and speeds could be modelled separately and the variances of these could simply be combined to determine the uncertainty of estimated animal density. This makes the iREM attractive, as it leads to smaller dimensional optimization problems. However, if more complicated modelling is required, for example to account for unobserved variability in animal density, we would recommend the joint-likelihood for estimating animal density and its variance. These are difficult to obtain analytically, so numerical approximation are required and therefore, the iREM estimator is favoured over the simple REM estimator or modelling of the counts and speed separately. The iREM is also flexible to estimate density of animals moving in groups, providing that some assumptions of estimating this density of animals moving in groups from camera trap data are met. Camera traps are similar to point transects in distance sampling (Buckland et al., 2001), which are both fixed at a given position, recording images of passing animals. However, there are inherent difficulties with the use of camera traps in assessing group sizes. If the detection probability is dependent on both the distance from the point (in this case the camera trap) and group size, there would be difficulties in obtaining an unbiased estimate of the expected group size. This dependence arises because large groups are more likely to be detected further away from the camera, while small groups might remain undetected. This phenomenon would cause an overestimation of the expected group size because too few small groups are detected, i.e., they are under-represented in the sample. Another complication arises as distances should be measured from the point to the geometric centre of the group (see Buckland et al., 2001, Ch. 1). In camera trapping, the distance from the camera to the centre of the group is unobservable, and it becomes impossible to quantify the detection zone, particularly for larger, more dispersed groups and estimation of the density becomes difficult (Rowcliffe et al., 2011). In particular, large groups near the camera would be detected, but their centres may lie outside of the detection zone given the narrow width of the detection zone near the camera trap. Buckland et al. (2001, pp 75-76) suggest that the problems of estimating average group size may be avoided by taking the sampling unit to be the object, not the group. However, in this case, the independence assumption would be violated. Alternative resampling methods such as the bootstrap can be used to provide valid variance estimation in this case, but analytical variance estimation and model selection procedures would not be valid. This remains an avenue for future research.

Both the REM and the iREM can give reliable estimates related to animal abundance and answer key ecological questions, but the REM lacks the potential to account for the sampling variability in the speed of movement and camera random effects. Although the iREM is flexible to incorporate multiple sources of variability, model fitting can be complex and computer-intensive, especially the iREM with both random effects and habitat covariates. It is also possible to test the robustness of both the REM and iREM since long term camera trap data sets, designed for population estimation do exist (e.g., Barro Colarado (BCI), Panama) (Rowcliffe et al., 2011). However, the sampling design differs from the WWAP data set and would require applications of distance sampling theory for animal density estimation, which is outside the scope of this work.

References

Barrull, J., Mate, I., Ruiz-Olmo, J., Casanovas, J., Gosàlbez, J., and Salicrú, M. (2014). Factors and mechanisms that explain coexistence in a mediterranean carnivore assemblage: an integrated study based on camera trapping and diet. *Mammalian Biology-Zeitschrift für Säugetierkunde*, 79(2):123–131.

Besbeas, P., Freeman, S. N., Morgan, B. J., and Catchpole, E. A. (2002). Integrating mark–recapture–recovery and census data to estimate animal abundance and demographic parameters. *Biometrics*, 58(3):540–547.

Bridges, A. S. and Noss, A. J. (2011). Behavior and activity patterns. In *Camera Traps in Animal Ecology*, pages 57–69. Springer.

Briggs, A. H., Mooney, C. Z., and Wonderling, D. E. (1999). Constructing confidence intervals for cost-effectiveness ratios: an evaluation of parametric and non-parametric techniques using monte carlo simulation. *Statistics in Medicine*, 18(23):3245–3262.

Buckland, S., Breiwick, J., Cattanach, K., and Laake, J. (1993). Estimated population size of the california gray whale. *Marine Mammal Science*, 9(3):235–249.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D., and Thomas, L. (2001). Introduction to distance sampling estimating abundance of biological populations.

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Bayne, E., and Boutin, S. (2015). Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, 52(3):675–685.

Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J., Griffiths, M., Holden, J., Kawanishi, K., Kinnaird, M., et al. (2001). The use of photographic rates to estimate densities of tigers and other cryptic mammals. In *Animal Conservation Forum*, volume 4, pages 75–79. Cambridge University Press.

Carpenter, J. and Bithell, J. (2000). Bootstrap confidence intervals: when, which, what? a practical guide for medical statisticians. *Statistics in medicine*, 19(9):1141–1164.

Chandler, R. B., Royle, J. A., et al. (2013). Spatially explicit models for inference about density in unmarked or partially marked populations. *The Annals of Applied Statistics*, 7(2):936–954.

Chaudhary, M. A. and Stearns, S. C. (1996). Estimating confidence intervals for cost-effectiveness ratios: an example from a randomized trial. *Statistics in Medicine*, 15(13):1447–1458.

Cole, D. J. and McCrea, R. S. (2016). Parameter redundancy in discrete state-space and integrated models. *Biometrical Journal*, 58(5):1071–1090.

Cole, D. J., Morgan, B. J., and Ridout, M. S. (2003). Generalized linear mixed models for strawberry inflorescence data. *Statistical Modelling*, 3(4):273–290.

Dinh, P. and Zhou, X.-H. (2006). Nonparametric statistical methods for cost-effectiveness analyses. *Biometrics*, 62(2):576–588.

Dufour, J.-M. (1997). Some impossibility theorems in econometrics with applications to structural and dynamic models. *Econometrica: Journal of the Econometric Society*, pages 1365–1387.

Efford, M. G., Dawson, D. K., and Borchers, D. L. (2009). Population density estimated from locations of individuals on a passive detector array. *Ecology*, 90(10):2676–2682.

Fieller, E. C. (1944). A fundamental formula in the statistics of biological assay, and some applications. *Quarterly Journal of Pharmacy and Pharmacology*, 17(2):117–123.

Fieller, E. C. (1954). Some problems in interval estimation. *Journal of the Royal Statistical Society: Series B (Methodological)*, 16(2):175–185.

Franz, V. H. (2007). Ratios: A short guide to confidence limits and proper use. *arXiv preprint arXiv:0710.2024*.

Gleser, L. J. and Hwang, J. T. (1987). The nonexistence of 100 (1-α)% confidence sets of finite expected diameter in errors-in-variables and related models. *The Annals of Statistics*, pages 1351–1362.

Green, P. J. (1984). Iteratively reweighted least squares for maximum likelihood estimation, and some robust and resistant alternatives. *Journal of the Royal Statistical Society. Series B (Methodological)*, pages 149–192.

Hilbe, J. M. (2011). *Negative Binomial Regression.* Cambridge University Press.

Howe, E. J., Buckland, S. T., Després-Einspenner, M.-L., and Kühl, H. S. (2017). Distance sampling with camera traps. *Methods in Ecology and Evolution*, 8(11):1558–1565.

Hutchinson, J. and Waser, P. M. (2007). Use, misuse and extensions of "ideal gas" models of animal encounter. *Biological Reviews*, 82(3):335–359.

Jennelle, C. S., Runge, M. C., and MacKenzie, D. I. (2002). The use of photographic rates to estimate densities of tigers and other cryptic mammals: a comment on misleading conclusions. *Animal Conservation*, 5(2):119–120.

McCallum, J. (2013). Changing use of camera traps in mammalian field research: habitats, taxa and study types. *Mammal Review*, 43(3):196–206.

McCrea, R. S. and Morgan, B. J. (2014). *Analysis of capture-recapture data.* CRC Press.

Miller, D. L., Burt, M. L., Rexstad, E. A., and Thomas, L. (2013). Spatial models for distance sampling data: recent developments and future directions. *Methods in Ecology and Evolution*, 4(11):1001–1010.

Morgan, B. J. (2008). *Applied Stochastic Modelling.* CRC press.

Newman, K., Buckland, S., Morgan, B. J., King, R., Borchers, D., Cole, D. J., Besbeas, P., Gimenez, O., and Thomas, L. (2014). *Modelling population dynamics.* Springer.

O'Brien, B. J., Drummond, M. F., Labelle, R. J., and Willan, A. (1994). In search of power and significance: issues in the design and analysis of stochastic cost-effectiveness studies in health care. *Medical Care*, pages 150–163.

O'Brien, T. G., Kinnaird, M. F., and Wibisono, H. T. (2003). Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. In *Animal Conservation Forum*, volume 6, pages 131–139. Cambridge University Press.

Polsky, D., Glick, H. A., Willke, R., et al. (1997). Confidence intervals for cost-effectiveness ratios: a comparison of four methods. *Health Economics*, 6(3):243–252.

Puth, M.-T., Neuh´auser, M., and Ruxton, G. D. (2015). On the variety of methods for calculating confidence intervals by bootstrapping. *Journal of Animal Ecology*, 84(4):892–897.

R Core Team (2017). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ridout, M. S. and Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, 14(3):322–337.

Rowcliffe, J. M., Field, J., Turvey, S. T., and Carbone, C. (2008). Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, 45(4):1228–1236.

Rowcliffe, J. M., Kays, R., Carbone, C., and Jansen, P. A. (2013). Clarifying assumptions behind the estimation of animal density from camera trap rates. *Journal of Wildlife Management*.

Rowcliffe, M., Carbone, C., Jansen, P. A., Kays, R., and Kranstauber, B. (2011). Quantifying the sensitivity of camera traps: an adapted distance sampling approach. *Methods in Ecology and Evolution*, 2(5):464–476.

Royle, J. A. and Young, K. V. (2008). A hierarchical model for spatial capture–recapture data. *Ecology*, 89(8):2281–2289.

Satterthwaite, F. E. (1946). An approximate distribution of estimates of variance components. *Biometrics Bulletin*, 2(6):110–114.

Sherman, M., Maity, A., and Wang, S. (2011). Inferences for the ratio: Fieller's interval, log ratio, and large sample based confidence intervals. *AStA Advances in Statistical Analysis*, 95(3):313.

Van Kempen, G. and Van Vliet, L. (2000). Mean and variance of ratio estimators used in fluorescence ratio imaging. *Cytometry Part A*, 39(4):300–305.

Winkelmann, R. (2008). *Econometric analysis of count data*. Springer Science & Business Media.

Zhou, M., McCrea, R. S., Matechou, E., Cole, D. J., and Griffths, R. A. (2019). Removal models accounting for temporary emigration. *Biometrics*, 75:24–35.

Table 1: Average estimated animal density $\hat{\rho}$ from the REM and iREM, estimators. The proportion of confidence intervals (CI) that include the true value from the relevant confidence interval methods (mean width of the CI (mCI) in parentheses) is also given. The simulation is 1000 times with 1000 bootstrap replicates.

		REM						**iREM**	
		Delta		**Bootstrap**		**Fieller's**		**Delta**	
Scenarios	$\hat{\rho}$	Large-sample (mCI width)	Log-scale (mCI width)	Bias-corrected (mCI width)	Percentile (mCI width)	(mCI width)	%infinite CI	Large-sample (mCI width)	Log-scale (mCI width)
1. Fixed sample sizes									
$n = 42$; $m = 15$									
$\rho = 25$	26.74	0.90 (52.62)	0.96 (62.72)	0.93 (61.24)	0.92 (59.03)	0.94 (68.35)	0%	0.91 (53.80)	0.96 (65.00)
$\rho = 68$	73.73	0.90 (118.40)	0.93 (132.52)	0.92 (139.38)	0.91 (138.22)	0.93 (203.59)	0.1%	0.90 (119.21)	0.93 (133.73)
$\rho = 119$	126.23	0.91 (186.30)	0.94 (204.90)	0.93 (216.86)	0.93 (214.97)	0.94 (968.63)	0.1%	0.91 (186.45)	0.94 (205.18)
$\rho = 468$	495.77	0.92 (673.06)	0.94 (730.02)	0.94 (797.67)	0.93 (804.50)	0.96 (1313.48)	0.3%	0.92 (669.05)	0.94 (724.34)
2. Varying sample sizes									
$\rho = 25$									
$n = m = 50$	25.10	0.91 (41.73)	0.96 (47.46)	0.93 (43.26)	0.92 (42.08)	0.92 (44.42)	0%	0.91 (43.04)	0.96 (49.66)
$n = m = 100$	25.19	0.93 (30.18)	0.95 (32.16)	0.94 (30.71)	0.93 (30.25)	0.93 (31.08)	0%	0.93 (30.59)	0.95 (32.66)
$n = m = 200$	25.15	0.94 (21.40)	0.95 (22.07)	0.94 (21.54)	0.94 (21.37)	0.94 (21.71)	0%	0.94 (21.49)	0.95 (22.18)
$n = m = 500$	25.11	0.95 (13.59)	0.95 (13.76)	0.95 (13.61)	0.95 (13.56)	0.95 (13.67)	0%	0.95 (13.63)	0.95 (13.80)
$\rho = 468$									
$n = m = 50$	474.38	0.91 (464.46)	0.93 (484.04)	0.93 (478.76)	0.93 (472.83)	0.94 (495.42)	0%	0.92 (470.56)	0.94 (490.58)
$n = m = 100$	470.98	0.93 (327.41)	0.94 (334.19)	0.94 (331.36)	0.94 (329.05)	0.94 (337.46)	0%	0.94 (330.90)	0.95 (337.84)
$n = m = 200$	470.09	0.95 (232.96)	0.95 (235.38)	0.94 (233.72)	0.94 (232.99)	0.95 (236.40)	0%	0.95 (223.83)	0.95 (236.26)
$n = m = 500$	468.98	0.95 (147.29)	0.95 (147.90)	0.94 (147.17)	0.94 (146.83)	0.94 (148.14)	0%	0.95 (147.67)	0.95 (148.14)

Table 2: Average estimates from the iREM with random effect and the iREM for $Q = 20$ quadrature points (average standard error in parentheses). The Standard deviation (Sd), Root Mean Square Error (RMSE) and percentage bias are given.

Sample sizes		**True Values**			**iREM with random effect**			**iREM**	
		ρ	μ	σ_b	$\hat{\rho}$	$\hat{\mu}$	$\hat{\sigma}_b$	$\hat{\rho}$	$\hat{\mu}$
$n = m = 25$		75	0.71	0.10	79.92 (19.92)	0.70 (0.13)	0.08 (0.23)	80.78 (18.95)	0.70 (0.13)
	Sd				20.62	0.13	0.13	20.70	0.14
	RMSE				19.82	0.13	0.23	19.81	0.13
	%bias				+6.56%	−1.75%	−20.30%	+7.71%	−1.75%
		75	0.71	0.60	85.95 (25.36)	0.71 (0.13)	0.51 (0.24)	99.86 (23.37)	0.70 (0.13)
	Sd				27.02	0.14	0.25	33.25	0.14
	RMSE				27.63	0.13	0.25	34.13	0.13
	%bias				+14.60%	−2.10%	−14.70%	+33.15%	−2.10%
$n = m = 100$		75	0.71	0.10	76.13 (9.08)	0.71 (0.07)	0.06 (0.12)	76.53 (8.80)	0.71 (0.07)
	Sd				9.77	0.07	0.08	9.81	0.07
	RMSE				9.15	0.07	0.13	8.93	0.07
	%bias				+1.50%	−0.16%	−35.48%	+2.04%	−0.16%
		75	0.71	0.60	77.40 (14.72)	0.71 (0.07)	0.54 (0.13)	89.59 (10.31)	0.71 (0.07)
	Sd				18.35	0.07	0.17	21.03	0.07
	RMSE				14.91	0.07	0.15	17.87	0.07
	%bias				+3.20%	+0.63%	−10.79%	+19.45%	0.63%

Table 3: Density from the census ρ (in km^2) compared with estimated animal density from using the REM and iREM with habitat. Standard errors are estimated from the large-sample and bootstrap methods. Estimated mean and median from the bootstrap methods are also given with approximate 95% confidence intervals from the log-scale, bias-corrected and percentile methods.

Species	Habitat	Census	Estimate	Bootstrap estimates		Standard error of $\hat{\rho}$			Confidence intervals			
				REM		**REM**		**iREM with habitat**	**REM**			**iREM with habitat**
		ρ	$\hat{\rho}$	$\hat{\rho}$ (mean)	$\hat{\rho}$ (median)	Large-sample	Bootstrap	Large-sample	Log-scale	Bias-corrected	Percentile	Log-scale
wallaby												
	Downs	1101	834	1098	872	447.24	677.50	629.78	(292, 2386)	(361, 2673)	(384, 2840)	(190, 3663)
	IP	760	1177	1506	1217	621.14	885.13	918.55	(418, 3311)	(516, 3597)	(553, 3797)	(255, 5433)
	OF	803	809	1008	819	432.04	574.20	627.14	(284, 2304)	(351, 2399)	(358, 2450)	(117, 3696)
	CP	96	334	451	353	202.39	335.68	157.44	(102, 1095)	(112, 1164)	(119, 1226)	(133, 841)
	$\hat{\rho}_{mean}$	468	595	779	733	173.18	268.01	247.45	(337, 1053)	(311, 918)	(407, 1392)	(263, 1345)
water deer												
	Downs	73	86	111	87	37.90	212.18	71.32	(36, 204)	(41, 261)	(42, 283)	(17, 437)
	IP	36	10	15	10	7.05	62.24	12.04	(3, 39)	(0, 41)	(0, 39)	(1, 102)
	OF	577	326	475	339	136.79	1850.34	256.62	(138, 409)	(160, 909)	(167, 1010)	(62, 1568)
	CP	72	248	346	253	113.79	1131.53	130.97	(101, 610)	(108, 789)	(112, 819)	(88,968)
	$\hat{\rho}_{mean}$	119	190	267	207	65.59	657.84	95.82	(98, 375)	(95, 386)	(116, 569)	(71, 511)
mara												
	Downs	30	5	6	4	3.26	6.41	7.31	(1.16, 18.41)	(0.00, 21.25)	(0.00, 18.70)	(0.21, 102.56)
	IP	7	3	3	2	3.06	4.98	5.42	(0.34, 23.66)	(0.00, 18.77)	(0.00, 15.73)	(0.07, 121.61)
	OF	0	5	7	5	3.94	9.96	8.12	(0.98, 18.11)	(0.00, 26.81)	(0.00, 26.49)	(0.18, 129.78)
	CP	108	11	13	10	7.34	13.81	8.10	(2.72, 41.22)	(0.00, 46.91)	(0.00, 44.75)	(2.36, 47.43)
	$\hat{\rho}_{mean}$	68	8	10	8	4.19	7.93	5.23	(2.68, 22.37)	(1.69, 25.75)	(1.90, 27.55)	(2.06, 29.07)

Table 4: Model comparison of the four methods proposed above using AIC: iREM, iREM with haitat, iREM with random effect and iREM with habitat and random effect. Density from the census ρ and its estimate $\hat{\rho}$ or $\hat{\rho}_{mean}$(in km^2) are also given for each method (estimated standard error in parentheses).

Species	Census	iREM		iREM with habitat		iREM with random effect		iREM with habitat and random effect	
	ρ	$\hat{\rho}$	ΔAIC	$\hat{\rho}$	ΔAIC	$\hat{\rho}_{mean}$	ΔAIC	$\hat{\rho}_{mean}$	ΔAIC
wallaby	468	816 (337.58)	27.98	595 (247.45)	20.74	768 (325.51)	28.9	497 (223.21)	0
water deer	119	155 (76.58)	69.34	190 (96.23)	19.20	61 (34.19)	11.64	160 (90.87)	0
mara	68	3 (1.70)	1.24	8 (5.23)	5.76	1 (1.74)	0	5 (5.20)	5.02

Table 5: Estimated density $\hat{\rho}$ (km^2) and census density ρ of wallaby and water deer in each habitat (standard errors are in parentheses), along with model parameter estimates for expected speed μ, random effect variance σ_b, and probability of zero-response category ω.

	Habitat							
	CP	Downs	IP	OF	$\hat{\rho}_{mean}$	$\hat{\mu}$	$\hat{\sigma}_b$	$\hat{\omega}$
wallaby								
ρ	96	1101	760	803	468			
$\hat{\rho}$	271 (163.49)	684 (782.36)	1133 (1338.99)	561 (677.79)	497 (223.21)	0.71 (0.28)	0.62 (0.15)	0.20 (0.16)
water deer								
ρ	72	73	36	577	119			
$\hat{\rho}$	214 (133.00)	58 (65.09)	8 (11.84)	272 (296.68)	160 (90.87)	1.17 (0.56)	0.68 (0.21)	0.40 (0.26)
mara								
ρ	108	30	7	0	68			
$\hat{\rho}$	7 (8.45)	3 (6.28)	2 (4.72)	3 (6.44)	5 (5.20)	2.56 (1.21)	1.13 (0.67)	0.30 (0.21)