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Continuous-time spatially explicit capture–recapture models, with an application to a jaguar camera-trap survey

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Summary

1. Many capture–recapture surveys of wildlife populations operate in continuous time, but detections are typically aggregated into occasions for analysis, even when exact detection times are available. This discards information and introduces subjectivity, in the form of decisions about occasion definition.

2. We develop a spatiotemporal Poisson process model for spatially explicit capture–recapture (SECR) surveys that operate continuously and record exact detection times. We show that, except in some special cases (including the case in which detection probability does not change within occasion), temporally aggregated data do not provide sufficient statistics for density and related parameters, and that when detection probability is constant over time, our continuous-time (CT) model is equivalent to an existing model based on detection frequencies. We use the model to estimate jaguar density from a camera-trap survey and conduct a simulation study to investigate the properties of a CT estimator and discrete-occasion estimators with various levels of temporal aggregation. This includes investigation of the effect on the estimators of spatiotemporal correlation induced by animal movement.

3. The CT estimator is found to be unbiased and more precise than discrete-occasion estimators based on binary capture data (rather than detection frequencies) when there is no spatiotemporal correlation. It is also found to be only slightly biased when there is correlation induced by animal movement, and to be more robust to inadequate detector spacing, while discrete-occasion estimators with binary data can be sensitive to occasion length, particularly in the presence of inadequate detector spacing.

4. Our model includes as a special case a discrete-occasion estimator based on detection frequencies, and at the same time lays a foundation for the development of more sophisticated CT models and estimators. It allows modelling within-occasion changes in detectability, readily accommodates variation in detector effort, removes subjectivity associated with user-defined occasions and fully utilizes CT data. We identify a need for developing CT methods that incorporate spatiotemporal dependence in detections and see potential for CT models being combined with telemetry-based animal movement models to provide a richer inference framework.

Key-words: animal movement, data aggregation, density estimation, statistical methods, sufficiency

Introduction

Monitoring elusive species such as forest-dwelling carnivores that occur at low densities and range over wide areas is difficult, as is monitoring species that are difficult to trap or detect visually, but many such species are of high conservation concern. The estimation of density and detectability are common in population monitoring and are crucial parameters for elusive species (Stuart *et al*. 2004, Thompson 2004).

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Technological advances in non-invasive sampling methods such as scat or hair collection for genetic analysis, camera-trapping and acoustic detection have led to new ways of 'capturing' individuals, that are particularly useful for species that are difficult to survey using more conventional methods. Camera-trap arrays in particular have become an important tool for assessment and management of species that are hard to detect by other means. They have been used with capture–recapture (CR) methods for various species that are individually identifiable from photographs, including felids, canids, ursids, hyaenids, procyonoids, tapirids and dasypodids (see references in

Foster & Harmsen 2012), and are increasingly used with spatially explicit capture–recapture (SECR) methods. SECR incorporates spatial information on capture locations and allows inferences to be drawn about the underlying process governing the locations of individuals, as well as providing estimates of density without the need for separate estimates of the effective sampling area (Efford 2004, Borchers & Efford 2008, Efford, Borchers & Byrom 2009a, Royle *et al*. 2009).

When a CR study (conventional or SECR) involves physically capturing individuals, the survey process generates well-defined sampling occasions. But, when there is no physical capture and release, as in the case of camera-trap studies or acoustic CR surveys that record times of detection, there is no well-defined sampling occasion. In such cases, aggregating data into capture occasions introduces subjectivity (the occasion length chosen by the analyst) and discards some information (the exact times of capture). Continuous-time (CT) models avoid these problems. The earliest CT model is probably that of Craig (1953). It assumed equal catchability for all individuals at all times, but has since been extended to allow individual heterogeneity (Boyce *et al*. 2001). Most CT estimators use martingale estimating functions (Becker 1984; Yip 1989; Becker & Heyde 1990; Yip, Huggins & Lin 1995; Lin & Yip 1999; Yip *et al*. 1999; Hwang & Chao 2002; Yip & Wang 2002), although Nayak (1988), Becker & Heyde (1990) and Hwang, Chao & Yip (2002) developed maximum likelihood estimators (MLEs) and Chao & Lee (1993) developed a CT estimator based on sample coverage. Of the CT models in the literature, only the models of Nayak (1988), Yip (1989) and Hwang, Chao & Yip (2002) estimate detectability and abundance simultaneously, in common with the estimator we develop below.

There is no consensus on the utility of CT estimators. Some authors concluded that the use of a discrete-occasion model to analyse a CT data set will bias estimates (Yip & Wang 2002; Barbour, Ponciano & Lorenzen 2013), while others found no benefit over discrete-occasion estimators (e.g. Chao & Lee 1993; Wilson & Anderson 1995). We show in Appendix S3 that Chao & Lee's (1993) conclusion that capture times are uninformative about abundance does not hold in general. We develop CT SECR likelihoods and MLEs which, unlike any existing CT models, are parameterised in terms of population density rather than abundance, and crucially, incorporate a model for (unobserved) individual activity centres. An activity centre is the centre of gravity of an individual's locations over the duration of the survey. It may have biological interpretation, for example as a home range centre, but need not. Our model is obtained by formulating the SECR survey process as a non-homogeneous spatiotemporal Poisson process, in which events are detections at points in space and time (see Cook & Lawless 2007, for a comprehensive overview of recurrent event processes, of which Poisson processes are a special case). We note that the interaction between recurrent event processes and CR methods was identified by Chao & Huggins (2005), p. 85) as 'a fruitful area for future research', which we explore in this paper.

We focus on the development of SECR methods for data from camera-trap surveys, but our models are also appropriate for any CR survey with continuous sampling in which capture times are recorded. This includes acoustic SECR surveys such as those described in Efford, Dawson & Borchers (2009b), Dawson & Efford (2009) or Borchers *et al*. (2013), although recapture identification may be difficult in such surveys. CT SECR models also provide the basis for varying-effort SECR methods such as those of Efford, Borchers and Mowat (2013), and we show how discrete-occasion models arise from a CT formulation.

We assume independence between captures, conditional on activity centre location. This is almost certainly violated to some degree in camera-trap studies because individuals are only detected when they move within range of a camera, and an individual's locations are temporally correlated. We investigate sensitivity to violation of this assumption.

We develop a general CT SECR likelihood and then evaluate models under the assumptions of constant detection probability over time and constant intensity of the spatial point process governing the number and locations of activity centres. In this case, the CT likelihood is equivalent to a single-occasion Poisson count likelihood spanning the whole survey, in which the data are the capture frequencies of each individual at each detector (see Appendix S3). Simulations are used to compare the CT estimator for this case with discrete-occasion estimators based on binary data within occasions and detectors (i.e. in which, each individual's capture frequency at each detector within an occasion is reduced to a binary indicator of detection or not). We compare various levels of temporal aggregation both when the assumption of independence holds and when it is violated by simulating correlated animal movement.

Materials and methods

STUDY SITE AND CAMERA TRAPPING OF JAGUARS

Jaguars (*Panthera onca*) are near threatened and their global population is declining (Caso *et al*. 2008), and population monitoring is difficult because they occur at low densities, range widely and are elusive, often inhabiting thick habitat. Over the past decade, the challenge of detecting jaguars for population estimation has been facilitated by camera traps, following the work of Silver *et al*. 2004; however, reliable and robust density estimates of jaguars are rarely obtained (see Foster & Harmsen 2012; Tobler & Powell 2013).

We estimate male jaguar density in the Cockscomb Basin Wildlife Sanctuary in Belize from camera-trap data. The sanctuary encompasses 490 km^2 of secondary tropical moist broadleaf forest at various stages of regeneration following anthropogenic and natural disturbance (for more details, see Harmsen *et al*. 2010b). To the west, the sanctuary forms a contiguous forest block with the protected forests of the Maya Mountain Massif ($\approx$ 5000 km^2 of forest). To the east, the sanctuary is partially buffered by unprotected forest beyond which is a mosaic of pine savannah, shrub land and broadleaf forest, inter-dispersed with villages and farms. Jaguars are found throughout this landscape (Foster, Harmsen & Doncaster 2010). There are 65 km of trails, all within the eastern part of the sanctuary (see Fig. 1). Male jaguars routinely walk the trail system; trail use overlaps extensively. Although they frequently leave the trails to move through the forest, they are rarely detected off-trail by camera traps (Harmsen *et al*. 2010a). Nineteen paired camera stations (Pantheracam v3) were deployed along the trail network within the eastern basin and maintained for 90 days (April to July 2011).

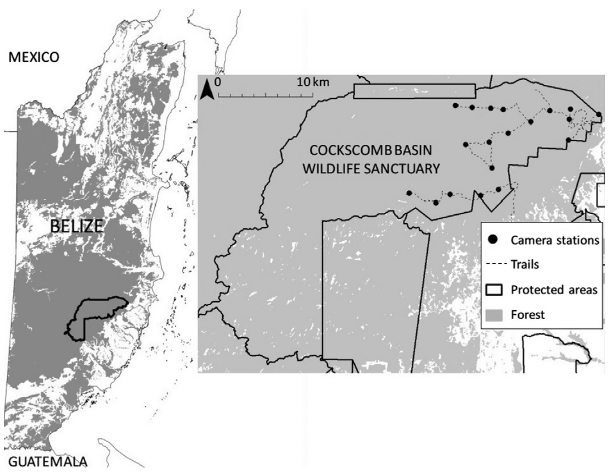

Fig. 1. Camera-trap locations within Cockscomb Basin Wildlife Sanctuary, Belize.

Neighbouring stations had an average spacing of 2·0 km (1·1 to 3·1 km). The cameras used have an enforced 8 s delay between consecutive photos, and digital photographic data were downloaded every 2 weeks.

CONTINUOUS-TIME MODELS FOR PROXIMITY DETECTORS

We refer to both capture and detection as 'detection', and to all detectors, including traps, as 'detectors'.

We model the process generating detections as a non-homogeneous Poisson process (NHPP) in space and time, in which the events are detections. This model is governed by a hazard of detection, which can vary with location and time and is equal to the expected number of detections per unit time at the location and time. The model allows this hazard to change with location (to accommodate lower capture probability for individuals with activity centres farther from detectors, for example), time (to accommodate different animal activity levels at different times of day, for example) and other explanatory variables, but we assume initially that the hazard for any individual at any time is independent of the individual's capture history up to that time. We develop a model and estimator under this assumption and then investigate its performance when the hazard of detection does depend on where and when individuals were previously detected (as a consequence of correlated animal movement). Parameters and standard errors were estimated using a Newton-type algorithm with function `nlm` in R (R Core Team, 2013).

Continuous-time proximity detector likelihood

We consider a survey in which we have an array of K continuously sampling proximity detectors. The key difference between the likelihood presented here and a discrete-occasion SECR likelihood is that there are no longer occasions, but instead, a continuous survey running for a period $(0,T)$. Instead of a capture history of length S (if there were S occasions) for the ith individual at detector k, we have ω_{ik} captures of the individual at detector k at times $\boldsymbol{t}_{ik} = (t_{ik1}, \ldots, t_{ik\omega_{ik}})$. For brevity, we let $\boldsymbol{t} = \{\boldsymbol{t}_{ik}\}$ $(i = 1,\ldots,n; k = 1,\ldots,K)$ denote the set of all detection times.

To simplify presentation of the likelihood, we start by considering a single individual (the ith individual), with activity centre at $\boldsymbol{x}_i$, and a single detector (the kth detector). By considering $\boldsymbol{t}_{ik}$ to be a realization of an NHPP in time, we obtain an expression for the probability density function (pdf) of $\boldsymbol{t}_{ik}$. This is analogous to the probability of obtaining a capture history at detector k for individual i in a discrete-occasion formulation, but it is worth noting that both the length of $\boldsymbol{t}_{ik}$ (i.e. ω_{ik}) and the times that it contains are random variables, whereas for a discrete-occasion survey, the length of a capture history is fixed by the number of occasions used.

Using the pdf of $\boldsymbol{t}_{ik}$, we obtain an expression for the probability of detecting individual i at all. Then, following Borchers & Efford (2008), we assume that the (unobserved) activity centres of detected individuals are realizations of a filtered spatial NHPP, with filter at a location $\boldsymbol{x}$ being the detection probability at that location. This gives rise to a joint probability model for the number of individuals detected (n) and their detection times at detectors ($\boldsymbol{t}$). When considered as a function of the unknown model parameters, this is the CT SECR likelihood function.

The pdf of $\boldsymbol{t}_{ik}$. In a CT formulation, the discrete-occasion expression for the probability of detecting individual i at detector k on an occasion is replaced by a detection hazard function that specifies the expected detection rate per unit time at detector k of an individual, at time t, given the location of its activity centre ($\boldsymbol{x}_i$ for individual i). This hazard function $h_k(t,\boldsymbol{x}_i;\boldsymbol{\theta})$ depends on the distance from detector k to the individual's activity centre ($\boldsymbol{x}_i$), and we make this explicit when we specify models for $h_k(t,\boldsymbol{x}_i;\boldsymbol{\theta})$, but for notational, brevity we do not make the dependence on distance explicit otherwise. The hazard function has an unknown vector of detection function parameters $\boldsymbol{\theta}$. The 'survivor function' for individual i at detector k over the whole survey (the probability of individual i not being detected on the detector by time T) is $S_k(T,\boldsymbol{x}_i;\boldsymbol{\theta}) = \exp\left(-\int_0^T h_k(u,\boldsymbol{x}_i;\boldsymbol{\theta})\,\mathrm{d}u\right)$ and hence $1-S_k(T,\boldsymbol{x}_i;\boldsymbol{\theta})$ is the probability of detection in $(0,T)$.

In a similar vein, the link between a CT detection hazard and a discrete-occasion detection probability, $p_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})$ for detector k on occasion s, of length $T_s = t_s - t_{s-1}$ (running from t_{s-1} to t_s) is: $p_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta}) = 1 - \exp\left(-\int_{t_{s-1}}^{t_s} h_{ks}(t,\boldsymbol{x}_i;\boldsymbol{\theta})\,\mathrm{d}u\right)$. Under the assumption of a constant hazard, solving this for $h_{ks}(t,\boldsymbol{x}_i;\boldsymbol{\theta})$ leads to a hazard with the following form:

$$h_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta}) = -\log\{1 - p_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})\}/T_s \qquad \text{eqn 1}$$

In our analyses, we use hazard functions in which $p_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})$ for a specified occasion length has a half-normal form: $p_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta}) = g_{0,T_s} \exp^{\{-d_k(\boldsymbol{x}_i)^2/(2\sigma^2)\}}$, where $d_k(\boldsymbol{x}_i)$ is the distance from $\boldsymbol{x}_i$ to detector k, and g_{0,T_s} and σ are parameters to be estimated. The parameter g_{0,T_s} is the probability that an individual with activity centre located at a detector is detected in a time period of length T_s, while σ is the scale parameter of the half-normal detection function, and determines the range over which an individual is detectable.

Assuming that, conditional on the activity centre location, the times of detections are independent, we can model the number of detections, ω_{ik}, and the detection times $\boldsymbol{t}_{ik}$ as a nonhomogeneous Poisson process with pdf as follows [see Cook & Lawless 2007, Theorem 2·1 on page 30, and Equation (2·13) on page 32]:

$$f_k(\boldsymbol{t}_{ik}|\boldsymbol{x}_i;\boldsymbol{\theta}) = S_k(T,\boldsymbol{x}_i;\boldsymbol{\theta}) \prod_{r=1}^{\omega_{ik}} h_k(t_{ikr},\boldsymbol{x}_i;\boldsymbol{\theta}) \qquad \text{eqn 2}$$

(We omit ω_{ik} from the LHS for brevity, because given $\boldsymbol{t}_{ik}$, ω_{ik} is known.) For those familiar with the definition of hazard functions in terms of the pdf and survivor function, we note that $h_k(t_{ikr},\boldsymbol{x}_i;\boldsymbol{\theta}) = f_k(t_{ikr}|\boldsymbol{x}_i;\boldsymbol{\theta})/S_k((t_{ikr}-t_{ik(r-1)}),\boldsymbol{x}_i;\boldsymbol{\theta})$.

Equation (2) is a generalization of the expression obtained by Hwang *et al.* (2000, p. 43) for their model M_t (given by their expression for L_i), and of the expression of Chao & Huggins (2005, p. 80) for the case in which $h_k(t_{ikr},\boldsymbol{x}_i;\boldsymbol{\theta})$ is constant. Both sets of authors use λ for the hazard, whereas we use $h()$. In addition to locating these models in the

Poisson process literature, our generalization involves the inclusion of $\boldsymbol{x}$ as a latent variable (see below), and extension to multiple detectors.

Multiple detectors and individuals. An individual's overall detection frequency across the K detectors is denoted $\omega_{i\cdot} = \sum_{k=1}^{K}\omega_{ik}$, and the event $\omega_{i\cdot} > 0$ indicates detection by some detector. The combined detection hazard over all detectors at time t is $h_{\cdot}(t, \boldsymbol{x}_i; \boldsymbol{\theta}) = \sum_{k=1}^{K} h_k(t, \boldsymbol{x}_i; \boldsymbol{\theta})$, and the overall probability of detection in $(0,T)$ over all detectors is $p_{\cdot}(\boldsymbol{x}_i;\boldsymbol{\theta}) = p(\omega_{i\cdot} > 0|\boldsymbol{x}_i;\boldsymbol{\theta}) = 1 - S_{\cdot}(T,\boldsymbol{x}_i;\boldsymbol{\theta})$, where $S_{\cdot}(T, \boldsymbol{x}_i; \boldsymbol{\theta}) = \exp\left(-\int_0^T h_{\cdot}(t, \boldsymbol{x}_i; \boldsymbol{\theta})\right)$ is the overall survivor function.

Following Borchers & Efford (2008), we assume that activity centres occur independently in the plane according to an NHPP with intensity $D(\boldsymbol{x};\boldsymbol{\phi})$ at $\boldsymbol{x}$, where $\boldsymbol{x}$ is any point in the survey region and $\boldsymbol{\phi}$ is a vector of unknown parameters that govern the intensity and hence the distribution of activity centres. $D(\boldsymbol{x};\boldsymbol{\phi})$ is the expected activity centre density at $\boldsymbol{x}$. Activity centres are assumed not to move during the survey.

The likelihood for $\boldsymbol{\phi}$ and $\boldsymbol{\theta}$ is the joint distribution of the number of animals captured n, and the density of the outcome 'ω_{ik} events, at times $t_{ik1} < \ldots < t_{ik\omega_{mikr}}$', for all i and k. This can be written in terms of the marginal distribution of n and the conditional distribution of $\boldsymbol{t}$ given n.

$$L(\boldsymbol{\theta}, \boldsymbol{\phi} \mid n, \boldsymbol{t}) = P(n \mid \boldsymbol{\phi}, \boldsymbol{\theta}) f_t(\boldsymbol{t}|n, \boldsymbol{\theta}, \boldsymbol{\phi}) \qquad \text{eqn 3}$$

If individuals are detected independently, n is a Poisson random variable with parameter $\lambda(\boldsymbol{\theta},\boldsymbol{\phi}) = \int_A D(\boldsymbol{x};\boldsymbol{\phi}) p_{\cdot}(\boldsymbol{x};\boldsymbol{\theta})\, \mathrm{d}\boldsymbol{x}$, where $p_{\cdot}(\boldsymbol{x};\boldsymbol{\theta})$ is the probability of an individual with activity centre at $\boldsymbol{x}$ being detected at all and the integral is over all points $\boldsymbol{x}$ in the area A in which activity centres occur.

We obtain an expression for $f_t(\boldsymbol{t}|n,\boldsymbol{\theta},\boldsymbol{\phi})$ in Appendix S1 and show that, given the detection times of all detected individuals, $\boldsymbol{t}$, the likelihood for $\boldsymbol{\phi}$ and $\boldsymbol{\theta}$ is

$$L(\boldsymbol{\phi}, \boldsymbol{\theta}|n, \boldsymbol{t}) = \frac{\exp^{-\lambda(\boldsymbol{\phi},\boldsymbol{\theta})}}{n!} \prod_{i=1}^{n} \int_A D(\boldsymbol{x}_i; \boldsymbol{\phi}) S_{\cdot}(T, \boldsymbol{x}_i; \boldsymbol{\theta}) \prod_{k=1}^{K} \prod_{r=1}^{\omega_{ik}} h_k(t_{ikr}, \boldsymbol{x}_i; \boldsymbol{\theta})\, \mathrm{d}\boldsymbol{x} \qquad \text{eqn 4}$$

The integral is over all possible activity centre locations that could have led to a detection on the survey. (See section 4·2 of Borchers & Efford 2008, for a brief discussion of this issue.)

It is sometimes useful to write this likelihood in terms of the marginal distribution of ω_{ik} and the conditional distribution of $\boldsymbol{t}_{ik}$ given ω_{ik}. The capture frequency over the survey for individual i at detector k has a Poisson distribution with parameter $H_k(\boldsymbol{x}_i; \boldsymbol{\theta}) = \int_0^T h_k(t, \boldsymbol{x}_i; \boldsymbol{\theta})\, \mathrm{d}t$ [see Cook & Lawless 2007, Equation (2·15) on page 32]:

$$P_k(\omega_{ik}|\boldsymbol{x}_i; \boldsymbol{\theta}) = \frac{H_k(\boldsymbol{x}_i; \boldsymbol{\theta})^{\omega_{ik}} \exp^{-H_k(\boldsymbol{x}_i;\boldsymbol{\theta})}}{\omega_{ik}!} = \frac{H_k(\boldsymbol{x}_i; \boldsymbol{\theta})^{\omega_{ik}} S_k(T, \boldsymbol{x}_i; \boldsymbol{\theta})}{\omega_{ik}!} \qquad \text{eqn 5}$$

It follows from this and eqn (2) that the conditional pdf of detection times $\boldsymbol{t}_{ik}$, given ω_{ik}, for the ith animal is

$$f_{t|\omega,k}(\boldsymbol{t}_{ik}|\omega_{ik}, \boldsymbol{x}_i; \boldsymbol{\theta}) = \omega_{ik}! \prod_{r=1}^{\omega_{ik}} \frac{h_k(t_{ikr}|\boldsymbol{x}_i; \boldsymbol{\theta})}{H_k(\boldsymbol{x}_i; \boldsymbol{\theta})} \qquad \text{eqn 6}$$

and hence that

$$L(\boldsymbol{\phi}, \boldsymbol{\theta}|n, \boldsymbol{t}) = \frac{e^{-\lambda(\boldsymbol{\theta},\boldsymbol{\phi})}}{n!} \prod_{i=1}^{n} \int_A D(\boldsymbol{x}_i; \boldsymbol{\phi}) \prod_{k=1}^{K} P_k(\omega_{ik}|\boldsymbol{x}_i; \boldsymbol{\theta}) \prod_{r=1}^{\omega_{ik}} f_{t|\omega,k}(\boldsymbol{t}_{ik}|\omega_{ik}, \boldsymbol{x}_i; \boldsymbol{\theta})\, \mathrm{d}\boldsymbol{x} \qquad \text{eqn 7}$$

Constant density, constant hazard likelihood

One simple special case arises when density is uniform, that is the spatial Poisson process governing activity centre locations is homogeneous, and the detection hazards do not change with time. In this case, $D(\boldsymbol{x};\boldsymbol{\phi})$ is a constant (D), $\lambda(\boldsymbol{\theta},\boldsymbol{\phi}) = Da(\boldsymbol{\theta})$ (where $a(\boldsymbol{\theta}) = \int_A p_{\cdot}(\boldsymbol{x};\boldsymbol{\theta})\quad \mathrm{d}\boldsymbol{x}$ is the effective survey area), $h_k(t,\boldsymbol{x}_i;\boldsymbol{\theta}) = h_k(\boldsymbol{x}_i;\boldsymbol{\theta})$ and so $H_k(\boldsymbol{x}_i;\boldsymbol{\theta}) = Th_k(\boldsymbol{x}_i;\boldsymbol{\theta})$. As a result, eqn (6) becomes $f_{t|\omega,k}(\boldsymbol{t}_{ik}|\omega_{ik}, \boldsymbol{x}_i; \boldsymbol{\theta}) = \omega_{ik}! \prod_{r=1}^{\omega_{ik}} T^{-1}$ and the likelihood eqn (7) simplifies to

$$L(D, \boldsymbol{\theta}|n, \boldsymbol{t}) = \left(\frac{D^n e^{-Da(\boldsymbol{\theta})}}{n!} \prod_{i=1}^{n} \int_A \prod_{k=1}^{K} P_k(\omega_{ik}|\boldsymbol{x}_i; \boldsymbol{\theta})\, \mathrm{d}\boldsymbol{x} \right) \left(\prod_{i=1}^{n} \prod_{k=1}^{K} \omega_{ik}! \prod_{r=1}^{\omega_{ik}} \frac{1}{T} \right) \qquad \text{eqn 8}$$

The second term in large brackets is the pdf of the detection times $\boldsymbol{t}$, given the detection frequencies $\{\omega_{ik}\}$ ($i = 1,\ldots,n; k = 1,\ldots,K$). Because this term does not contain any model parameters, and the term in the first large brackets contains the parameters and the detection frequencies $\{\omega_{ik}\}$ but not the detection times, it follows (from the Fisher–Neyman Factorization Theorem for sufficiency) that in this case, the detection frequencies are sufficient statistics for the parameters $\boldsymbol{\theta}$ and D, that is, that no information about D is lost by discarding the detection times. Chao & Lee (1993) obtained this result for the case with a single detector, no $\boldsymbol{x}$, and a model parameterised in terms of abundance N rather than density D – but the result does not hold in general, as we discuss below.

Relationship to Poisson count models

One can see from eqn (8) that under the above assumptions, the CT model gives rise to a Poisson count model, as $P_k(\omega_{ik})$ is a Poisson probability mass function (pmf) with rate parameter $T_s h_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})$ and the term in the second large bracket can be neglected because it is constant with respect to the parameters. This model was proposed in Appendix S1 of Efford, Dawson & Borchers (2009b), and a similar model was proposed by Royle *et al.* (2009). The CT model provides an interpretation of the Poisson rate parameter of these models as the cumulative detection hazard, $T_s h_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})$. Both Efford, Dawson & Borchers (2009b) and Royle *et al.* (2009) proposed modelling $T_s h_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})$ using the same functional forms as are used for the probability of detecting an individual within an occasion, but allowing an intercept greater than 1. This may be a reasonable strategy, but modellers should be aware that $p_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})$ and $h_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})$ necessarily have different shapes because $p_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta}) = 1 - \exp\{-T_s h_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})\}$. So for example, assuming a half-normal shape for the Poisson rate parameter (as do Royle *et al.* 2009), $T_s h_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta}) = \lambda_0 exp\{-d_k(\boldsymbol{x}_i)^2/\sigma^2\}$ generates a shape for the detection function $p_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})$ that is not half-normal.

Lack of sufficiency of detection frequencies

In Appendix S3, we show that the discrete-occasion Bernoulli, binomial and Poisson models are reduced-data versions of the CT model and that the detection histories or detection frequencies $\boldsymbol{\Omega} = \{\omega_{iks}\}$ ($i = 1,\ldots,n; k = 1,\ldots,K; s = 1,\ldots,S$, where S is the number of occasions in the survey) are not in general sufficient statistics for $\boldsymbol{\theta}$ and $\boldsymbol{\phi}$, that is that in general detection time is informative. A notable exception is when the detection hazard is constant within occasions. In this case, discarding detection times does not discard information about population density. Reducing counts to a binary event does however discard information, and the consequences of this reduction are explored in the first simulation below.

MODELS WITH VARIABLE EFFORT

Continuous-time models readily accommodate detectors that are operational for different periods of time, by setting the detection hazard at a detector to zero while the detector is out of operation (i.e. $h_k(t,\boldsymbol{x};\boldsymbol{\theta}) = 0$ if detector k was not operating at time t). This is the basis of the varying-effort model for binary detectors and counts in Efford, Borchers & Mowat (2013). It is more difficult to accommodate detectors when their time of failing is unknown, and we do not address that problem here.

SIMULATION TESTING CAMERA-TRAP ESTIMATORS

If animals are detected as a consequence of their moving close to a detector, the expected detection rate of the animal at any given detector depends on when and where the animal was last detected, because animals' locations are temporally correlated. But if times between detections are sufficiently long that the pdf of an animal's location at time t is independent of where it was last detected, then we can model the process generating detection times using the model derived above.

In addition, to investigate the properties of the CT estimator for camera-trap surveys when detections are temporally correlated, we conducted simulations using a generating process in which probability of detection at any detector depends on when and where an animal was last detected. Because our focus is on the application of CT estimators to jaguar camera-trap survey data, we model dependence by constructing individual movement models that are plausible for jaguar movement.

For all simulation scenarios, we also investigated the properties of a binary discrete-occasion proximity detector SECR model (in which ω_{iks} is binary) using a half-normal detection function and a range of aggregation levels: (i) 360 occasions of length $T_s = 6$ h (ii) 90 occasions of length $T_s = 24$ h (iii) 30 occasions of length $T_s = 72$ h and (iv) 18 occasions of length $T_s = 120$ h. In all cases, we assumed constant intensity, D, in the survey region.

The density estimates obtained from fitting a variety of models to the jaguar survey data (see below) were used to inform the simulation scenarios and led to the use of $D = 4$ individuals per 100 km^2. The movement model (below) is not parameterised in terms of the parameters g_0 and σ that are used for the independence simulation model. In order to facilitate comparison of results across the two kinds of simulations, the values used for these parameters in the independence simulations were based on estimates obtained by fitting the CT model to data from the movement simulations. All simulations involved twenty detectors arranged on a 4 × 5 grid. Three different grid spacings were used: 1500 m (62·5% of σ), 3000 m (125% of σ) and 4500 m (187·5% of σ).

Independence simulations

Function `sim.popn` from the R package `secr` (Efford 2013) was used to simulate populations of N individuals with activity centres $\boldsymbol{x}_1,\ldots,\boldsymbol{x}_N$, where N is stochastic and varied from simulation to simulation (see Fewster & Buckland 2004, for details of the simulation method). A time-constant hazard $h_k(\boldsymbol{x}_i;\boldsymbol{\theta})$ $(k = 1,\ldots,K)$ was assumed for the duration of the survey $(0,T)$, and the frequency with which individual i was detected by detector k (ω_{ik}) was obtained as a draw from a Poisson distribution with rate parameter $T \times h_k(\boldsymbol{x}_i;\boldsymbol{\theta})$. Detection times were generated by independent draws from a uniform distribution on $(0,T)$.

Separate detection hazards were used to simulate data for the different aggregation levels, so as to have discrete-occasion detection functions with half-normal forms at each level (to facilitate discrete-occasion estimation with the `secr` package). The corresponding CT model estimator was also applied to each simulated data set. For an occasion of length T_s, $h_{\text{ks}}(\boldsymbol{x}_i;\boldsymbol{\theta}_{T_s})$ is equal to eqn (1), where $p_{\text{ks}}(\boldsymbol{x}_i;\boldsymbol{\theta}_{T_s}) = g_{0,T_s}\exp\{-d_k(\boldsymbol{x}_i)^2/(2\sigma^2)\}$, $d_k(\boldsymbol{x}_i)$ is the distance from $\boldsymbol{x}_i$ to detector k, $\boldsymbol{\theta}_6 = (g_{0,6} = 0{\cdot}01, \sigma = 2400)$, $\boldsymbol{\theta}_{24} = (g_{0,24} = 0{\cdot}05, \sigma = 2400)$, $\boldsymbol{\theta}_{72} = (g_{0,72} = 0{\cdot}15, \sigma = 2400)$ and $\boldsymbol{\theta}_{120} = (g_{0,120} = 0{\cdot}25, \sigma = 2400)$.

Movement model simulations

Activity centres were simulated as above. Animals were moved in time steps of 1 h according to the movement model described below. Whenever a path crossed a 250×250 m grid cell containing a detector, detection occurred with probability P_{GC} (where subscript GC stands for 'Grid Cell' as these probabilities operate at the level of grid cells). The lower P_{GC}, the less temporally clustered are detections and the closer the model is to the independence model. This is because a correlated time series becomes less correlated when randomly thinned.

The movement model: a mixture of random walks. There is considerable literature on the modelling of animal movement using various types of random walks (Morales *et al.* 2004; Codling, Plank & Benhamou 2008; Smouse *et al.* 2010; Langrock *et al.* 2012). Movement can conveniently be simulated by generating a step length and a turning angle from appropriate distributions at each time step (Morales *et al.* 2004). Different turning angle distributions produce different types of random walks. For example, for a biased random walk (BRW), the turning angle for the next step is drawn from a distribution with mean oriented towards some focal point, whereas for a correlated random walk (CRW), the mean is the current direction of movement.

In order to reproduce both the tendency of individuals to persist in the direction in which they are currently moving and the tendency not to stray too far from their activity centre, we constructed a movement model in which individuals transition stochastically between two states. In the first state (state $s = 0$), they follow a CRW, and in the second state (state $s = 1$), a BRW with bias towards an activity centre. The probability of being in a particular state depends on the distance the individual is from its activity centre. Specifically, the state s of an individual at distance d from its activity centre has the following Bernoulli distribution $s|d \sim \gamma(d)^s(1-\gamma(d))^{1-s}$, where $\gamma(d)$ is the probability of being in state 1, which is modelled as a logistic function of distance: $\gamma(d) = (1+\exp\{\alpha+\beta d\})^{-1}$. For example, the parameter values used in the simulation (Table 1) result in a probability of being in state 0 (CRW) of 0·95 at a distance of zero, 0·5 at a distance of 2500 m and 0·05 at a distance of 5000 m from the activity centre.

Table 1. Movement model parameter values used in the movement simulations. CRW refers to a correlated random walk and BRW to a biased random walk. Only the von Mises parameters are state dependent; 0^o indicates movement in the same direction, while ϕ_t represents a turning angle from the current location back towards the activity centre

Parameter	CRW (state $s = 0$)	BRW (state $s = 1$)
α	3	3
β	−0·0012	−0·0012
a	750	750
b	450	450
$\kappa(s)$	6	0·5
$\mu(s)$	0^o	ϕ_t

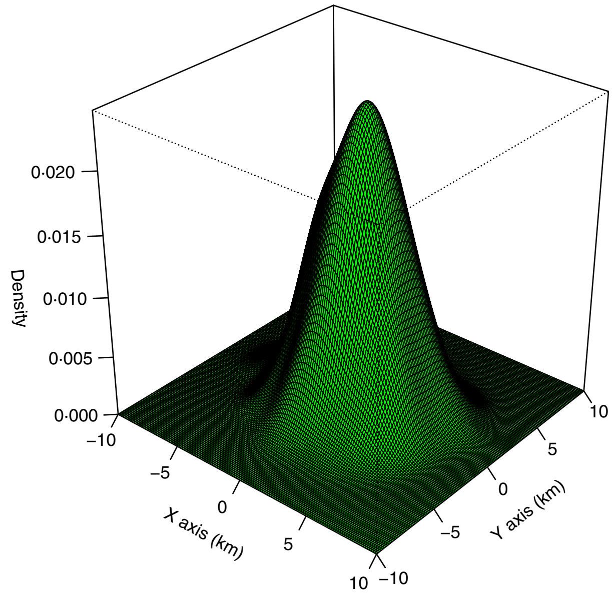

Fig. 2. Example of simulated movement for a 90-day period in hourly steps, showing the number of times each cell is visited in the period and smoothed with a nonparametric smoother.

The size of each movement step (l) is a draw from a gamma distribution with mean step length a and standard deviation b: $l \sim \text{Gamma}(a^2/b^2, b^2/a)$. The turning angle ($\phi$), given that the individual is in state s, is drawn from a von Mises distribution $\phi|s \sim \text{von Mises}(\mu(s), \kappa(s))$ where $\mu(s)$ is the mean and $\kappa(s)$ the concentration parameter. Values for $\kappa(s)$ close to zero generate something close to a uniform distribution on the circle, whereas larger values will place increasing mass around the mean value. Table 1 shows the movement model parameter values used in the movement simulations and, Fig. 2 shows a realization of the model over T = 2160 h (90 days). Because the objective is to generate correlated detection times rather than to make inferences about the underlying behaviour, a large standard deviation for step length was used to reflect movement of a range of behavioural states (resting, hunting, travelling, etc).

Results

BELIZE JAGUAR SURVEY

Females have very different home range sizes to males, so that modelling both sexes would require separate parameters for each sex. Because very few female jaguars were detected, this analysis only uses male detections. A total of 207 detections of 17 identifiable males were made, of which six males (35%) were detected at least twice in a day at the same detector. Not all detectors operated for the 90 days of the survey; therefore, we set the detection hazard for the detector to zero for all of the failed days in the case of the CT model, and removed the detector from occasions on which it was out of action in the case of the discrete-occasion model.

In addition to models with no covariates, models with a behavioural response in the form of separate g_0 and/or σ parameters before and after first detection were considered. This led to models with a behavioural response for g_0 but not σ being selected on the basis of AIC$_c$ (see Table 2). Estimates from a discrete-occasion model with T_s = 24 h are shown in Table 3, together with estimates from the comparable CT model. Variances were estimated using the inverse of the observed Fisher information matrix, and normality was assumed to estimate confidence intervals.

Table 2. Model selection summary for the Belize jaguar data. '(b)' indicates that a behavioural response was included. ΔAIC$_c$: difference in AIC$_c$ between the current and the best model (AIC$_c$ is Akaike information criterion corrected for small sample size); wt, Akaike weight; npar, number of estimated parameters

Model	ΔAIC$_c$	wt	npar
Discrete-occasion models			
D(.) g_0(.) σ(.)	1·29	0·28	3
D(.) g_0(b) σ(.)	0·00	0·53	4
D(.) g_0(.) σ(b)	3·83	0·08	4
D(.) g_0(b) σ(b)	3·04	0·12	5
Continuous-time models			
D(.) g_0(.) σ(.)	8·97	0·01	3
D(.) g_0(b) σ(.)	0·00	0·81	4
D(.) g_0(.) σ(b)	8·18	0·01	4
D(.) g_0(b) σ(b)	3·16	0·17	5

SIMULATION RESULTS

Independence simulation results

The estimated biases of estimators as a percentage of true parameter values (%Bias) are shown together with their standard errors for the three different detector spacings in Table 4. The percentage bias in density for the discrete-occasion models was particularly high for closely spaced traps, more so when many short occasions were used. The number of individuals detected per survey increased with detector spacing because greater spacing leads to a larger area being sampled.

With 1500 m detector spacing, 12% of individuals were detected at least twice a day at the same detector, on average. This reduced to 9% and 6% with spacing of 3000 m and 4500 m, respectively. These values are substantially lower than the 35% observed in the survey data.

Movement model simulation results

Table 5 summarizes the results from the movement simulations. The pattern of bias is similar to that from the independent simulations though the bias is worse when P_{GC} is high (compare results from Table 4 for 125%σ with the corresponding spacing in Table 5 when P_{GC} = 0·9).

Reducing P_{GC} in the movement simulation effectively thins the detection time process and consequently reduces temporal correlation. For spacing of 3000 m, when P_{GC} = 0·9, on average, 85% of individuals were detected at least twice in a day at the same detector, and this proportion drops to 52% when P_{GC} = 0·3. Results were similar for the larger detector spacing.

Table 3. Estimates from the selected SECR proximity model with $T_s = 24$ h and a continuous-time (CT) model fitted to the male jaguar data. Estimated density ($\hat{D}$) is individuals per 100 km^2; $\hat{g}_{00}$ and $\hat{g}_{01}$ are estimated detection function intercepts before and after initial detection, respectively; $\hat{\sigma}$ (in km) is estimated detection function scale parameter. The CT model used a hazard that is consistent with a half-normal detection function shape over an interval of 24 h

T_s	$\hat{D}$ (95% CI)	$\hat{g}_{00}$ (95% CI)	$\hat{g}_{01}$ (95% CI)	$\hat{\sigma}$ (95% CI)
24	3·6 (2·14 ; 6·05)	0·034 (0·016 ; 0·068)	0·067 (0·055 ; 0·094)	2·737 (2·419 ; 3·095)
CT	3·4 (2·02 ; 5·68)	0·028 (0·014 ; 0·055)	0·077 (0·061 ; 0·096)	2·942 (2·624 ; 3·299)

Table 4. % Bias and associated standard error of density and other estimators, from simulations with independent data, with discrete-occasion models with interval length T_s ranging from 6 to 120 h, and the corresponding continuous-time (CT) model. 'CT (t)' indicates that a CT model with detection hazard form that generates a half-normal detection shape over t hours was used. True density was four individuals per 100 km^2, $\sigma = 2400$ m, $g_0 = 0{\cdot}01$ for $T_s = 6$, $g_0 = 0{\cdot}05$ for $T_s = 24$, $g_0 = 0{\cdot}15$ for $T_s = 72$, $g_0 = 0{\cdot}25$ for $T_s = 120$. Twenty detectors spaced at 1500 m, 3000 m and 4500 m apart were used, and the survey duration was $T = 2160$ h. 'Detections' is mean number of detections per survey, 'Unique' is mean number of individuals detected per survey and 'Reps' is number of surveys that did not result in estimation error or warning messages (such estimates were excluded)

Detector spacing	T_s	%Bias D (SE)	%Bias g_0 (SE)	%Bias σ (SE)	Detections	Unique	Reps
62·5% σ (1500)	6	85·43 (2·51)	−41·13 (0·69)	−25·43 (0·44)	103·7	10·0	979
	CT (6)	8·35 (1·31)	−3·01 (0·75)	−2·28 (0·46)	103·8	9·9	1000
	24	69·35 (2·21)	−36·94 (0·73)	−21·62 (0·41)	130·6	10·6	988
	CT (24)	8·69 (1·16)	−4·10 (0·65)	−2·49 (0·38)	132·3	10·5	998
	72	36·15 (1·66)	−21·17 (0·77)	−13·49 (0·43)	129·6	10·4	995
	CT (72)	6·64 (1·19)	−3·40 (0·64)	−1·92 (0·41)	134·7	10·4	999
	120	21·75 (1·39)	−11·99 (0·75)	−8·01 (0·41)	130·0	10·5	998
	CT (120)	6·42 (1·15)	−3·55 (0·62)	−1·27 (0·40)	139·1	10·5	1000
125% σ (3000)	6	1·81 (0·81)	−2·97 (0·53)	−1·35 (0·25)	101·8	16·0	995
	CT (6)	−0·51 (0·79)	−0·01 (0·54)	0·10 (0·25)	102·0	16·0	1000
	24	0·01 (0·82)	−0·31 (0·44)	−0·68 (0·22)	128·1	16·7	991
	CT (24)	−0·95 (0·81)	0·61 (0·44)	−0·14 (0·22)	129·5	16·6	1000
	72	−0·84 (0·78)	0·42 (0·46)	−0·05 (0·23)	127·6	16·7	981
	CT (72)	−1·14 (0·77)	0·17 (0·44)	−0·06 (0·23)	132·4	16·6	1000
	120	−0·24 (0·81)	0·23 (0·43)	0·15 (0·22)	128·0	16·8	950
	CT (120)	−0·86 (0·80)	0·24 (0·40)	0·06 (0·21)	136·6	16·7	1000
187·5% σ (4500)	6	1·25 (0·67)	1·22 (0·52)	−0·02 (0·23)	105·2	24·6	994
	CT (6)	1·18 (0·67)	1·18 (0·51)	−0·02 (0·23)	105·4	24·6	1000
	24	0·89 (0·65)	0·74 (0·45)	−0·09 (0·20)	130·9	25·6	982
	CT (24)	0·84 (0·64)	0·84 (0·44)	−0·11 (0·20)	132·8	25·6	1000
	72	1·07 (0·68)	−0·02 (0·45)	0·29 (0·19)	130·9	25·8	924
	CT (72)	0·89 (0·65)	0·22 (0·41)	0·12 (0·18)	136·3	25·7	1000
	120	1·51 (0·69)	1·29 (0·46)	−0·20 (0·21)	131·6	25·9	865
	CT (120)	1·15 (0·64)	1·16 (0·41)	−0·25 (0·19)	141·0	25·8	1000

Discussion

BELIZE JAGUAR SURVEY RESULTS

The percentage of individuals that are detected at least twice in a day at the same camera gives a rough indication of spatio-temporal clustering. The differences between the real data (35%) and the simulated movement data (52% and 85%) suggest that the Belize jaguar data are closer to satisfying the independence assumptions of the continuous-time (CT) model than are either of the movement simulation scenarios. Although the assumption of independent activity centres is not realistic for territorial species, no SECR model yet exists that accommodates the 'repulsive' effect that activity centres of territorial species exert on one another's activity centres, and modelling this is challenging. Efford, Borchers & Byrom (2009a) found SECR estimators of density to be robust to violation of the independent activity centre distribution assumption in the form of clustering (overdispersion), and they may also be robust to violation in the form of underdispersion.

As no bait or lure was used, it is unlikely that the behavioural response in g_0 is a true trap-happiness effect. The camera stations are located on trails resulting in a higher probability of detecting the individuals that habitually use those trails; hence, the behavioural response parameter may be acting as a proxy for individual heterogeneity (Soisalo & Cavalcanti 2006, Royle *et al.* 2009).

ESTIMATOR PROPERTIES

Like Efford, Dawson & Borchers (2009b), we found that a SECR count model estimator with a single sampling interval (equivalent to our CT estimator with constant hazards) can give precise and unbiased density estimates. In addition, we

Table 5. % Bias and associated standard error of density estimators is shown for two levels of P_{GC} and for two different detector spacings (in metres), using half- normal detection functions, from simulations with an animal movement model, with occasion lengths ranging from T_s=6 to T_s=120 h spanning a survey duration of T=2160 h. Simulated survey design is as per Table 4. P_{GC} is the probability that an individual is detected when it is in a 250m×250m cell containing a camera. 'Detections' is mean number of detections per survey, 'Unique' is mean number of individuals detected per survey and 'Reps' is number of surveys that did not result in estimation error or warning messages (such estimates were excluded). The continuous-time (CT) model uses a hazard that is consistent with a half-normal detection function over an interval size of 24 h

Detector spacing	T_s	%Bias D (SE)	Detections	Unique	Reps
3000 m	P_{GC} = 0·9				
	6	35·33 (1·21)	367·17	19·81	990
	24	13·76 (0·90)	332·07	19·77	997
	72	3·82 (0·76)	303·64	19·78	995
	120	0·82 (0·81)	283·49	19·77	865
	CT (24)	−4·33 (0·71)	468·17	19·77	1000
	P_{GC} = 0·3				
	6	8·00 (0·86)	143·20	17·24	992
	24	2·48 (0·81)	138·09	17·25	998
	72	1·49 (0·81)	133·16	17·25	995
	120	1·50 (0·81)	129·35	17·26	990
	CT (24)	0·38 (0·85)	153·63	17·28	898
4500 m	P_{GC} = 0·9				
	6	5·39 (0·64)	361·73	29·15	997
	24	−0·03 (0·60)	327·11	29·12	976
	72	−0·12 (0·60)	299·25	29·16	987
	120	−0·98 (0·62)	278·07	28·93	853
	CT (24)	−4·45 (0·57)	461·89	29·16	1000
	P_{GC} = 0·3				
	6	−0·91 (0·64)	142·02	25·56	1000
	24	−0·26 (0·65)	137·00	25·65	960
	72	−0·47 (0·64)	131·85	25·56	988
	120	−0·47 (0·65)	128·05	25·56	969
	CT (24)	−1·83 (0·64)	153·64	25·56	986

show that when there is inadequate spacing between detectors, the estimator from a count model with a single sampling interval performs substantially better than binary model estimators in which the interval is divided into multiple occasions.

Information loss with binary data

In general, information is lost if exact detection times are discarded, although this is not the case if the hazard of detection is constant and count data are retained. There is a loss if count data are reduced to binary data although Efford, Dawson & Borchers (2009b) found the loss to be small in the scenarios they considered. Similarly, we found little difference between the performance of binary discrete-occasion estimators and CT estimators with constant detection hazard when using detector spacings of 1·25σ and 1·88σ. However, when detector spacing was reduced to 0·625σ, the CT estimator performed substantially better than the binary discrete-occasion estimators.

To understand this behaviour, we investigated simulated data sets in which no count was greater than 1 in any interval. The binary and CT estimators produced different estimates in these cases, although they operate on identical data. This is because the binary likelihood models the probability of at least one detection in an interval, whereas the CT likelihood models the probability of exactly one detection, and the latter is more informative about individual activity centre location. For example, the fact that an individual was detected exactly once by the detector suggests that the centre was not very close to the detector (if it was, more than one detection would be likely), whereas the fact that an individual was detected *at least* once includes the possibility that it was detected many times, in which case, the centre could be very close to the detector. Consequently, the binary data model tends to 'attract' centres to detectors, which can lead to negatively biased effective sampling area estimates and positively biased density estimates (Fig. 3). This effect is more pronounced for activity centres that are on the edge of the detector array, which explains why the bias is worse for smaller detector arrays. When an activity centre is surrounded by detectors, the presence of other detectors limits the extent to which the binary model can 'attract' the centre to any detector (Fig. 3).

Data aggregation

Except in some special cases, data aggregation involves information loss. Aggregation can be useful when modelling unaggregated data is difficult, but aggregation without good reason is not a good practice. When SECR data are recorded in continuous time, we are not aware of any reason not to use a CT model if detections are independent events. If the detection hazard is constant, the CT model is identical to a count model spanning a single occasion, but the CT formulation can be extended to incorporate time-varying hazards within occasion and therefore enables extensions that are not available without a CT formulation. When detection hazards depend on observable time-varying covariates (time of day, temperature or some other time-varying environmental variables for example), there may be advantage in modelling this using exact detection times even if there is no inherent interest in the nature of the varying hazard, and there is certainly benefit in modelling the effect of time-varying covariates on detection hazard when there is interest in how the hazard function depends on such covariates.

When there is spatiotemporal correlation in detections (e.g. due to movement) and a design with adequate detector spacing is used, there may be merit in aggregating data across time and using binary discrete-occasion models with appropriate occasion lengths. However, our simulations suggest that (a) the bias of binary discrete-occasion density estimators can be quite sensitive to the length of occasions, particularly when detectors are too close together, and that (b) the CT point estimator of density is moderately robust to inadequate detector spacing and levels of spatiotemporal correlation that are substantially higher than is apparent in the jaguar field data.

We have not in this paper considered the adequacy of interval estimators based on the observed Fisher information matrix. If detections of the same animal are not independent across detector locations and time (due to correlated animal

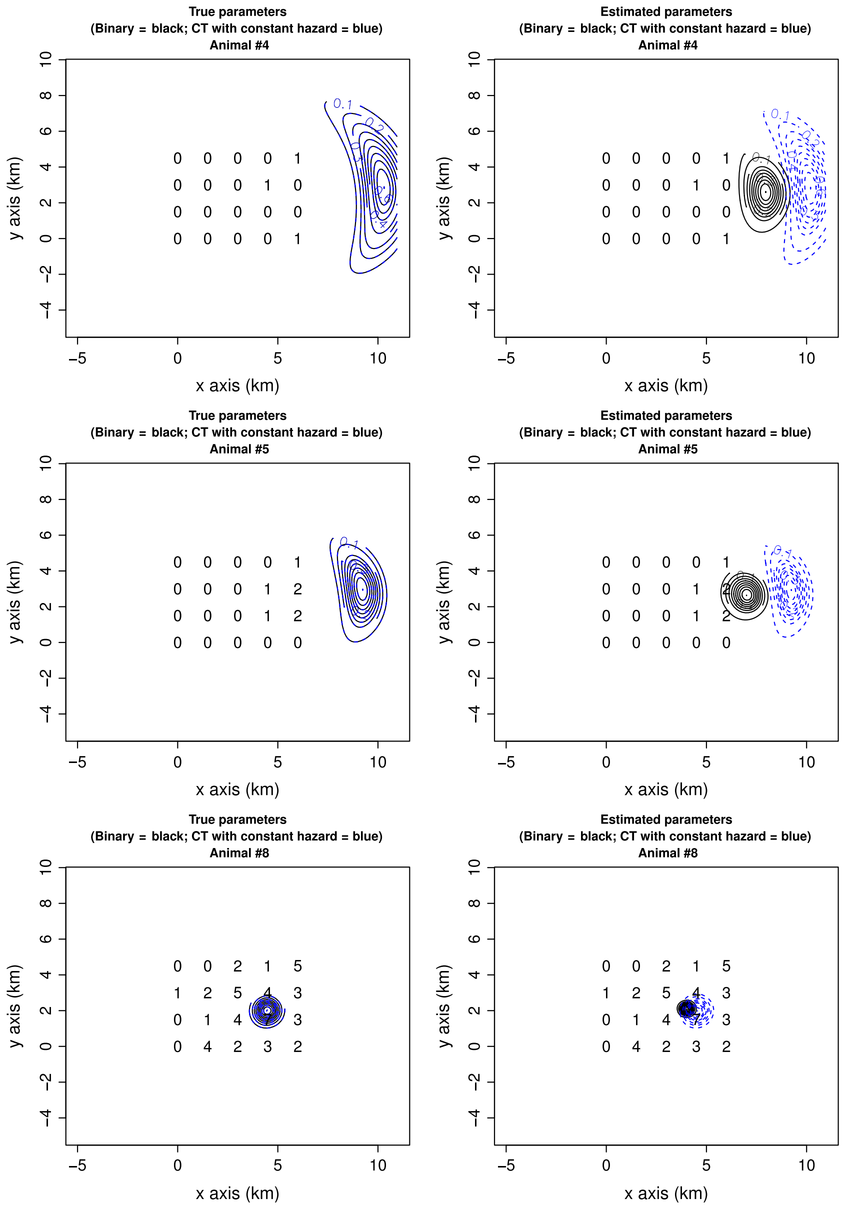

Fig. 3. Probability contours for the location of activity centres, given the spatial capture histories for selected individuals from a simulated data set, generated from both a binary likelihood and a continuous-time (CT) likelihood with a constant hazard. The left panels show the contours when the true detection function parameters are used for both models, whereas the right panels do the same using the estimated detection function parameters. Numbers show locations and detection frequencies for each individual on each detector.

movement, for example), variance estimates may be biased and confidence interval estimates may have incorrect coverage probability. One way of dealing with this would be to consider the likelihood eqn (4) to be an approximation to the correct likelihood and use a version the ABC bootstrap method of Efron (1987) that incorporates an animal movement model (as per our movement simulation model, for example), to obtain corrected point and interval estimates.

Conclusion

We have shown that CT SECR methods, unlike discrete-occasion methods, fully use the available data when detections are made continuously, and they have a number of other advantages over methods that aggregate data into discrete occasions. We therefore recommend that CT methods be considered when detection times are available, and we recommend collecting detection times whenever possible.

Although CT SECR methods are not yet as well developed as discrete-occasion methods (e.g. models incorporating individual covariates or unobserved individual-level heterogeneity remain to be developed), this is a temporary obstacle that will soon be overcome. A more substantial obstacle in the case of camera-trap studies may be the development of CT models that incorporate spatiotemporal dependence in detections due to individual movement. This seems challenging, but we see potential for CT models being combined with telemetry-based animal movement models to provide a richer inference framework than is currently available.

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Data accessibility

Data deposited in the Dryad repository: http://datadryad.org/resource/doi:10.5061/dryad.mg5kv

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Continuous-time proximity likelihood derivation.

Appendix S2. Discrete-occasion proximity likelihood derivation.

Appendix S3. Lack of sufficiency of Ω.

A Continuous-time proximity likelihood derivation

Consider a SECR survey of duration T with continuously-sampling proximity detectors and suppose that the ith detected individual is detected by detector k at times $\boldsymbol{t}_{ik} = (t_{ik1}, \ldots, t_{ik\omega_{ik}})$, where ω_{ik} is the number of times individual i is detected by detector k. Assuming that, conditional on its activity centre location ($\boldsymbol{x}_i$), the times of detections are independent, we can model the detection times as a nonhomogeneous Poisson process with pdf $f_k(\boldsymbol{t}_{ik}|\boldsymbol{x}_i;\boldsymbol{\theta}) = S_k(T,\boldsymbol{x}_i;\boldsymbol{\theta}) \prod_{r=1}^{\omega_{ik}} h_k(t_{ikr},\boldsymbol{x}_i;\boldsymbol{\theta})$, where $h_k(t,\boldsymbol{x}_i;\boldsymbol{\theta})$ is the non-homogeneous event intensity or hazard at time t, $\boldsymbol{\theta}$ is an unknown parameter, and $S_k(T,\boldsymbol{x}_i;\boldsymbol{\theta}) = e^{-\int_0^T h_k(u,\boldsymbol{x}_i;\boldsymbol{\theta})\,du}$ is the "survivor function" for detector k (the probability of individual i not being detected on the detector by time T).

We need to define a few more things for convenient expression of the likelihood function. Noting that $\omega_{i\cdot} = \sum_{k=1}^{K} \omega_{ik}$ is the individual's overall detection frequency and the event $\omega_{i\cdot}{>}0$ indicates detection by some detector, we let $\boldsymbol{\omega}_{\cdot} = \{\omega_{i\cdot}\}$ $(i = 1, \ldots, n)$ and let $\boldsymbol{\omega}_{\cdot}{>}0$ indicate detection by some detector of individuals $i = 1, \ldots, n$. $\boldsymbol{t} = \{\boldsymbol{t}_{ik}\}$ $(i = 1, \ldots, n; k = 1, \ldots, K)$ denotes the set of all detection times. We also note that the combined detection hazard over all detectors at time t is $h_{\cdot}(t,\boldsymbol{x}_i;\boldsymbol{\theta}) = \sum_{k=1}^{K} h_k(t,\boldsymbol{x}_i;\boldsymbol{\theta})$ and the probability of detection in $(0,T)$ is $p_{\cdot}(\boldsymbol{x}_i;\boldsymbol{\theta}) = p(\omega_{i\cdot}{>}0|\boldsymbol{x}_i;\boldsymbol{\theta}) = 1 - S_{\cdot}(T,\boldsymbol{x}_i;\boldsymbol{\theta})$, where $S_{\cdot}(T,\boldsymbol{x}_i;\boldsymbol{\theta}) = \prod_k S_k(T,\boldsymbol{x}_i;\boldsymbol{\theta}) = \exp^{-\int_0^T h_{\cdot}(u,\boldsymbol{x}_i;\boldsymbol{\theta})du}$.

This likelihood derivation is very similar to that in Borchers & Efford (2008) and Equations (10) and (11) below are also derived in that paper.

The reader may find it useful to refer to Borchers & Efford (2008) when reading this derivation. We assume that, conditional on activity centre locations of detected individuals ($\boldsymbol{X} = (\boldsymbol{x}_1, \ldots, \boldsymbol{x}_n)$), the times and locations of detections of individuals are independent, and that individuals are detected independently. Suppose also that activity centres are realisations of a non-homogeneous Poisson process (NHPP) in the plane, with intensity $D(\boldsymbol{x}; \boldsymbol{\phi})$ at $\boldsymbol{x}$, and that $\boldsymbol{\phi}$ is an unknown parameter vector. Then the likelihood for the parameters $\boldsymbol{\phi}$ of the NHPP governing activity centre locations and the parameters $\boldsymbol{\theta}$ of the detection process, is obtained from the pdf of the number of detected individuals n ($P(n|\boldsymbol{\phi}, \boldsymbol{\theta})$), the pdf of the activity centre locations given detection ($f_X(\boldsymbol{X}|\boldsymbol{\omega}.{>}0; \boldsymbol{\phi}, \boldsymbol{\theta})$), and the pdf of detection times $\boldsymbol{t}$, given $\boldsymbol{X}$ and detection ($f_t(\boldsymbol{t}|\boldsymbol{X}, \boldsymbol{\omega}. > 0; \boldsymbol{\theta})$), after integrating over the unknown locations $\boldsymbol{X}$, as follows:

$$\begin{aligned} L(\boldsymbol{\phi}, \boldsymbol{\theta}|n, \boldsymbol{t}) &= P(n|\boldsymbol{\phi}, \boldsymbol{\theta}) f_t(\boldsymbol{t}|n, \boldsymbol{\theta}, \boldsymbol{\phi}) \\ &= P(n|\boldsymbol{\phi}, \boldsymbol{\theta}) \int_A f_X(\boldsymbol{X}|\boldsymbol{\omega}.{>}0; \boldsymbol{\phi}, \boldsymbol{\theta}) f_t(\boldsymbol{t}|\boldsymbol{X}, \boldsymbol{\omega}.{>}0; \boldsymbol{\theta})\, d\boldsymbol{X} \end{aligned} \tag{9}$$

where

$$P(n|\boldsymbol{\phi}, \boldsymbol{\theta}) = \frac{\lambda(\boldsymbol{\theta}, \boldsymbol{\phi})^n e^{-\lambda(\boldsymbol{\theta}, \boldsymbol{\phi})}}{n!} \tag{10}$$

with $\lambda(\boldsymbol{\theta}, \boldsymbol{\phi}) = \int_A D(\boldsymbol{x}; \boldsymbol{\phi}) p.(\boldsymbol{x}; \boldsymbol{\theta})\, d\boldsymbol{x}$ (where the integral is over all points $\boldsymbol{x}$ in the area A in which activity centres occur), and

$$f_X(\boldsymbol{X}|\boldsymbol{\omega}.{>}0; \boldsymbol{\phi}, \boldsymbol{\theta}) = \prod_{i=1}^{n} \frac{D(\boldsymbol{x_i}; \boldsymbol{\phi}) p.(\boldsymbol{x}_i; \boldsymbol{\theta})}{\lambda(\boldsymbol{\theta}, \boldsymbol{\phi})} \tag{11}$$

$$
\begin{aligned}
f_t(\boldsymbol{t}|\boldsymbol{X},\boldsymbol{\omega}.{>}0;\boldsymbol{\theta}) &= \prod_{i=1}^{n} \frac{\prod_{k=1}^{K} f_k(\boldsymbol{t}_{ik}|\boldsymbol{x}_i;\boldsymbol{\theta})}{p.(\boldsymbol{x}_i;\boldsymbol{\theta})} \\
&= \prod_{i=1}^{n} \frac{1}{p.(\boldsymbol{x}_i;\boldsymbol{\theta})} \prod_{k=1}^{K} S_k(T,\boldsymbol{x}_i;\boldsymbol{\theta}) \prod_{r=1}^{\omega_{ik}} h_k(t_{ikr},\boldsymbol{x}_i;\boldsymbol{\theta}).
\end{aligned} \tag{12}
$$

If we substitute Equations (11) and (12) into the integral in Equation (9), note that $\prod_k S_k(T,\boldsymbol{x}_i;\boldsymbol{\theta}) = \prod_k e^{-\int_0^T h_k(u,\boldsymbol{x}_i;\boldsymbol{\theta})\,du} = e^{-\int_0^T h.(u,\boldsymbol{x}_i;\boldsymbol{\theta})\,du} = S.(T,\boldsymbol{x}_i;\boldsymbol{\theta})$ and cancel $p.(\boldsymbol{x}_i;\boldsymbol{\theta})$ we get

$$
\begin{aligned}
f_t(\boldsymbol{t}|n,\boldsymbol{\theta},\boldsymbol{\phi}) &= \int_A \prod_{i=1}^{n} \frac{D(\boldsymbol{x_i};\boldsymbol{\phi})}{\lambda(\boldsymbol{\theta},\boldsymbol{\phi})} S.(T,\boldsymbol{x}_i;\boldsymbol{\theta}) \prod_{k=1}^{K} \prod_{r=1}^{\omega_{ik}} h_k(t_{ikr},\boldsymbol{x}_i;\boldsymbol{\theta})\; d\boldsymbol{X} \\
&= \prod_{i=1}^{n} \int_A \frac{D(\boldsymbol{x_i};\boldsymbol{\phi})}{\lambda(\boldsymbol{\theta},\boldsymbol{\phi})} S.(T,\boldsymbol{x}_i;\boldsymbol{\theta}) \prod_{k=1}^{K} \prod_{r=1}^{\omega_{ik}} h_k(t_{ikr},\boldsymbol{x}_i;\boldsymbol{\theta})\; d\boldsymbol{X}.
\end{aligned}
$$

(We can take the product over n outside the integral because the n $\boldsymbol{x}_i$s are independent.) Substituting this in Equation (9) and cancelling $\lambda(\boldsymbol{\theta},\boldsymbol{\phi})$ gives Equation (4).

B Discrete-occasion proximity likelihood derivation

The likelihood for $\boldsymbol{\phi}$ and $\boldsymbol{\theta}$ for the discrete-occasion case in which there are S occasions can be obtained in a similar way to that in which the continuous-time (CT) likelihood was obtained, but replacing the pdf of detection times, given detection: $f_t(\boldsymbol{t}|\boldsymbol{X},\boldsymbol{\omega}.{>}0;\boldsymbol{\theta})$ with the pdf of detection histories, given detection, $P_\Omega(\boldsymbol{\Omega}|\boldsymbol{X},\boldsymbol{\omega}.{>}0;\boldsymbol{\theta})$, where $\boldsymbol{\Omega} = \{\boldsymbol{\omega}_{ik}\}$ $(i = 1,\ldots,n; k = 1,\ldots,K)$ and $\boldsymbol{\omega}_{ik} = (\omega_{ik1},\ldots,\omega_{ikS})$ is individual i's detection history on detector k

over the S occasions:

$$L(\boldsymbol{\phi},\boldsymbol{\theta}|n,\boldsymbol{\omega}_{ik}) = P(n|\boldsymbol{\phi},\boldsymbol{\theta}) \int_A f_X(\boldsymbol{X}|\boldsymbol{\omega}_{\cdot}{>}0;\boldsymbol{\phi},\boldsymbol{\theta}) P_\Omega(\boldsymbol{\Omega}|\boldsymbol{X},\boldsymbol{\omega}_{\cdot}{>}0;\boldsymbol{\theta})\, d\boldsymbol{X}. \tag{13}$$

This is the likelihood obtained by Borchers & Efford (2008).

In 13 above $P_\Omega(\boldsymbol{\Omega}|\boldsymbol{X};\boldsymbol{\theta})$ is conditioned on being caught ($\boldsymbol{\omega}_{\cdot}{>}0$) and leads to another term entering the likelihood $p_{\cdot}(\boldsymbol{x},\boldsymbol{\theta})^{-1}$. Two forms of $P_\Omega(\boldsymbol{\Omega}|\boldsymbol{X};\boldsymbol{\theta})$ have been proposed for proximity detectors: one in which ω_{iks} is binary, indicating detection or not of individual i on detector k on occasion s, and one in which ω_{iks} is a count of the number of times individual i was detected by detector k on occasion s. Both have the form

$$P_\Omega(\boldsymbol{\Omega}|\boldsymbol{X};\boldsymbol{\theta}) \;=\; \prod_{i=1}^{n}\prod_{s=1}^{S}\prod_{k=1}^{K} P(\omega_{iks}|\boldsymbol{x}_i;\boldsymbol{\theta}). \tag{14}$$

The two forms of discrete-occasion SECR model differ in the form they use for $P(\omega_{iks}|\boldsymbol{x}_i;\boldsymbol{\theta})$. We show that when a CT detection process is discretised into discrete occasions this gives rise to a Bernoulli model in the case of binary data, and to binomial and Poisson SECR models in the case of count data. (Binomial and Poisson models have been proposed for the case in which there is only one occasion ($S = 1$) but are easily extended to multi-occasion scenarios, as we show below.) To do this, we divide the time interval $(0,T)$ into S subintervals with interval s running from t_{s-1} to t_s, of length $T_s = t_s - t_{s-1}$, and with $t_0 = 0$.

With a CT model, the probability of detecting individual i at least once in detector k in this interval is $p_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta}) = 1 - e^{-H_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})}$, where

$H_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta}) = \int_{t_{s-1}}^{t_s} h_k(u,\boldsymbol{x}_i;\boldsymbol{\theta})du$. Specifying a model for $p_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})$ implies a model for $h_k(t,\boldsymbol{x}_i;\boldsymbol{\theta})$, although not a unique one. The mean value of the detection hazard in interval s must be $\bar{h}_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta}) = -\log\{1 - p_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})\}/T_s$ and any $h_k(t,\boldsymbol{x}_i;\boldsymbol{\theta})$ with this mean is consistent with $p_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})$. When the hazard is constant in the interval there is a one-to-one relationship between the detection hazard and the detection probability: $h_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta}) = -\log\{1 - p_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})\}/T_s$.

Bernoulli model This is obtained from a continuous-time model as $P_{Bern}(\omega_{iks}|\boldsymbol{x}_i;\boldsymbol{\theta}) = p_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})^{\omega_{iks}}\{1 - p_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})\}^{1-\omega_{iks}}$, with $p_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta}) = 1 - e^{-H_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})}$ and binary ω_{iks}.

Binomial count model Efford, Dawson & Borchers (2009b) proposed this for the case in which the S original intervals are collapsed into $S^*(< S)$ intervals and ω_{iks^*} is the count in the new interval s^*, which comprises N_{s^*} adjacent original intervals. In this case $P_{Binom}(\omega_{iks^*}|\boldsymbol{x}_i;\boldsymbol{\theta}) = \binom{N_{s^*}}{\omega_{iks^*}} p_{ks^*}(\boldsymbol{x}_i;\boldsymbol{\theta})^{\omega_{iks^*}}\{1 - p_{ks^*}(\boldsymbol{x}_i;\boldsymbol{\theta})\}^{1-\omega}$ where $p_{ks^*}(\boldsymbol{x}_i;\boldsymbol{\theta}) = 1 - e^{-H_{ks^*}(\boldsymbol{x}_i;\boldsymbol{\theta})}$, and $H_{ks^*}(\boldsymbol{x}_i;\boldsymbol{\theta}) = \sum_{s=1}^{N_{s^*}} H_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})$.

Poisson count model A NHPP with intensity $h_k(t,\boldsymbol{x}_i;\boldsymbol{\theta})$ at time t gives rise to an event count (ω_{iks}) in a time interval (t_{s-1}, t_s) that has the Poisson pmf $P_P(\omega_{iks}|\boldsymbol{x}_i;\boldsymbol{\theta}) = H_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})^{\omega_{iks}} \exp^{\{-H_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})\}}/(\omega_{iks}!)$, where $H_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta}) = \int_{t_{s-1}}^{t_s} h_k(u,\boldsymbol{x}_i;\boldsymbol{\theta})du$ and event counts in non-overlapping intervals are independent.

C Lack of sufficiency of $\boldsymbol{\Omega}$

To investigate the sufficiency of $\boldsymbol{\Omega}$ for the unknown parameters $\boldsymbol{\theta}$ and $\boldsymbol{\phi}$, we consider the term $f_k(\boldsymbol{t}_{ik}|\boldsymbol{x}_i;\boldsymbol{\theta})$.

The conditional distribution of detection times, $\boldsymbol{t}_{ik}^{(s)} = t_{ik1}^{(s)}, \ldots, t_{ik\omega_{iks}}^{(s)}$, in interval s, given that ω_{iks} detections occurred in the interval is as follows:

$$f_{t_s}(\boldsymbol{t}_{ik}^{(s)}|\omega_{iks};\boldsymbol{\theta}) = \omega_{iks}! \prod_{r=1}^{\omega_{iks}} \frac{h_k(t_{ikr},\boldsymbol{x}_i;\boldsymbol{\theta})}{H_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})}. \tag{15}$$

We can now factorise $f_k(\boldsymbol{t}_{ik}|\boldsymbol{x}_i;\boldsymbol{\theta})$ into the pmf for the count ω_{iks} in interval s and the pdf for the detection times, given the count, as follows:

$$\begin{aligned} f_k(\boldsymbol{t}_{ik}|\boldsymbol{x}_i;\boldsymbol{\theta}) &= \prod_{s=1}^{S} \frac{H_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})^{\omega_{iks}} \exp^{\{-H_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})\}}}{(\omega_{iks}!)} \left[\omega_{iks}! \prod_{r=1}^{\omega_{iks}} \frac{h_k(t_{ikr},\boldsymbol{x}_i;\boldsymbol{\theta})}{H_{ks}(\boldsymbol{x}_i;\boldsymbol{\theta})}\right] \\ &= \prod_{s=1}^{S} P_P(\omega_{iks}|\boldsymbol{x}_i;\boldsymbol{\theta}) f_{t_s}(\boldsymbol{t}_{ik}^{(s)}|\omega_{iks};\boldsymbol{\theta}) \end{aligned} \tag{16}$$

The likelihood Equation (4) can then be written as

$$L(\boldsymbol{\phi},\boldsymbol{\theta}|n,\boldsymbol{t}) = \frac{e^{-\lambda(\boldsymbol{\phi},\boldsymbol{\theta})}}{n!} \prod_{i=1}^{n} \int_A D(\boldsymbol{x}_i;\boldsymbol{\phi}) \prod_{k=1}^{K} \prod_{s=1}^{S} P_P(\omega_{iks}|\boldsymbol{x}_i;\boldsymbol{\theta}) f_{t_s}(\boldsymbol{t}_{ik}^{(s)}|\omega_{iks};\boldsymbol{\theta})\, d\boldsymbol{x} \tag{17}$$

The likelihood for the Poisson count model proposed by Efford, Dawson & Borchers (2009b) is this likelihood with a single occasion ($S = 1$) and without $f_{t_s}(\boldsymbol{t}_{ik}^{(s)}|\omega_{iks};\boldsymbol{\theta})$). It ignores the times of detection and because $f_{t_s}(\boldsymbol{t}_{ik}^{(s)}|\omega_{iks};\boldsymbol{\theta})$ involves $\boldsymbol{\theta}$, the detection frequencies alone (without the times of detection) are not in general sufficient for $\boldsymbol{\theta}$. And because $\boldsymbol{\phi}$ occurs in a product inside the integral, we can't factorise the likelihood into a component with $\boldsymbol{\phi}$ and without $\boldsymbol{t}_{ik}^{(s)}$, so that (by the Fisher-Neyman Factorization Theorem) $\boldsymbol{\Omega}$ is neither sufficient for $\boldsymbol{\theta}$ nor $\boldsymbol{\phi}$. Finally, because neither the binomial nor the Bernoulli models involve the detection times, $\boldsymbol{\Omega}$ is not sufficient for $\boldsymbol{\theta}$ and $\boldsymbol{\phi}$ with any of these models either.

There are two notable exceptions. The first is when $h_k(t, \boldsymbol{x}_i; \boldsymbol{\theta})$ is constant within intervals. In this case $f_{t_s}(\boldsymbol{t}_{ik}^{(s)}|\omega_{iks}; \boldsymbol{\theta}) = \omega_{iks}!/T_s^{\omega_{iks}}$, which does not involve $\boldsymbol{\theta}$ (or the detection times) and so counts with the Poisson model are sufficient for $\boldsymbol{\theta}$ and $\boldsymbol{\phi}$. Note that in this case, the multi-occasion ($S > 1$) likelihood is identical to a single-occasion likelihood with occasion duration $T = \sum_{s=1}^{S} T_s$ (the only difference being the multiplicative constant $\omega_{iks}!/T_s^{\omega_{iks}}$). A consequence of this is that when detection hazards do not depend on time, the notion of occasion is redundant when using a Poisson count model – since the likelihood is identical whether or not it involves occasions.

The second is when density is constant, i.e. $D(\boldsymbol{x}; \boldsymbol{\phi}) = D$. In this case D can be factorised out of the integral and n is conditionally sufficient for $\boldsymbol{\phi}$, given $\boldsymbol{\theta}$.