



## RESEARCH ARTICLE

# A spatial capture–recapture model to estimate call rate and population density from passive acoustic surveys

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**Handling Editor:** Chris Sutherland**Abstract**

1. Spatial capture–recapture (SCR) models are commonly used to estimate animal population density from detections and subsequent redetections of individuals across space. In particular, acoustic SCR models deal with detections of animal vocalisations across an array of acoustic detectors. Previously published acoustic SCR methods either estimate call density (calls per unit space per unit time) rather than animal density itself, require an independently estimated call rate to estimate animal density, or discard data from all but one detected call from each individual.
2. In this manuscript, we develop a new spatial capture–recapture model that estimates both call rate and animal density from the acoustic survey alone, without requiring an independently estimated call rate. Our approach therefore alleviates the need for the additional fieldwork of physically locating and monitoring individual animals. We illustrate our method and compare it to an existing approach using a simulation study and an application to data collected on an acoustic survey of the visually cryptic Cape peninsula moss frog *Arthroleptella lightfooti*.
3. In the context of our acoustic survey, our calling animal density estimator has low bias, good precision and confidence intervals with appropriate coverage, yielding results that are consistent with previous studies of the same species.
4. Our method can obtain accurate and precise estimates of animal density while eliminating the fieldwork burden associated with separately estimating call rate. We discuss how the development of our model's likelihood reveals a clear path to further extensions, which may incorporate features such as animal movement processes and uncertain individual identification.

**KEYWORDS**

animal density, anurans, automated recording systems, call density, detection function, passive acoustic monitoring

## 1 | INTRODUCTION

Passive acoustic surveys are becoming increasingly popular for monitoring animal populations because they offer a fast, cheap, safe and noninvasive alternative to relying on visual sightings or physical capture (Marques et al., 2013). Although there has been a particular focus on passive acoustic surveys for the study of cetaceans (e.g.

Harris et al., 2018; Klinck et al., 2012; Marques et al., 2012), they have also been used to monitor taxa such as birds (e.g. Buxton et al., 2013; Dawson & Efford, 2009; Dent & Molles, 2016; Sebastián-González et al., 2018) and anurans (e.g. Benevides et al., 2019; Measey et al., 2017).

Estimating population density is a primary objective of many acoustic surveys. Marques et al. (2013) provide a review of statistical methods that have been developed to meet this goal. A major

challenge is that not all vocalisations are detected. Those produced close to recorders are easier to detect than those further away, and missed vocalisations must be accounted for in order to estimate density. A common way to overcome uncertain detection is to model the detection process with a detection function (e.g. Dawson & Efford, 2009; Marques et al., 2009, 2012; Sebastián-González et al., 2018; Stevenson et al., 2015), which describes how the probability of detection decreases with an increasing distance between the vocalisation and a detector.

Distance sampling (Buckland et al., 2001) can be used to estimate the detection function, and requires observed distances between detectors and detected vocalisations. However, the locations at which detected vocalisations were produced are not often observed on an acoustic survey, and so neither are the distances. Although properties of acoustic signals such as the received strength can be used to estimate distances, it is not often possible to do so with high precision for all (e.g. see Sebastián-González et al., 2018). Obtaining distances with negligible error is a fundamental assumption of distance sampling, violation of which causes biased density estimators (Borchers et al., 2010; Marques, 2004).

Spatial capture–recapture (SCR) models (Borchers & Efford, 2008; Efford, 2004; Royle et al., 2013; Royle & Young, 2008) provide a way to estimate a detection function directly from a single survey without observing exact distances between individuals and detectors. Although the first SCR methods were developed for live-trapping and area-search surveys, there has been recent development for acoustic surveys (Borchers et al., 2015; Dawson & Efford, 2009; Efford et al., 2009; Stevenson et al., 2015). Instead of requiring call locations to be observed, acoustic SCR models treat them as latent variables. Estimation of the detection function involves either integrating (for estimation by maximum likelihood) or sampling (for estimation via MCMC under a Bayesian framework) over all points at which each call may have been located. Borchers et al. (2015) developed a method to incorporate auxiliary data like times of arrival, received signal strengths and estimated bearings into acoustic SCR models, providing additional information about call locations. Importantly, their method models measurement error in these variables, so like other SCR approaches, it does not require that the locations of the calls are perfectly resolved. So far, acoustic SCR models have been applied to populations of birds (Efford et al., 2009), whales (Marques et al., 2012), primates (Kidney et al., 2016) and frogs (Measey et al., 2017).

There are two primary disadvantages of the SCR methods developed by Efford et al. (2009) and Borchers et al. (2015). The first is that they estimate call density (calls produced per unit area per unit time), which confounds the two parameters that are usually of interest: animal density (individuals per unit area) and call rate (calls produced per individual per unit time). Using ideas from Marques et al. (2013) and Stevenson et al. (2015) showed that unbiased estimation of animal density can be calculated via the quotient of the call density estimate from SCR and an independently estimated call rate. The latter can be established by monitoring a random sample of individuals from the population separately to—but alongside—the

main acoustic survey. Collecting these data can be time-consuming and costly, but avoiding this exercise by applying a call rate estimated from data collected at another location or time can introduce bias. For example, call rates of ectotherms may vary with temperature (Llusia & Márquez, 2013) and between different populations of the same species (Zuk et al., 2001).

The second primary disadvantage is that their likelihoods are constructed under an assumption that call locations are a realisation of a Poisson point process, effectively assuming the location of one call is independent of all others. This assumption provides tractable estimates that can be computed in realistic time frames—but does not accurately describe the way call locations are distributed throughout the survey area. Two calls produced by the same individual will have the same location if animals do not move, or similar locations if they do. Stevenson et al. (2015) showed that point estimates of call density (and animal density, if computed via an independently estimated call rate) are unbiased despite this model misspecification—but standard errors are negatively biased and confidence intervals (CIs) fail to meet their nominal coverage levels. They used a parametric bootstrap method to provide appropriate estimates of parameter uncertainty. Because their point estimates still relied on maximising a misspecified likelihood, their method cannot make use of likelihood-based tools, for example AIC and BIC for model selection. The remaining acoustic SCR method, that of Dawson and Efford (2009), avoids both of the disadvantages described above by only analysing a single call from each detected individual. However, this approach discards data from all subsequent calls, which are informative about the detection function.

Finally, in some cases, animal distribution is of interest in addition to density, which can be estimated by SCR using an inhomogeneous Poisson process for the latent locations (Borchers & Efford, 2008; Royle et al., 2013, pp. 307–327). However, inhomogeneous processes cannot be implemented to estimate animal distribution in existing acoustic SCR methods, because they directly model call locations rather than animal locations. Applying an inhomogeneous Poisson process to call locations provides an estimated density surface that confounds spatial clustering of animals with clustering of different calls from the same animal. In other words, such an approach would not be able to distinguish between a region with high call density due to the presence of many animals, or a region with high call density due to the presence of a single animal that is particularly vocally active.

In this paper, we develop a new SCR method to analyse detection data from acoustic surveys. Our method directly estimates a detection function, the call rate and animal density without requiring the collection of any independent data and without discarding available data. Unlike existing methods, we directly model animal locations rather than call locations, so we can fit inhomogeneous animal density surfaces if desired. We present our method in Sections 2.1–2.3. Unlike the model of Stevenson et al. (2015), parameter estimation for our method involves maximisation of a correctly specified likelihood, so we can rely on the usual variance estimators from maximum likelihood theory without resorting to a bootstrap procedure. We

can also use other likelihood-based tools such as AIC and BIC. Like that of Dawson and Efford (2009), our method requires that individuals can be identified by their calls and that animals do not move substantially during the survey.

We are able to generate plausible detection-to-call and call-to-individual matchings for an application of our method to an acoustic survey of the Cape peninsula moss frog *Arthroleptella lightfooti*, described in Section 2.4, and present a simulation study investigating point and variance estimator performance in Section 2.5. Our method paves the way for the development of extensions that are applicable to mobile species and/or those that cannot be identified from their calls, which we discuss in Section 4.

## 2 | MATERIALS AND METHODS

### 2.1 | Data and notation

Notation used in this manuscript is summarised in Table 1. We consider a survey of duration  $z$  with  $m$  acoustic recorders at known locations, which detect calls produced by animals. Let  $\mathbf{x}_k$  be the Cartesian coordinates for the location of the  $k$ th detector. We denote our survey region  $S \subset \mathbb{R}^2$ , the set of all locations at which a calling individual could possibly be detected by the detector array. Like existing acoustic SCR models (Borchers et al., 2015; Dawson & Efford, 2009; Efford et al., 2009; Stevenson et al., 2015), we require that detections can be matched to calls, so we can determine when a single call is detected by more than one detector. Like Dawson and Efford (2009), we impose the additional requirement that calls can be matched to individuals, so we can determine when a single animal produces multiple detected calls.

SCR models require observed capture histories, each of which denotes a spatial pattern of detections (Borchers, 2012). In our case, each call has a capture history representing which microphones it was detected by. Let  $\omega_{ij} = (\omega_{ij1}, \dots, \omega_{ijm})$  be the capture history for the  $j$ th call produced by the  $i$ th individual, where  $\omega_{ijk} = 1$  if the call was detected by the  $k$ th detector and  $\omega_{ijk} = 0$  if not. The  $i$ th animal therefore has a capture history matrix,  $\Omega_i$ , the rows of which are the capture histories for its individual calls. The number of rows in  $\Omega_i$  is equal to  $c_i$ , the number of calls the animal produced during the survey, and the number of columns is equal to  $m$ . Some calls may not be detected and have capture histories of  $\mathbf{0}_m$ , containing only zeroes. Likewise, some animals may not produce any calls that are detected, and therefore have capture history matrices containing only zeroes.

We may also collect auxiliary data from each detection informative about call location, incorporation of which can greatly improve density estimator precision (see Borchers et al., 2015). Here we consider the collection of precise times that acoustic signals from detected calls arrived at the detectors, where  $t_{ijk}^*$  provides the time that the  $j$ th call from the  $i$ th individual arrived at the  $k$ th microphone. Let  $\mathbf{t}_{ij}$  be a vector and  $\mathbf{T}_i$  be a matrix of arrival times associated with detections in  $\omega_{ij}$  and  $\Omega_i$ , respectively.

**TABLE 1** A summary of notation used throughout this manuscript

Group	Notation	Definition
Survey design	$m$	The number of detectors
	$\mathbf{x}_k$	The location of the $k$ th detector
	$S$	The set of all points in the survey region
	$z$	The duration of the survey
Latent data	$n$	The number of calling animals in $S$
	$c_i$	The number of calls produced by the $i$ th animal during the survey
	$\omega_{ijk}$	A detection indicator of the $j$ th call by the $i$ th animal at the $k$ th detector
	$\omega_{ij}$	The capture history of the $j$ th call by the $i$ th animal, where $\omega_{ij} = (\omega_{ij1}, \dots, \omega_{ijm})$
	$\Omega_i$	The capture history matrix of the $i$ th animal, where $\Omega_i = (\omega_{i1}, \dots, \omega_{ic_i})$
	$\mathbf{T}_i$	Signal arrival times for the $i$ th animal, comprising an arrival time $t_{ijk}^*$ for all $\{i, j, k: \omega_{ijk} = 1\}$
Observed data	$n^*$	The number of animals with at least one detected call
	$c_i^*$	The number of calls produced by the $i$ th detected animal that were detected by at least one detector
	$\omega_{ijk}^*$	A detection indicator for the $j$ th detected call by the $i$ th detected animal at the $k$ th detector
	$\omega_{ij}^*$	The capture history of the $j$ th detected call by the $i$ th detected animal, where $\omega_{ij}^* = (\omega_{ij1}^*, \dots, \omega_{ijm}^*)$
	$\Omega_i^*$	The capture history matrix of the $i$ th detected animal, where $\Omega_i^* = (\omega_{i1}^*, \dots, \omega_{ic_i^*}^*)$
	$\mathbf{T}_i^*$	Signal arrival times for the $i$ th detected animal, comprising an arrival time $t_{ijk}^*$ for all $\{i, j, k: \omega_{ijk}^* = 1\}$
Parameters	$\beta$	A vector of coefficients characterising spatially varying calling animal density, where $\beta = (\beta_0, \dots, \beta_Q)$
	$\psi$	A vector of call detection function parameters, where $\psi = (\lambda_0, \sigma)$ for the hazard halfnormal
	$\mu$	The expected number of calls an animal produces per unit time
	$\sigma_t$	The standard deviation of measurement error for recorded signal arrival times
Functions	$D(\mathbf{s})$	Calling animal density at location $\mathbf{s}$ . Abbreviated to $D$ for homogeneous density models
	$x_q(\mathbf{s})$	Measurement of the $q$ th spatial covariate or spline basis function at location $\mathbf{s}$
	$d(\mathbf{x}, \mathbf{y})$	The Euclidean distance between locations $\mathbf{x}$ and $\mathbf{y}$

(Continues)

TABLE 1 (Continued)

Group	Notation	Definition
	$g_c(d)$	The probability a call is detected at a detector at distance $d$
	$g(d)$	The probability at least one call from an animal is detected by a detector at distance $d$
	$p_c(\mathbf{s})$	The probability a call at $\mathbf{s}$ is detected by at least one detector
	$p(\mathbf{s})$	The probability at least one call from an animal at $\mathbf{s}$ is detected by at least one detector

On our survey, we obtain a truncated version of the data described above, because capture histories of calls that are not detected and capture history matrices of animals that have no detected calls are unobservable. We denote the truncated versions of these variables with an asterisk. We do not observe the total number of calls produced by the  $i$ th individual,  $c_i$ , instead we observe the total number of its calls that were detected by at least one detector,  $c_i^*$ . We do not observe all  $c_i$  rows of its capture history matrix  $\Omega_i$ , we only observe the  $c_i^*$  rows associated with its detected calls, together given by  $\Omega_i^*$ . Every row of  $\Omega_i^*$  is not  $\mathbf{0}_m$  and has at least one detection. We denote  $\omega_{ij}^*$  to be the capture history of  $j$ th detected call produced by the  $i$ th animal, whereas the potentially unobserved  $\omega_{ij}$  is its  $j$ th call, regardless of detection. We also only observe  $t_{ijk}^*$ ,  $t_{ij}^*$  and  $T_i^*$ , comprising arrival times of calls that were detected. Finally, we do not observe  $n$ , the total number of animals in  $S$ , we only observe the number of detected animals,  $n^*$ .

In the development of our likelihood below, we use  $f$  to denote a probability density function (PDF) or probability mass function (PMF), but do not distinguish between functions for different variables, relying on their arguments to resolve ambiguity.

## 2.2 | The model

In the following sections, we develop a likelihood for acoustic surveys based on the observed data described above:  $n^*$ ,  $\mathbf{c}^* = (c_1^*, \dots, c_n^*)$ ,  $\Omega^* = (\Omega_1^*, \dots, \Omega_n^*)$  and  $\mathbf{T}^* = (T_1^*, \dots, T_n^*)$ .

### 2.2.1 | Animal density

Let  $\mathbf{s}_i$  be the physical location of the  $i$ th animal during the survey. Following Borchers and Efford (2008), we assume animals' locations are a realisation of an inhomogeneous Poisson process over the survey region, with intensity (i.e. animal density)  $D(\mathbf{s})$  at location  $\mathbf{s} \in S$ . Spatially varying animal density can be modelled via a loglinear relationship

$$\log \{D(\mathbf{s})\} = \beta_0 + \sum_{q=1}^Q \beta_q x_q(\mathbf{s}), \quad (1)$$

where  $x_q(\mathbf{s})$  is the measurement of the  $q$ th spatial covariate measured at location  $\mathbf{s}$ , and  $\boldsymbol{\beta} = (\beta_0, \dots, \beta_Q)$  are parameters characterising the intensity function. Alternatively,  $x_q(\mathbf{s})$  might be a basis function of a regression spline, for example allowing a spatially smoothed density surface that varies independently of any covariates (Borchers & Kidney, 2014). This Poisson point process model implies that  $n \sim \text{Poisson} \left\{ \int_S D(\mathbf{s}) d\mathbf{s} \right\}$  (see Borchers et al., 2015), and that animals' locations are independent of one another given the intensity surface.

### 2.2.2 | Call and individual detection probabilities

The closer an individual is to a recorder, the more easily its calls are detected. We model this detection process using a call detection function,  $g_c(d)$ , which provides the probability that a call is detected by a recorder that is located distance  $d$  from where the call was produced. There are various parametric forms for detection functions available in the distance sampling and SCR literature. Here we consider the hazard halfnormal function

$$g_c(d) = 1 - \exp \left\{ -\lambda_0 \exp \left( \frac{-d^2}{2\sigma^2} \right) \right\}, \quad (2)$$

because it allows perfect detection within some distance  $b$  such that  $g_c(d) \approx 1$  for  $0 < d < b$ , which is often the case for acoustic data.

Let  $d(\mathbf{x}, \mathbf{y})$  be the Euclidean distance between the locations  $\mathbf{x}$  and  $\mathbf{y}$ , and so  $d(\mathbf{x}_k, \mathbf{s}_i)$  is the distance between the  $k$ th detector and the  $i$ th animal. By assuming independence between detections of the same call at different detectors conditional on the animal's location, the probability that a single call located at  $\mathbf{s}$  is detected at all (i.e. by at least one detector) is the complement of the probability of no detection by any detector,  $p_c(\mathbf{s}) = 1 - \prod_{k=1}^m [1 - g_c \{d(\mathbf{x}_k, \mathbf{s})\}]$ .

The number of calls produced by the  $i$ th individual has the PMF  $f(c_i)$ . Conditional on both its location,  $\mathbf{s}_i$ , and the total number of calls it produced,  $c_i$ , the number of calls from the  $i$ th animal that are detected by at least one detector has a binomial distribution with  $c_i$  trials and probability of success  $p_c(\mathbf{s}_i)$ . The PMF  $f(c_i^* | c_i, \mathbf{s}_i^*)$ , for the number of detected calls from the  $i$ th detected animal, conditional on having produced  $c_i$  total calls from location  $\mathbf{s}_i$ , is that of the zero-truncated (ZT) binomial distribution. The truncation is because detected individuals must have produced at least one detected call.

Because we do not observe  $c_i$ , we require the PMF for the number of detected calls from a detected animal conditional only on  $\mathbf{s}_i^*$ , which is given by

$$f(c_i^* | \mathbf{s}_i^*) = \sum_{c_i=1}^{\infty} f(c_i^* | c_i, \mathbf{s}_i^*) f(c_i). \quad (3)$$

A special case arises if we assume that calls are produced by a Poisson process at the same rate for all calling individuals, which results in a closed-form expression for the sum. In this scenario, we have  $c_i \sim \text{Poisson}(\mu z)$ , where the call rate  $\mu$  is the expected number of calls produced per unit time per individual. This provides

$(c_i^* | s_i^*) \sim \text{ZT Poisson} \{ \mu z p_c (s_i^*) \}$ , because the call detection process is a thinning of the call production process by the call detection probability, and a thinned Poisson process is itself a Poisson process. We proceed using this Poisson assumption, but our method can incorporate alternative distributions for  $c_i$  if desired, for example to accommodate between-individual variation in call rates.

The probability that an animal located at  $s$  is detected at all (i.e. at least one of its calls is detected by at least one of the detectors) is then given by the complement of the probability that none of its calls were detected,

$$p(s) = 1 - f(c^* = 0 | s). \quad (4)$$

Although not explicitly used in our likelihood below, the individual detection function,  $g(d)$ , is the probability that at least one call produced by an individual animal is detected by a particular detector at distance  $d$  from its location, and is given by

$$g(d) = \sum_{c=0}^{\infty} \left[ 1 - \{1 - g_c(d)\}^c \right] f(c). \quad (5)$$

The area effectively sampled by the detectors is given by  $\int_S p(s) ds$  (Borchers, 2012).

### 2.2.3 | PMFs for capture histories conditional on location

From Section 2.2.2, we assume that  $(\omega_{ijk} | s_i) \sim \text{Bernoulli} [g_c(d(x_k, s_i))]$  and that a detection of a single call at one detector is independent of detection at others, conditional on the call's location—these are standard acoustic SCR assumptions. The PMF of the capture history for the  $j$ th call produced by the  $i$ th animal conditional on its location is therefore given by the following product of Bernoulli PMFs:

$$f(\omega_{ij} | s_i) = \prod_{k=1}^m g_c \{ d(x_k, s_i) \}^{\omega_{ijk}} [1 - g_c \{ d(x_k, s_i) \}]^{1 - \omega_{ijk}}. \quad (6)$$

However, observed capture histories of calls are zero-truncated (i.e. it is impossible to observe  $\omega_{ij} = \mathbf{0}_m$ ), because we only observe those relating to detected calls. We can account for this truncation using the call detection probabilities from Section 2.2.2, and so the PMF of the capture history of the  $j$ th detected call from the  $i$ th detected animal is

$$f(\omega_{ij}^* | s_i^*) = \frac{f(\omega_{ij} = \omega_{ij}^* | s_i = s_i^*)}{p_c(s_i^*)}. \quad (7)$$

The PMF of a detected animal's capture history matrix, given its location and the number of its calls that were detected, is

$$f(\Omega_i^* | c_i^*, s_i^*) = \prod_{j=1}^{c_i^*} f(\omega_{ij}^* | s_i^*). \quad (8)$$

### 2.2.4 | Individual locations

In Section 2.2.3, we assumed that individuals' locations are a realisation of an inhomogeneous Poisson process with intensity  $D(s)$  at location  $s$ , which implies that the PDF of a randomly selected individual's location is  $f(s) = D(s) / \int_S D(s') ds'$ . However, the location of a randomly selected detected individual does not come from this distribution, because inhomogeneity in detected animals' locations is additionally affected by spatially varying detectability: animals situated closer to the detectors are more likely to have at least one of their calls detected.

We proceed using the standard maximum likelihood SCR approach (Borchers & Efford, 2008), but with an individual's detection probability specified as per our new formulation in Equation (4). Locations of detected individuals are a thinned Poisson process, with thinning via the function  $p(s)$ . The intensity function of the thinned process at location  $s$  is  $D(s)p(s)$ , which is proportional to the PDF of a detected individual's location, providing the PDF of the  $i$ th detected individuals location:

$$f(s_i^*) \propto D(s_i^*) p(s_i^*) = \frac{D(s_i^*) p(s_i^*)}{\int_S D(s) p(s) ds}. \quad (9)$$

Because locations of detected individuals are a realisation of a thinned Poisson process, we have  $n^* \sim \text{Poisson} \{ \int_S D(s) p(s) ds \}$  with PDF

$$f(n^*) = \frac{\{ \int_S D(s) p(s) ds \}^{n^*} \exp \{ - \int_S D(s) p(s) ds \}}{n^*!}. \quad (10)$$

### 2.2.5 | Incorporating auxiliary information

We use the same approach of Borchers et al. (2015) and Stevenson et al. (2015) to incorporate observed TOAs. Their method estimates independent measurement error for each detection, with standard deviation  $\sigma_t$ . This procedure acknowledges that TOAs are not observed perfectly and do not deterministically resolve call locations—even when a single call is detected by many detectors.

In Appendix S1, we describe their formulation of  $f(\mathbf{T}_i^* | \Omega_i^*, c_i^*, s_i^*)$ , the PDF of the observed TOAs, conditional on the observed capture histories, detected call counts, and detected animal locations.

### 2.2.6 | The likelihood

Our likelihood function is a joint density of our observed data as a function of the model parameters,  $\theta$ , comprising the following:  $\beta$ , coefficients characterising animal density;  $\psi$ , a vector of call detection function parameters with  $\psi = (\lambda_0, \sigma)$  for the hazard halfnormal detection function;  $\mu$ , the call rate and  $\sigma_t$ , measurement error for observed TOAs, if they have been collected. The likelihood is

$$L(\theta) = f(n^*, c^*, \Omega^*, \mathbf{T}^*). \quad (11)$$

Assuming independence between individuals and building in dependence on call locations as latent variables provides

$$= f(n^*) \prod_{j=1}^{n^*} \int_S f(c_i^*, \Omega_i^*, T_i^*, s_i^*) ds_i^*, \quad (12)$$

$$= f(n^*) \prod_{j=1}^{n^*} \int_S f(T_i^* | \Omega_i^*, c_i^*, s_i^*) f(\Omega_i^* | c_i^*, s_i^*) f(c_i^* | s_i^*) f(s_i^*) ds_i^*. \quad (13)$$

Here,  $f(n^*)$  is provided in Equation 10, and the four functions in the product of the integrand are provided in Appendix S1 and Equations 8, 3 and 9, respectively.

Estimation can be achieved in the standard way under a maximum likelihood framework. Maximising  $\log\{L(\theta)\}$  over provides point estimates, while standard errors are available by taking the square root of the diagonal elements of the inverse of the Hessian. The standard errors can be used to construct Wald CIs, although likelihood ratio CIs can also be computed.

## 2.3 | Software implementation

A software implementation of the method described above is available on GitHub and archived on Zenodo (Stevenson et al., 2020), and is described in Appendix S2. The log-likelihood function is written in C++, which is maximised using the `nlminb()` function from the `stats` package in R (R Core Team, 2020).

## 2.4 | The *A. lightfooti* survey

### 2.4.1 | Survey description

We applied our method to data collected on two acoustic surveys of *A. lightfooti*, conducted 18 days apart on 16 May and 3 June 2012, on Steenberg Plateau in Silvermine Nature Reserve, Table Mountain National Park, South Africa. On both occasions, six microphones were placed in identical configurations in the same seepage inhabited by calling *A. lightfooti* males. These are two of many such surveys described by Measey et al. (2017), who analysed the resulting data using the method of Stevenson et al. (2015) and used a proxy call rate to convert from call to animal density. Here we use our method to estimate both animal density and the call rate directly.

### 2.4.2 | Call and individual identification

The process we used to match detections to calls (i.e. to determine which detections by different microphones are recordings of the same call) is described by Measey et al. (2017) and Stevenson et al. (2015). We then manually allocated a plausible matching

of detected calls to individual identities using the timings of calls, plausible call locations and received call frequencies, as described in Appendix S3. We recognise that our matching procedure was a subjective exercise. We discuss this further in Section 4.1.

### 2.4.3 | Data analysis

We analysed a 30-s subset of each recording, although the full surveys were longer. If animals are stationary, then increasing survey length does not collect additional independent data because the array continues to repeatedly detect the same individuals. Lengthening the survey beyond some limit provides a negligible improvement in terms of animal density estimator precision; the small improvement may be outweighed by data processing and computational costs. Stevenson et al. (2015) found that this limit was approached at about 25 s for their survey of *A. lightfooti*.

Our goal here is to illustrate the application of our method, which is able to estimate calling animal density and call rate in addition to call density, and is hereafter referred to as the ASCR-AD model. We also compare these results to those obtained using the method of Stevenson et al. (2015), which only directly estimates call density, and is hereafter referred to as the ASCR-CD model. We fitted the ASCR-CD model using the R package `ASCR` (Stevenson, 2020). We fitted ASCR-AD and ASCR-CR models to the data, considering the two surveys as independent sessions.

Calling animal density, the call detection function and the TOA measurement error were assumed to be the same for both surveys. Because the microphone array spanned a small area (the largest distance between a pair of microphones was 9.22 m), it is reasonable to assume spatially homogeneous calling animal density across our survey region. Elsewhere, we refer directly to the spatially constant calling animal density,  $D$ , rather than coefficients  $\beta$ . We also refer to call density,  $D_c = D\mu$ , which represents the density of calls produced  $\text{ha}^{-1} \text{min}^{-1}$ .

## 2.5 | Simulation study

We conducted a simulation study to establish the performance of the ASCR-AD animal density estimator used in Section 2.4, and make comparisons to the ASCR-CD method. In particular, our simulation study answers the following questions in the context of our *A. lightfooti* analysis: (a) does the ASCR-AD model provide an unbiased point estimator of calling animal density, and CIs with nominal coverage? (b) How do the properties of the ASCR-AD call density estimator compare to those of the ASCR-CD call density estimator?

We simulated 1,000 datasets under the ASCR-AD model described in Sections 2.2, using the detector configuration and parameter estimates from our analysis described above. We fitted both the ASCR-AD and ASCR-CD model to each dataset.

### 3 | RESULTS

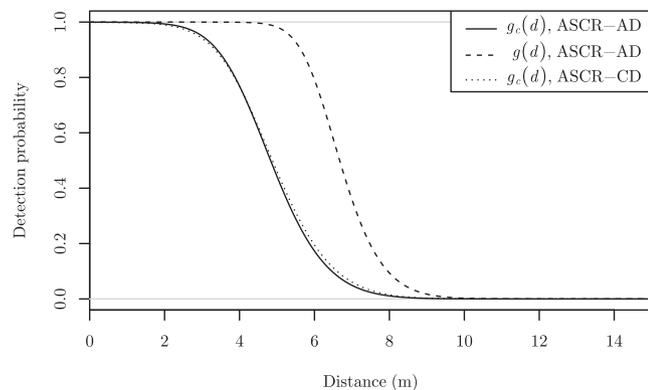
#### 3.1 | The *A. lightfooti* survey

In total, 86 calls from 11 individuals were detected on 16 May 2012, and 98 calls from 14 individuals by the same array on 3 June 2012. Our ASCR-AD model estimated calling animal density and call rate separately with good precision, providing estimates (with 95% CIs) of  $\hat{D} = 358.5$  (240.4, 534.6) calling individuals per hectare and  $\hat{\mu} = 18.1$  (15.5, 21.2) calls per individual per minute. Coefficients of variation (CVs) for  $\hat{D}$  and  $\hat{\mu}$  were 20.4% and 8.0%, respectively. We estimate that the area effectively sampled by each of the two surveys was 350 m<sup>2</sup>. See Table 2 for estimates, standard errors, CVs and 95% CIs for all parameters provided by our ASCR-AD model, and Figure 1 for the estimated call and individual detection functions, based on estimates  $\hat{\lambda}_0$ ,  $\hat{\sigma}$  and  $\hat{\mu}$ .

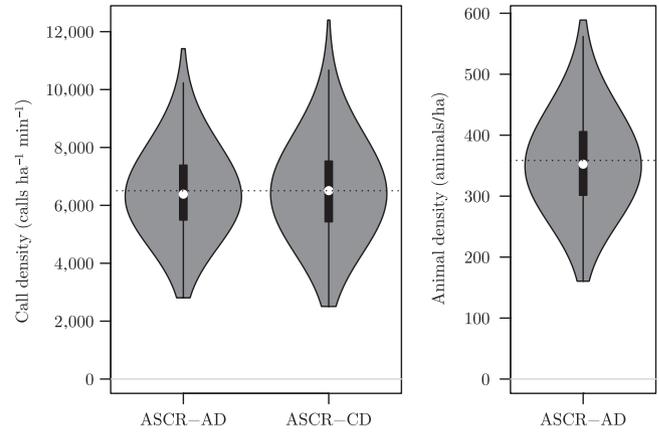
These results are consistent with those from the ASCR-CD model fitted to the same data, which provided a call density estimate of  $\hat{D}_c = 7,470$  calls ha<sup>-1</sup> min<sup>-1</sup>. A derived estimate of call density from our ASCR-AD model is  $\hat{D}\hat{\mu} = 6,504$  calls ha<sup>-1</sup> min<sup>-1</sup>. The two models provided very similar estimated call detection functions (Figure 1). The ASCR-CD model cannot compute standard errors or CIs without an independently estimated call rate, so we are unable to directly compare standard errors, CVs or CIs between the two models.

**TABLE 2** Parameter estimates, standard errors, CVs and CIs from the ASCR-AD model. The parameter *D* is reported in calling animals/ha,  $\sigma$  in m,  $\mu$  in calls/min, and  $\sigma_t$  in s ( $\times 10^{-4}$ )

Parameter	Estimate	SE	CV (%)	95% CI
<i>D</i>	358.5	73.1	20.4	(240.4, 534.6)
$\lambda_0$	7.5	1.1	14.2	(5.7, 9.9)
$\sigma$	2.2	0.1	3.6	(2.1, 2.4)
$\mu$	18.1	1.4	8.0	(15.5, 21.2)
$\sigma_t$	10.4	0.5	4.8	(9.5, 11.4)



**FIGURE 1** Call and individual detection functions ( $g_c(d)$  and  $g(d)$ , respectively) estimated from the acoustic survey data by the ASCR-AD model, and the call detection function estimated by the ASCR-CD model. The ASCR-CD model does not estimate an individual detection function



**FIGURE 2** Violin plots of call density (left) and animal density (right) estimates from our simulation study. Horizontal dotted lines indicate the true density values used to simulate the data

#### 3.2 | Simulation study

Based on our simulations, we estimate percentage bias of the call density estimators for our survey scenario to be -0.5% and 0.6% for the ASCR-AD and ASCR-CD models, respectively, with CVs of 21.4% and 23.5%. Our ASCR-AD calling animal density estimator has an estimated bias of -0.6%, with a CV of 20.3%. See Figure 2 for violin plots of call and animal density estimates from the two models. In total, 95.9% of the 95% CIs for animal density from the ASCR-AD model captured the true parameter value.

### 4 | DISCUSSION

We have described a novel method to estimate calling animal density from acoustic surveys. Importantly, we disentangle call density and animal abundance, allowing separate estimates of animal density and call rates from the acoustic survey alone—which is not possible using acoustic SCR models in the existing literature.

Parameter estimates from our application are consistent with previous studies of *A. lightfooti*. Based on seven surveys conducted at the same site, Measey et al. (2017) estimated similar call densities to us, and call detection functions that also dropped to zero by a distance of 10 m (see our estimate in Figure 1). Stevenson et al. (2015) physically located and monitored calls from eight individuals, which produced 16.2 calls individual per minute, on average, consistent with our estimate (with 95% CI) of 18.1 (15.5, 21.2).

Our simulation study reveals that our ASCR-AD model provides an animal density estimator with negligible bias and an associated CI with near-nominal coverage. For comparison, if we were to treat the objective function maximised by the ASCR-CD model as the correct likelihood function, then only 55.0% of the 95% CIs for call density capture the true parameter value. This replicates the finding of Stevenson et al. (2015) that likelihood-based CIs from the ASCR-CD model do not reach their nominal coverage levels due to the likelihood failing to acknowledge dependence

between capture histories of calls produced by the same individual. Moreover, our simulations demonstrate that our model produces more precise estimates of call density than the ASCR-CD model, presumably because we make use of observed animal identities, and because our model is fitted by maximising a correctly specified likelihood.

In the remainder of this section, we discuss extensions to our method that are now possible based on likelihood described in Section 2, and the application of our method more generally to survey scenarios other than what we have considered here.

#### 4.1 | Individual identification

Although we could allocate a plausible set of individual identities to detected calls from *A. lightfooti* (Section 2.4), we may not have allocated identities perfectly. Nevertheless, we anticipate accurate identification from acoustic signals will become more common in the future with the development of methods to distinguish animal identities from properties of vocalisations, similarly to current efforts in identifying individual animals from photographs. Our application illustrates the utility of our model when applied to such datasets.

Developing models that account for uncertain animal identities is a research topic of particular recent focus (e.g. see Augustine et al., 2018, 2019; Borchers et al., in press; Chandler & Royle, 2013; Stevenson et al., 2019), but, at present, existing methods in the literature are not directly applicable to the type of acoustic survey we have considered here. Sampling from possible matchings of detections to individuals is one way to deal with uncertain animal identities in capture–recapture models (Augustine et al., 2018, 2019), while another is maximising a likelihood computed via a sum over all such allocations (Borchers et al., in press). Both introduce considerable computational complexity to model fitting. Either approach involves a likelihood conditional on a proposed matching of detections to individuals, and this likelihood is what we have provided in Section 2.2.6. Future methods developed specifically for passive acoustic data could use properties of detected calls, such as their dominant frequencies, to inform plausible matchings to individuals.

The ASCR-CD model of Stevenson et al. (2015) does not require individual identification and performed comparably to our ASCR-AD model in estimating call density, despite using a misspecified likelihood. Although requiring independently collected call rate data to estimate animal density and produce standard errors and CIs, this approach remains a computationally efficient alternative to modelling uncertain identities via sampling or summing over possible allocations if call rates can be obtained. However, collecting call rate data from *A. lightfooti* individuals presents a substantial fieldwork burden due to their cryptic nature. In this scenario, methods that estimate animal density directly can alleviate this burden, either by dealing directly with observed identities (as ours does here) or by accounting for identification uncertainty.

#### 4.2 | Incorporating animal movement

We assumed that animals are stationary, and so all calls produced by the same individual have the same location. While our method may be seen as an iteration in the progression towards the estimation of calling animal density in all situations, it is already applicable to a wide range of uses. In many invertebrates, for example stridulation in Orthoptera (crickets, katydids, grasshoppers) and cicadas, males call from stationary positions and females travel towards the calling male (Fonseca, 2014; Greenfield, 1997). Calling vertebrate ectotherms, like reptiles and amphibians, have similar advertising systems. Volent calling endotherms, birds and bats, often call from roosting congregations where they can be recorded vocalising in relatively stationary positions (e.g. see Furmankiewicz et al., 2011).

Nevertheless, a possible extension is to allow for mobile animals, so that not all  $c_i$  calls produced by the  $i$ th animal have location  $s_i$ . Instead, each call could have a different location, where the  $j$ th call from the  $i$ th animal has location  $s_{ij}$ . Calls from the same animal still cannot be considered independent, because they will have similar locations if they are produced close together in time.

A movement model would be required to specify  $f(\mathbf{S}_i)$ , where  $\mathbf{S}_i$  is a matrix comprising all  $c_i$  locations of the  $i$ th animal's calls. Movement models for unobserved activity centres have been incorporated into SCR before (e.g. Ergon & Gardner, 2014; Glennie et al., 2019; Royle et al., 2016), but only for surveys where activity centres move between discrete sampling occasions. Accounting for movement within a single acoustic survey is more complicated because a continuous-time model is required instead. Locations of an individual are never directly observed; two possible methods to deal with the latent movement of each individual are (a) to integrate over possible animal movement trajectories to compute a likelihood to maximise, or (b) sample from these trajectories within an MCMC scheme under a Bayesian framework. Both provide a substantial computational challenge.

#### 4.3 | Accounting for between-individual and between-call heterogeneity

Unmodelled heterogeneity in detection probabilities introduces bias to density estimates provided by capture–recapture models (Otis et al., 1978). Acoustic SCR methods explicitly model one specific mechanism that induces heterogeneity: the call detection function accounts for the fact that calls produced closer to detectors are more likely to be detected than those produced further away. However, additional sources of heterogeneity may exist that cause calls to have different detection functions. For example, some individuals may consistently call louder than others making their calls more easily detected, and two calls from the same animal may not be equally detectable due to fluctuations in source signal strength or background noise.

Methods that do not acknowledge which calls were produced by which animal (e.g. Borchers et al., 2015; Efford et al., 2009;

Stevenson et al., 2015) cannot separate heterogeneity between individuals from heterogeneity between calls. However, our model could be extended by including hierarchical individual-level and call-level random effects in the detection function to account for both between-individual and between-call sources of heterogeneity.

#### 4.4 | Distribution of call frequencies

In our application and simulation study, we assumed a Poisson distribution for the number of calls produced by each individual, consistent with calling animals producing calls according to a Poisson process at the same underlying rate. We did so to provide simpler expressions for  $f(c_i^* | s_i^*)$  and  $g(d)$ , given our models were fitted primarily for illustrative purposes.

Nevertheless, if desired, our method can accommodate either underdispersion or overdispersion relative to the Poisson distribution by using an appropriate alternative for  $f(c_i)$ . This decision comes at the expense of added computational complexity due to the infinite sum in Equation (3).

#### 4.5 | Further applications

We applied our model to data collected on two passive acoustic surveys of *A. lightfooti* conducted in the same seepage. Other studies have established that SCR models like ours can be used more generally for other taxa, in more complex habitats, and at larger spatiotemporal scales.

Kidney et al. (2016) and Marques et al. (2012) have shown that acoustic SCR models can be applied to species that are detectable at much larger spatial scales, although larger spacings between adjacent detectors are required; one recommendation is a spacing of two times  $\sigma$  (Efford & Fewster, 2013). A practical consequence of a large spacing is an inability to connect all detectors to a recorder with a single clock, precluding the collection of TOAs that are comparable between detectors. Our method can be applied without TOAs simply by omitting the PDF  $f(T_i^* | \Omega_i^*, c_i^*, s_i^*)$  from the likelihood (Equation 12), although this affects estimator precision (Borchers et al., 2015).

Following Borchers and Efford (2008), our method accommodates estimation of inhomogeneous density for studies in more complex habitats. Moreover, SCR models that involve a homogeneous density assumption provide reliable estimates of abundance and average density even for complex habitats, for example with small patches of suitable habitat interspersed among large regions with no individuals (Efford & Fewster, 2013).

Cluster survey designs, which involve deploying small clusters of detectors at various locations across the landscape, are potentially useful for studies monitoring a large, complex region. Dawson and Efford (2009) used a cluster design for their acoustic survey of ovenbirds *Seiurus aurocapilla*. Clark (2019) conducted a comprehensive

simulation study investigating the performance of SCR density estimators applied to data from cluster designs.

## 5 | CONCLUSIONS

Although our method requires individual identification of calling animals and does not allow for animals relocating within the survey region, it provides a correctly specified likelihood under its assumptions. By doing so, we obtain point and variance estimates using standard maximum likelihood theory, and can use other likelihood-based tools like information-theoretic model selection criteria. Moreover, our model can fit an inhomogeneous density surface, and does not require supplementary data on call rate at the expense of fieldwork effort to identify call density from animal density.

We have provided clear direction towards new methods that relax our assumptions and data requirements. The potential models we described throughout Sections 4.1–4.3 introduce new latent components over and above the animal locations we dealt with in constructing our likelihood, and remain topics of future research.

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#### AUTHORS' CONTRIBUTIONS

B.C.S. conceived the ideas for this study; B.C.S. and C.K.Y.Y. developed the statistical methodology; B.C.S., P.v.D.-B. and C.K.Y.Y. wrote the software and conducted the simulation study; J.M. collected the data; B.C.S. and P.v.D.-B. analysed the data; B.C.S. led the writing of the manuscript. All authors contributed to revision of the original draft.

#### PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/2041-210X.13522>.

#### DATA AVAILABILITY STATEMENT

Data collected on the acoustical surveys of *A. lightfooti*, along with code to analyse these data and conduct the simulation study, are available in a GitHub repository (<https://github.com/b-steve/scr-cuerate>) and are archived on Zenodo (Stevenson et al., 2020).

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## REFERENCES

- Augustine, B. C., Royle, J. A., Kelly, M. J., Satter, C. B., Alonso, R. S., Boydston, E. E., & Crooks, K. R. (2018). Spatial capture–recapture with partial identity: An application to camera traps. *The Annals of Applied Statistics*, 12, 67–95. <https://doi.org/10.1214/17-AOAS1091>
- Augustine, B. C., Royle, J. A., Murphy, S. M., Chandler, R. B., Cox, J. J., & Kelly, M. J. (2019). Spatial capture–recapture for categorically marked populations with an application to genetic capture–recapture. *Ecosphere*, 10, e02627. <https://doi.org/10.1002/ecs2.2627>
- Benevides, F. L., Mauntz, W. J., Jacobsen, C. J., & Hara, A. H. (2019). Estimating density of calling male *Eleutherodactylus coqui* in Hawaii from audio recordings of the nighttime frog chorus. *Bioacoustics*, 28, 101–114.
- Borchers, D. L. (2012). A non-technical overview of spatially explicit capture–recapture models. *Journal of Ornithology*, 152, 435–444. <https://doi.org/10.1007/s10336-010-0583-z>
- Borchers, D. L., & Efford, M. G. (2008). Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics*, 64, 377–385. <https://doi.org/10.1111/j.1541-0420.2007.00927.x>
- Borchers, D. L., & Kidney, D. (2014). *Flexible density surface estimation for spatially explicit capture–recapture surveys*. CREEM Technical Report 2014-1. University of St Andrews.
- Borchers, D. L., Marques, T. A., Gunnlaugsson, T., & Jupp, P. (2010). Estimating distance sampling detection functions when distances are measured with errors. *Journal of Agricultural, Biological, and Environmental Statistics*, 15, 346–361.
- Borchers, D. L., Nightingale, P., Stevenson, B. C., & Fewster, R. M. (in press). A latent capture history model for digital aerial surveys. *Biometrics*.
- Borchers, D. L., Stevenson, B. C., Kidney, D., Thomas, L., & Marques, T. A. (2015). A unifying model for capture–recapture and distance sampling surveys of wildlife populations. *Journal of the American Statistical Association*, 110, 195–204. <https://doi.org/10.1080/01621459.2014.893884>
- Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2001). *Introduction to distance sampling: Estimating abundance of biological populations*. Oxford University Press.
- Buxton, R. T., Major, H. L., Jones, I. L., & Williams, J. C. (2013). Examining patterns in nocturnal seabird activity and recovery across the Western Aleutian Islands, Alaska, using automated acoustic recording. *The Auk*, 130, 331–341.
- Chandler, R. B., & Royle, J. A. (2013). Spatially explicit models for inference about density in unmarked or partially marked populations. *The Annals of Applied Statistics*, 7, 936–954.
- Clark, J. D. (2019). Comparing clustered sampling designs for spatially explicit estimation of population density. *Population Ecology*, 61, 93–101.
- Dawson, D. K., & Efford, M. G. (2009). Bird population density estimated from acoustic signals. *Journal of Applied Ecology*, 46, 1201–1209.
- Dent, J. M., & Molles, L. E. (2016). Call-based identification as a potential tool for monitoring great spotted kiwi. *Emu–austral Ornithology*, 116, 315–322.
- Efford, M. G. (2004). Density estimation in live-trapping studies. *Oikos*, 106, 598–610.
- Efford, M. G., Dawson, D. K., & Borchers, D. L. (2009). Population density estimated from locations of individuals on a passive detector array. *Ecology*, 90, 2676–2682.
- Efford, M. G., & Fewster, R. M. (2013). Estimating population size by spatially explicit capture–recapture. *Oikos*, 122, 918–928.
- Ergon, T., & Gardner, B. (2014). Separating mortality and emigration: Modelling space use, dispersal and survival with robust-design spatial capture–recapture data. *Methods in Ecology and Evolution*, 5, 1327–1336.
- Fonseca, P. J. (2014). Cicada acoustic communication. In B. Hedwig (Ed.), *Insect hearing and acoustic communication* (pp. 101–121). Springer.
- Furmankiewicz, J., Ruczyński, I., Urban, R., & Jones, G. (2011). Social calls provide tree-dwelling bats with information about the locations of conspecifics at roosts. *Ethology*, 117, 480–489.
- Glennie, R., Borchers, D. L., Murchie, M., Harmsen, B. J., & Foster, R. J. (2019). Open population maximum likelihood spatial capture–recapture. *Biometrics*, 75, 1345–1355.
- Greenfield, M. D. (1997). Acoustic communication in orthoptera. In S. K. Gangwere, M. C. Muralirangan, & M. Muralirangan (Eds.), *The bi- nomics of grasshoppers, katydids, and their kin* (pp. 197–230). CAB International.
- Harris, D. V., Miksis-Olds, J. L., Vernon, J. A., & Thomas, L. (2018). Fin whale density and distribution estimation using acoustic bearings derived from sparse arrays. *Journal of the Acoustical Society of America*, 143, 2980–2993.
- Kidney, D., Rawson, B., Borchers, D. L., Stevenson, B. C., Marques, T. A., & Thomas, L. (2016). An efficient acoustic density estimation method with human detectors applied to gibbons in Cambodia. *PLoS ONE*, 11, e0155066.
- Klinck, H., Mellinger, D. K., Klinck, K., Bogue, N. M., Luby, J. C., Jump, W. A., Shilling, G. B., Litchendorf, T., Wood, A. S., Schorr, G. S., & Baird, R. W. (2012). Near-real-time acoustic monitoring of beaked whales and other cetaceans using a Seaglider™. *PLoS ONE*, 7, e361282012.
- Llusia, D., & Márquez, R. (2013). Calling behaviour under climate change: Geographical and seasonal variation of calling temperatures in ectotherms. *Global Change Biology*, 19, 2655–2674.
- Marques, T. A. (2004). Predicting and correcting bias caused by measurement error in line transect sampling using multiplicative error models. *Biometrics*, 60, 757–763.
- Marques, T. A., Thomas, L., Martin, S. W., Mellinger, D. K., Jarvis, S., Morrissey, R. P., Ciminello, C., & DiMarzio, N. (2012). Spatially explicit capture–recapture methods to estimate minke whale density from data collected at bottom-mounted hydrophones. *Journal of Ornithology*, 152, 445–455.
- Marques, T. A., Thomas, L., Martin, S. W., Mellinger, D. K., Ward, J. A., Morettie, D. J., Harris, D., & Tyack, P. L. (2013). Estimating animal population density using passive acoustics. *Biological Reviews*, 88, 287–309.
- Marques, T. A., Thomas, L., Ward, J., DiMarzio, N., & Tyack, P. L. (2009). Estimating cetacean population density using fixed passive acoustic sensors: An example with Blainville's beaked whales. *The Journal of the Acoustical Society of America*, 125, 1982–1994.
- Measey, G. J., Stevenson, B. C., Scott, T., Altwegg, R., & Borchers, D. L. (2017). Counting chirps: Acoustic monitoring of cryptic frogs. *Journal of Applied Ecology*, 54, 894–902.
- Otis, D. L., Burnham, K. P., White, G. C., & Anderson, D. R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife Monographs*, 62, 3–135.
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org/>
- Royle, J. A., Chandler, R. B., Sollmann, R., & Gardner, B. (2013). *Spatial capture–recapture*. Academic Press.
- Royle, J. A., Fuller, A. K., & Sutherland, C. (2016). Spatial capture–recapture models allowing Markovian transience or dispersal. *Population Ecology*, 58, 53–62.
- Royle, J. A., & Young, K. V. (2008). A hierarchical model for spatial capture–recapture data. *Ecology*, 89, 2281–2289.
- Sebastián-González, E., Camp, R. J., Tanimoto, A. M., de Oliveira, P. M., Lima, B. B., Marques, T. A., & Hart, P. J. (2018). Density estimation of sound-producing terrestrial animals using single automatic acoustic recorders and distance sampling. *Avian Conservation and Ecology*, 13, 7.

- Stevenson, B. C. (2020). *ascr: Acoustic spatial capture–recapture in AD Model Builder*. R package version 2.2.2. Retrieved from <https://github.com/b-steve/ascr>
- Stevenson, B. C., Borchers, D. L., Altwegg, R., Swift, R. J., Gillespie, D. M., & Measey, G. J. (2015). A general framework for animal density estimation from acoustic detections across a fixed microphone array. *Methods in Ecology and Evolution*, 6, 38–48.
- Stevenson, B. C., Borchers, D. L., & Fewster, R. M. (2019). Cluster capture–recapture to account for identification uncertainty on aerial surveys of animal populations. *Biometrics*, 75, 326–336. <https://doi.org/10.1111/biom.12983>
- Stevenson, B. C., van Dam-Bates, P., Young, C. K. Y., & Measey, J. (2020). Code and data to accompany the paper 'A spatial capture–recapture model to estimate call rate and population density from passive acoustic surveys'. *Zenodo*, <https://doi.org/10.5281/zenodo.4083577>
- Zuk, M., Rotenberry, J. T., & Simmons, L. W. (2001). Geographical variation in calling song of the field cricket *Teleogryllus oceanicus*: The

importance of spatial scale. *Journal of Evolutionary Biology*, 14, 731–741. <https://doi.org/10.1046/j.1420-9101.2001.00329.x>

#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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