Using Camera Traps to Estimate Medium and Large Mammal Density: Comparison of Methods and Recommendations for Wildlife Managers

4 authors:

Jamie Clarke
University of Victoria
1 PUBLICATION   **0** CITATIONS

SEE PROFILE

Cole Burton
University of British Columbia
107 PUBLICATIONS   **5,234** CITATIONS

SEE PROFILE

Holger Bohm
Ministry of Forests
6 PUBLICATIONS   **158** CITATIONS

SEE PROFILE

Alexia Constantinou
British Columbia Institute of Technology
3 PUBLICATIONS   **5** CITATIONS

SEE PROFILE

Using Camera Traps to Estimate Medium and Large Mammal Density: Comparison of Methods and Recommendations for Wildlife Managers

Prepared by

Jamie Clarke, Wildlife Data Coordinator – WildCAM, BC Parks Foundation

In collaboration with

Holger Bohm, Provincial Ungulate Specialist – British Columbia Ministry of Forests

Dr. Cole Burton, Principal Investigator – Wildlife Coexistence Lab, University of British Columbia

Alexia Constantinou, Program Coordinator – WildCAM, BC Parks Foundation

February 17, 2023

WildCAM (Wildlife Cameras for Adaptive Management) is a Western Canadian network of camera trappers. The goal of the program is to support effective wildlife management by encouraging coordination in camera trap surveys and data synthesis. It is a grassroots network driven by the needs and desires of its users, with an eye toward tackling large-scale challenges and questions too difficult for individual projects to address. WildCAM is a community of practice that creates and shares knowledge within the scope of the network.

WildCAM is co-chaired by Dr. Cole Burton, Wildlife Coexistence Lab, University of British Columbia, and Dr. Jason Fisher, Applied Conservation Macro Ecology Lab, University of Victoria. It is administered by the BC Parks Foundation in conjunction with the Wildlife Coexistence Lab, and supported by the Government of British Columbia through the Together for Wildlife program and by the Canada Research Chairs program.

To find out more, visit our website: www.wildcams.ca.

To become a member and/or add your camera trap project to the WildCAM database, visit: https://wildcams.ca/join/?register=1.

To find out more about the BC Parks Foundation, visit: https://bcparksfoundation.ca/.

Table of Contents

1. Introduction

1.1 Density Estimation for Wildlife Conservation and Management

Accurate estimates of wildlife population metrics are critical for successful management (Rich et al. 2014). Measures of a population's size, composition, and distribution – and how they change over time – help guide conservation actions (Rönnegård et al. 2008), such as protecting threatened species (Mace et al. 2008), implementing recreation closures (Simpson and Terry 2000, https://www2.gov.bc.ca/gov/content/sports-culture/recreation/motor-vehicle-prohibitions/snowmobiling-in-bc/snowmobile-closures), and setting hunter harvest limits (Government of BC 2020). Such information can also be used to forecast population trends into the future, as wildlife face the compounding pressures of climate and landscape change (Stewart 2022).

Estimates of population density are of particular importance for conservation and management (Williams et al. 2002). Density is a measure of abundance (i.e., number of individuals) per unit area (e.g., animals/km^2; Becker et al. 2022, Green et al. 2020). It is often considered the "gold standard" of population metrics, as standardization across a unit of area allows unbiased comparison across study sites, periods, and species (Green et al. 2020, Morin et al. 2022, Sollmann 2018). For density estimates to be of ecological relevance and of conservation use, however, they must be accurate and precise, and produced at regular intervals (Burgar et al. 2018, Jiménez et al. 2017). Robust estimates of density are crucial not only to the management of wildlife, but also to building public trust and support – especially for controversial management decisions (e.g., culling or recreation closures; Jiménez et al. 2017).

1.2 Provincial Standards for Density Estimation

1.2.1 Summary of Provincial Standards

The province of British Columbia (BC), Canada, has standard protocols for measuring medium- and large-bodied mammal population densities. They are described in the

following documents – BC Ministry of Environment, Lands and Parks (1998a-c), BC Ministry of Sustainable Resource Management (2002) – and are summarized below.

Note the difference between a survey tool and a research method: a survey tool is a means of gathering information for statistical analysis; a research method is a means of analyzing data to produce a measurement or estimate.

Table 1. Summary table of BC's standard protocols for measuring population densities of medium and large mammals.

PROTOCOL NAME	SPECIES OR SPECIES GROUP	SURVEY TOOL	RESEARCH METHOD	ADVANTAGES	CHALLENGES
aerial survey	ungulates	helicopter or fixed-wing airplane	minimum count (sometimes adjusted for sightability) or Gassaway stratified	• access to remote and/or treacherous terrain • extensive spatial coverage • relatively short field efforts	• infrequent surveys (limited spatial and temporal coverage) • risk of injury and death to observers (Bruns 2019, Sasse 2003) • disturbance to wildlife (e.g., Côté et al. 2013, Crupi et al. 2020, Frid 2003) • sightability issues (e.g., limited to relatively open habitats; BC Ministry of Sustainable Resource Management 2002, Ransom 2012) • high costs (Bohm, personal communication) • single-species effort • environmental impacts of fuel (BC Ministry of Sustainable Resource Management 2002, US Energy Information Administration 2021)
snow track survey	wolves	helicopter	minimum count	• same as aerial surveys • produce accurate wolf density estimates compared to telemetry studies (Hayes et al. 1991)	• same as aerial surveys • limited to winter season
track probability sampling	cougars	helicopter	minimum count	• same as aerial surveys	• same as aerial surveys • surveys should be flown within two days of moderate snowfall
telemetry	most carnivores	live trapping, GPS/radio collars	population size and extent of home ranges (see McLellan 1998 for details)	• provides additional data on focal species biology (e.g., survival, reproduction, space use; BC Ministry of Environment, Lands and Parks 1998c, Johansson et al. 2022)	• should only be used for long-term, intensive research projects requiring a large sample of collared animals (BC Ministry of Environment, Lands and Parks 1998a) • all individuals in a population must be captured • invasive • high costs • labour-intensive • covers small sampling areas (BC Ministry of Environment, Lands and Parks 1998a, b) • for elusive species: prone to small sample sizes (BC Ministry of Environment, Lands and Parks 1998a, b)
capture-mark-resight	bears	helicopter or fixed-wing airplane, live trapping, GPS/radio collars	capture-mark-resight	• definition of survey area (Miller et al. 1997) • applicable to open populations (BC Ministry of Environment, Lands and Parks 1998a, Miller et al. 1997)	• same as aerial surveys • outdated (with advent of spatial mark-resight models) • poor applicability to low-density populations (Miller 1990) • high costs
DNA mark-recapture	mesocarnivores and bears	DNA sampling (e.g., hair snags, scat collection)	mark-recapture	• can produce accurate, precise and reliable estimates of population size (Arandjelovic and Vigilant 2018, Sawaya et al. 2011, Schoenecker et al. 2021) • depending on material collected: can reveal the sex, age class, reproductive status, diet, and/or stress levels of individuals (Lamb et al. 2019	• high costs • labour-intensive • outcomes depend on the quality, quantity and representativeness of DNA samples collected, and error-free genotyping (Sawaya et al. 2011, Solberg et al. 2006)

1.2.2 Towards New Provincial Standards

BC's provincial standards for inventorying medium- and large-bodied mammals have not been extensively updated since the late 1990s or early 2000s. This field has seen several important technological, methodological, and statistical advances in the past twenty-plus years. Wildlife managers adhering to outdated standards may not be aware of the many new research tools and statistical models now at their disposal.

Camera traps are one such tool. Over the past thirty years, camera traps (also called trail or remote wildlife cameras) have exploded in popularity (Burton et al. 2015, Deslisle et al. 2021). They are a minimally invasive, cost-effective method of monitoring mammals in all kinds of habitats and conditions, and over long periods of time (Kucera and Barrett 2011). Compared with other techniques, camera traps can be used to study a wider variety of landscapes and species (Palencia et al. 2021), including rare and elusive animals which are typically very difficult to research (e.g., Blanc et al. 2013). Camera traps can also be used to study community composition (e.g., Hedwig et al. 2018) and interactions (e.g., Smith et al. 2020), and to make inferences about vital rates (recruitment and survival; e.g., Hessami 2019), habitat selection (e.g., Dertien et al. 2017), prevalence of disease (e.g., Murray et al. 2021), body condition (e.g., Sashika et al. 2020), and animal behaviour (e.g., Windell et al. 2019).

Camera traps are being used as a research tool in BC. At least 61 projects are active or complete (https://wildcams.ca/project-database/, Clarke unpublished). Compared to Alberta, the Northwest Territories and neighbouring states, however – which all have large-scale, standardized camera trapping programs – wildlife managers in BC have yet to adopt a standardized protocol for camera trap data collection, and very few make use of cameras for density estimation.

1.3 Purpose of Review

This document is an overview of the literature on camera trap density estimation. Its purpose is four-fold: 1) to summarize how camera trap density models work; 2) to make clear the advantages, limitations, assumptions and uncertainties of each model; 3) to

provide examples of how each model has performed in simulated and field tests, in comparison to other camera trap density models and to "traditional" density estimation methods; and 4) to provide wildlife managers in BC with tools to select the camera trap model that best suits their study species, landscapes and needs. Our overarching goal is to supply wildlife managers and practitioners in BC (and beyond) with the information they need to decide whether camera traps are the right density estimation tool for their purposes, and, if so, which camera-based density models are most appropriate for their study system. Note that model explanations are primarily conceptual; for the underlying mathematics, readers should refer to the references cited. Note also that camera trap density research and model development is ongoing – it is our intention to update this document as the field evolves, and as models are further researched and developed.

This document is not a judgement on the value of camera traps as a research tool; the utility of cameras is well-established and well-described (see above for examples). Rather, this document is an overview and evaluation of how to use camera trap detection data for density estimation.

2. Overview of Density Models: What is Possible?

Here, we describe density models that can be applied to camera trap data. Some of these models (e.g., distance sampling) were initially designed for other data collection methods (e.g., ground-based surveys) and modified for use with camera trap data. Others (e.g., time in front of the camera) were designed specifically for camera trap research.

Camera trap data based density models fall into three categories: marked, unmarked, and partially-marked population models. Marked population models rely on individual identification using natural or artificial marks (e.g., coat patterns, scars, tags, collars; Figure 1) to resolve the number of animals in a population. Unmarked population models rely on supplementary data (e.g., animal movement speed) and/or assumptions as a surrogate for individual identification – that is, to distinguish multiple detections of the same individual from detections of multiple individuals at a camera station, when individuals do not carry unique features (Morin et al. 2022, Gilbert et al. 2021; Figure 2). Partially marked population models can be applied either to populations in which a proportion of all individuals carry marks, or to populations in which individuals themselves are partially marked (i.e., have a suite of partially identifying traits).
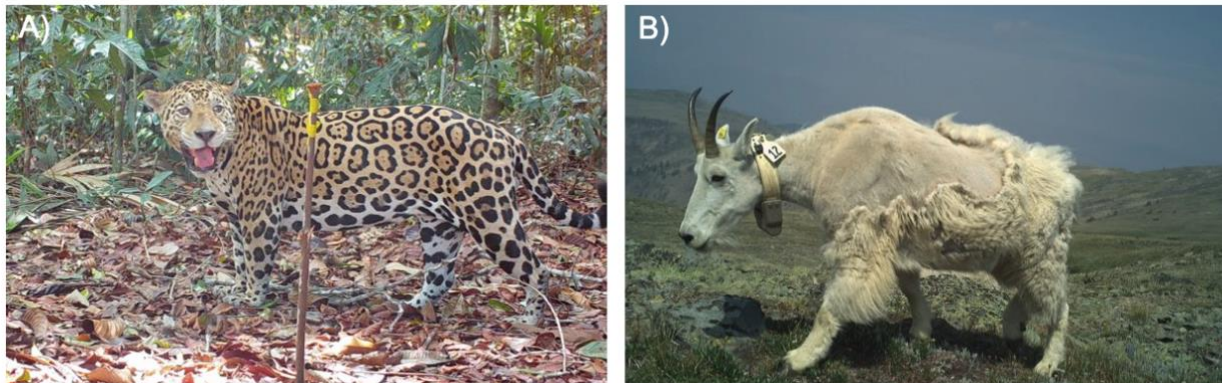
Figure 1. Examples of naturally (A) and artificially (B) marked animals. A) This jaguar's unique pattern of spots can be used to distinguish it from other individuals in its population. © Chris Beirne, Wildlife Coexistence Lab and Osa Conservation. B) This mountain goat was collared and marked prior to camera trapping. Its numbered tag clearly identifies which individual it is. © Mitchell Fennell, Wildlife Coexistence Lab.
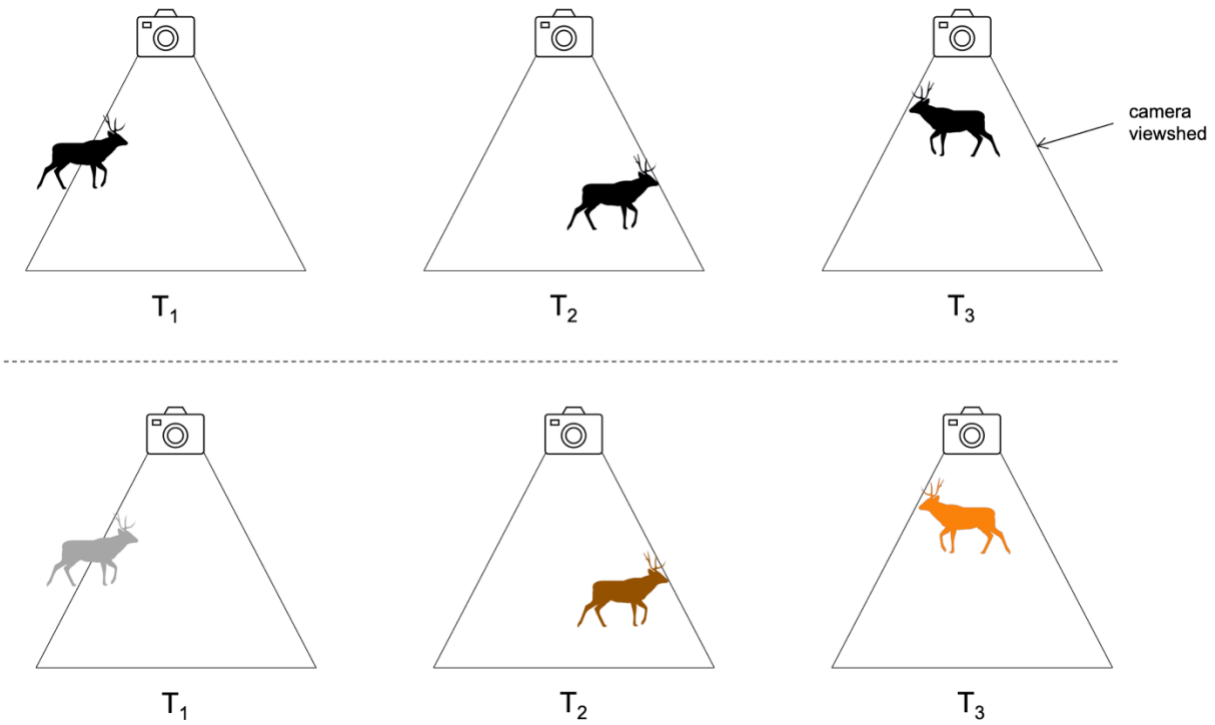
Figure 2. Part of the challenge of unmarked density estimation is distinguishing between many detections of a single individual (top) and detections of many different individuals (bottom) at a given camera station. Top panel: the same black deer passes in front of the camera at three different points in time. Bottom panel: three different deer – grey, brown and orange – pass in front of the camera at each timestamp. Unmarked models do not differentiate between the top and bottom scenarios directly (i.e., by individually identifying the deer), but use secondary information or model assumptions to tease them apart.

2.1 Marked Populations

2.1.1 Capture-Recapture (or Capture-Mark-Recapture or Mark-Recapture)

Of all the modelling frameworks discussed in this document, capture-recapture (CR) – also called capture-mark-recapture or mark-recapture – is perhaps the most well-known. Since the 19th century, CR has been used to measure population size by capturing, marking, releasing and recapturing individuals (Le Cren 1965, Otis et al. 1978). For species or populations that are challenging to physically trap and mark, CR can also be applied to DNA, acoustic and camera trap data (Royle et al. 2014). Here, we will discuss camera trap CR.

Figure 3. Adapted from Royle (2020). A detection history matrix for an example population. For each individual (1 through n) during each sampling occasion (1 through K), a value of 1 is assigned if that individual was detected at a camera trap and a value of 0 is assigned if it was not detected at a camera trap. Note that we do not detect individuals $n + 1, n + 2...N$ (0s for every sampling occasion), but they are still present and able to be detected.

To estimate density using camera trap CR, we must first estimate population size N. CR models use individuals' detection histories – that is, the record of when each individual was photographed or not photographed (i.e., (re)captured or not (re)captured) – to solve for N (Figure 3; Royle 2020). Population-level detection histories look like a matrix of 1s and 0s, where 1s signify that an individual was captured during a given sampling occasion k, and 0s signify that the individual was not captured during that occasion (Royle 2020, Royle et al. 2014). The number of individuals photographed at least once over the course of the study (i.e., the count of animals captured) is n.

Importantly, the count of animals is not the same as the size of the population (i.e., $n \neq N$). Some individuals will never be photographed during a study, even though they are present and able to be detected (i.e., they are in N but not in n; Royle 2020). Using the matrix of detection histories, we must therefore calculate the likelihood animals will be detected by an array of camera traps – that is, detection probability *p* (Royle 2020).

Taking this information together, we can calculate population size N as:

$$N = \frac{n}{p}$$

which is often referred to as the canonical estimator of population size (Royle 2020). Population size N can then be divided by an estimate of the area of the sampling frame A to obtain density.

CR models have important limitations – notably that they do not consider the spatial configuration of camera traps or the spatial pattern of animal detections. This gives rise to two major issues:

1) The sampling frame A is not known (Chandler and Royle 2013). In other words: the true area animals occupy is never measured, only approximated using ad-hoc approaches (e.g., using a buffer strip around the trap array; Rich et al. 2014, Sollmann 2018). Consequently, density cannot be calculated explicitly (Chandler and Royle 2013), and CR-derived density estimates are somewhat arbitrary and difficult to compare across studies (Green et al. 2020, Royle et al. 2014, Sollmann 2018).

2) Detection probability is assumed to be the same across all individuals and sampling occasions, even though the likelihood a given individual is detected at a given camera trap will change with its proximity to that trap. An animal that occupies territory far away from a trap is less likely to be detected there than one that lives nearby, for example (Morin et al. 2022).

The standard CR model has largely been phased out with the advent of spatially-explicit CR models (see *2.1.2 Spatial Capture-Recapture*; Burton et al. 2015, Sollmann 2008), which address the shortcomings of CR and have been shown to produce more accurate density estimates (e.g., Blanc et al. 2013, Obbard et al. 2010, Sollmann et al. 2011).

2.1.2 Spatial Capture-Recapture (or Spatially Explicit Capture-Recapture)

Borchers and Efford (2008), Royle and Young (2008)	
Assumptions	**Data Needed**
1) population closure	☐ individual detection histories
2) independence of detections	☐ camera trap coordinates
3) activity centres randomly dispersed	
4) activity centres stationary	
5) activity centres isotropic	

How the Model Works

Spatial capture-recapture (SCR) models can be applied to any survey method where animals are individually identifiable and trap locations are known: live trapping and tagging, DNA sampling, camera trapping, etc. (Royle et al. 2014). Here, we will discuss camera trap SCR.

SCR models break populations down into the activity, or home range, centres of individual animals. Let us first imagine we know the number and location of all individuals' activity centres in a population. If we did, we could easily estimate density:

$$D = \frac{\text{number of activity centres}}{\text{area encompassing all activity centres}}$$

assuming each member of the population has an activity centre, and so the number of activity centres is equivalent to population size; and since the area encompassing all activity centres is the total area sampled by the camera array (i.e., the sampling frame; Sollmann 2018). In reality, we do not know the number and location of activity centres – indeed, the estimated number and location of activity centres is the SCR model output.

To resolve the number and location of activity centres – and thus estimate density – SCR models combine information about 1) where animals are detected in space (using an observation model) and 2) how animals are distributed in space (using a spatial process model; Figure 4; Royle 2016).
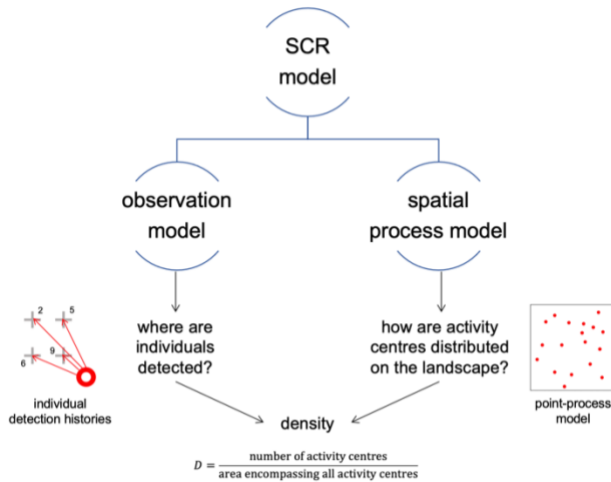
Figure 4. SCR models are made up of two sub-models: an observation model, which describes where individual animals are detected (i.e., their detection histories); and a spatial process model, which describes how animals' activity centres are distributed.

The observation model uses the record of where each individual was detected (i.e., individuals' detection histories) to infer the location of each individual's respective activity centre (Figure 5A; Chandler and Royle 2013, Royle 2016). It relies on the inverse relationship between detection probability and camera-trap-to-activity-centre distance: as the distance between a camera and an individual's activity centre increases, the likelihood that individual will be detected there decreases (Figure 5B; Royle et al. 2014). So, animals will be detected most frequently at camera traps near their activity centres, and least frequently (or not at all) at camera traps far from their activity centres. Because the locations of activity centres are unknown, we use a spatial process model to approximate their distribution. Point-process models are a common choice (Royle 2016). A point-process model is a random pattern of points in space (Baddeley, no date); it can be homogenous (completely spatially random) or inhomogeneous (the density of points depends on landscape/habitat covariates; Royle 2016).

Taken together: SCR essentially "downscales" density – a population-level estimator – to the level of the individual. The model asks: where does each animal live (Royle 2016)? Although the location of animals' activity centres is not known, we can use information about where individuals are captured (detection histories) and how activity centres are distributed in space (point-process model) to infer where they live, and thus estimate density (Royle 2016). SCR can be implemented using many statistical frameworks, including full likelihood estimation (Borchers and Efford 2008), data-augmented maximum likelihood estimation (Royle et al. 2014), and data-augmented Bayesian estimation (Royle and Young 2008; Morin et al. 2022).

15

When deploying cameras for SCR analysis, practitioners must balance the area covered by the camera array with trap spacing to maximize both the number of unique individuals captured and the number of spatial recaptures of each individual. A larger sampling area will yield a higher count of unique individuals; closely-spaced traps will yield a higher number of spatial recaptures (i.e., detections of the same individual at different camera traps; Royle et al. 2014). Both are important for SCR density estimation. Cameras should also be deployed across habitat types with different levels of use (Morin et al. 2022, Sun et al. 2014). Grid and clustered sampling designs can help meet all these needs (Clark 2019, Sun et al. 2014). Note that optimal camera trap placement and spacing will change with focal species, landscape and project limitations. See Clark (2019), Dupont et al. (2021), Fleming et al. (2021), McFarlane et al. (2020), Nawaz et al. (2021), Romairone et al. 2018, Sollmann et al. (2012) and Sun et al. (2014) for more detailed explorations of SCR study design.
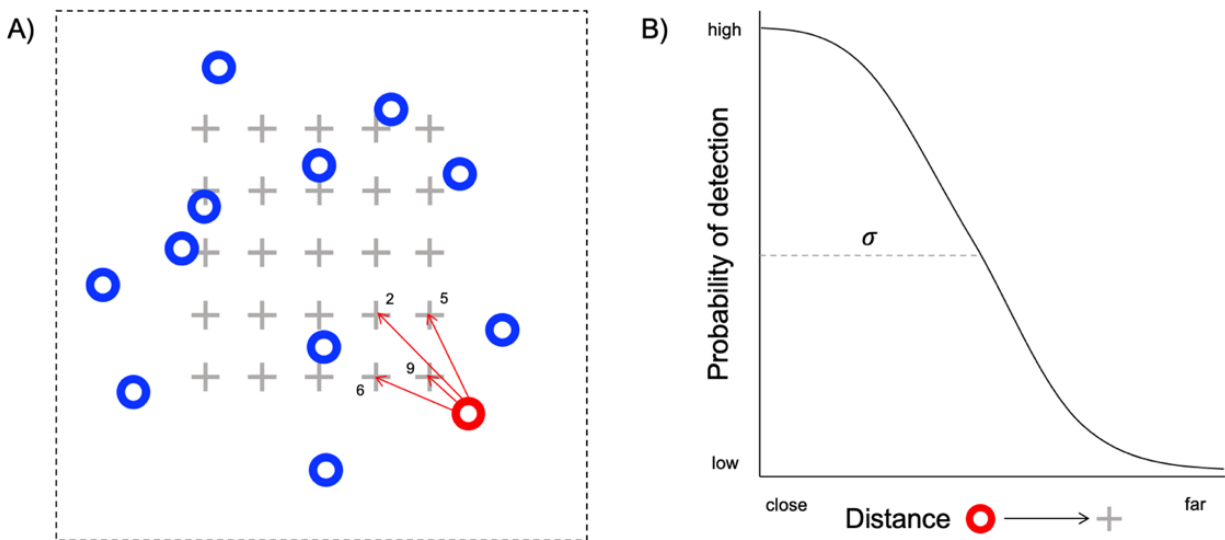
Figure 5. Adapted from Morin et al. (2022) and Royle et al. (2014). A) A diagram of how the individual activity centres (circles) that make up a population might overlap with a camera array (grey crosses). The red circle highlights an example individual's activity centre. The red arrows point towards camera stations where the red individual was detected; the numbers beside the camera stations show how many times the red individual was detected at each station. Note, the number and location of individual's activity centres is not known, but rather inferred from the spatial pattern of detections (i.e., the number of detections of each individual at camera stations of known location). B) An example graph showing how the probability the red individual is detected at a camera station decreases with distance from its activity centre. This is reflected in A); as the distance between the red individual's activity centre and a camera station increases, the number of detections dwindles. σ is the spatial scale parameter; it describes how detection probability decreases with increasing distance.

Another aspect of sampling design practitioners must consider is the number and configuration of cameras deployed at a station to identify animals to the individual. Left and right flanks may need to be photographed simultaneously, for example, to avoid assigning different identities to each side (Augustine et al. 2018); as another example, chest markings may need to be photographed from multiple angles at bait stations to be able to resolve identity (Proctor et al. 2022).

Assumptions

The assumptions listed below apply to basic SCR models. Note that many model extensions have been developed to account for violations of these assumptions, although they may require more statistical knowledge and computational power.

1) Population closure. Closed SCR models assume that there are no births, deaths, immigrations or emigrations over the course of the study. Changes in population size, whether through entries or exits, can result in the misestimation of detection probability or sampling area, and thus the misestimation of density (Green et al. 2020). To minimize violations of assumption 1, practitioners may choose to keep study length short or implement an open population SCR model (e.g., Gardner et al. 2010a, Shaub and Royle 2014). Note that open population models are designed for estimating population abundance an/or demographic parameters in populations that are not closed (e.g., Gardner et al. 2018).

2) Detections are independent. Detecting individual A at a camera station does not affect whether individual B will be detected at that camera station. Likewise, detecting an individual at camera station 1 does not affect the probability that individual will be detected at any other camera station (Green et al. 2020). This assumption is violated when animals travel in groups or prefer/avoid certain parts of the study area (Green et al. 2020). SCR appears to be fairly robust to group-travelling behaviour (Sun et al. 2022), but perhaps only at moderate levels (Bischof et al. 2020). Model extensions have been developed to account for violations of this assumption (see Gardner et al., 2010b, Royle et al., 2011).

3) Activity centres are randomly dispersed – that is, they follow a homogeneous point-process model. An individual's activity centre is equally likely to be anywhere within the sampling frame (Green et al. 2020). This assumption is violated when activity centres are clumped or overly spaced out, such as when habitats or features on the landscape attract or repel individuals. Model extensions for inhomogeneous point-process models, which account for landscape and habitat covariates, have been developed (Royle 2016).

4) Activity centres are stationary. They should not move throughout the duration of the study (i.e., home ranges do not shift). This assumption can be relaxed when information about animal movement is included in the model, allowing activity centres to "drift" (Green et al. 2020, Royle et al. 2016).

5) Activity centres are isotropic. Animals are assumed to travel the same distance in every direction from their activity centre (i.e., distances of equal magnitude from the activity centre). Basic SCR models further assume that animals have circular home ranges with use concentrated near the centre (i.e., bivariate normal home range utilization). Real animals do not move through real landscapes in this way; movement can instead be modelled using a host of other models (e.g., Fuller et al. 2016, Sutherland et al. 2015).

Advantages and Limitations

Advantages	Limitations
- Viewing a population as a collection of activity centres defines the sampling frame: the total area sampled is the area within which the activity centres of all individuals observed during a study are contained (Sollmann 2018). Density can therefore be thought of as the number of activity centres within the area encompassing all activity centres (Sollmann 2018). - Camera traps can target roads and trails, and can even be baited, to increase the number of (re)captures (Gerber et al. 2011, Hines et al. 2010). Maximizing the number of captures and recaptures increases the precision of estimates.	- All individuals within the study population must be marked and individually identifiable. Animals should be identifiable in every image. - SCR is difficult to implement at large spatial scales. The model relies on spatial recaptures – that is, detections of the same individual at many different camera stations – which requires high camera density (i.e., multiple cameras per home range; Ausband et al. 2022, Loonam et al. 2021b). Using SCR at the landscape level can therefore be inefficient (Ausband et al. 2022), although this is debated (Fisher, personal communication). - Practitioners must strike a balance between maximizing captures of unique individuals and

- SCR accounts for variation in individual detection probabilities (Chandler and Royle 2013, Royle et al. 2014).
- SCR can be used to model spatial variation in density (Morin et al. 2022).
- Many other processes can be modelled using SCR, including individual movement patterns, animal distribution, resource selection and population dynamics (Royle et al. 2014).

maximizing recaptures of individuals already detected (Morin et al. 2022).

Simulations and Field Studies

Camera trap SCR has primarily been used to estimate the densities of spotted and striped felids like tigers, jaguars and leopards (see the list of 95 papers in Green et al. (2020), Supplementary Table 1).

A recent metanalysis found that SCR was the only camera trap density model powerful enough to detect moderate-to-major population changes (i.e., 20-80% increases or decreases; Morin et al. 2022). This is in contrast with unmarked methods, which alarmingly often failed to detect even drastic population changes (i.e., 80-90% increases or decreases; Morin et al. 2022). Yet, SCR models are not "foolproof". Green et al. (2020) found less than ¼ of camera trap SCR studies produced density estimates precise enough for typical standards in wildlife management (i.e., coefficient of variation (CV) ≤ 0.20; Williams et al. 2002). SCR can also perform poorly when sampling design is not carefully considered (Morin et al. 2022).

Extensions of SCR for unmarked and partially-marked populations have been developed. These models are discussed in later sections (see *2.2.1 Spatial Count*, *2.3.1 Spatial Mark-Resight* and *2.3.2 Spatial Partial Identity Model*).

2.2 Unmarked Populations

2.2.1 Spatial Count (or Unmarked Spatial Capture-Recapture)

Chandler and Royle (2013)	
Assumptions	**Data Needed**
1) population closure	☐ camera-specific counts of animals
2) independence of detections	☐ camera trap coordinates
3) activity centres randomly dispersed	
4) activity centres stationary	
5) activity centres isotropic	

How the Model Works

A spatial count (SC) model is essentially a spatial capture-recapture (SCR; see *2.1.2 Spatial Capture-Recapture*) model with an extension to account for unmarked animals' unknown identities (Royle et al. 2014). SC, then, is formulated in much the same way as SCR: populations are treated as collections of individual activity (or home range) centres, and spatial detection data is used to infer the number and locations of these activity centres (see *How the Model Works* in the SCR section). Instead of identifying animals and constructing individual detection histories (i.e., each individual's spatial pattern of detections), however, SC uses trap-specific counts (i.e., the tally of animal detections at each trap of known location) and the correlation structure among trap-specific counts to estimate the number and location of activity centres (Royle et al. 2014, Sun et al. 2022).

Like SCR, an SC model is composed of a spatial process model and an observation model. The spatial process model, which describes how activity centres are distributed across the landscape, is a homogeneous point-process model – a completely random pattern of points in space (Baddeley, no date; Royle 2016). The observation model, which describes where individuals are detected on the landscape, is constructed as if we know each individual's detection history and the size of the population (Chandler

and Royle 2013). As Royle et al. (2014) put it: "[SC] is formulated in terms of the data we wish we had, i.e., the typical [detection] history data observed in [SCR] studies of marked animals." We can construct an SC model in this way because trap-specific counts of animals arise from those animals' detection histories; in other words, counts are a simplified version of the data that would have been collected, had individuals been identifiable (Chandler and Royle 2013, Sun et al. 2022).

To relate trap-specific counts to detection histories, we use the equation:

$$n_{jk} = \sum_{i=1}^{N} y_{ijk}$$

where n_{jk} is the count of animals at sampling location j and during sampling period k; N is population size; and y_{ijk} is individual i's detection history at sampling location j and during sampling period k (Royle et al. 2014). So, the trap- and period-specific count n_{jk} – the information we gather for SC – is the same as the sum of every individual's encounter history at that trap – the information we gather for SCR (Royle et al. 2014).

To approximate population size, we take a data augmentation approach. Population size N is treated as a subset of some larger, hypothetical population of size M (the "augmented" population; Royle and Dorazio 2012), such that:

$$N = \sum_{i=1}^{M} \omega_i$$

where $M \gg N$ and ω_i is the probability of existence of individual i within population N (Chandler and Royle 2013, Sun et al. 2022). ω_i is Bernoulli distributed – an animal can be present (i.e., $\omega_i = 1$) or absent (i.e., $\omega_i = 0$) – and depends on the number of detections at traps and the distance between traps and individuals' activity centres (Chandler and Royle 2013, Sun et al. 2022).

Note that, for SC, a "trap" is simply a tool or method for collecting count data. Trap types include hair snags, track plates, acoustic recording devices, human point-count

observers and camera traps (Chandler and Royle 2013, Royle et al. 2014). We will refer to camera traps for the remainder of this section.

The aim of SC sampling design is to infer the number and location of activity centres by inducing correlation (i.e., linear relation) between the number and location of detections (Burgar et al. 2019, Chandler and Royle 2013, Sollmann 2018, Sun et al. 2022). To this end, camera traps must be deployed close enough together that individuals will be detected at multiple locations (Chandler and Royle 2013). Grid or clustered designs may be best (Burgar et al. 2019, Clark 2019, Sun et al. 2014).

Assumptions

SC models make the same assumptions as SCR models (see above), but do not require individual identification.

Advantages and Limitations

Advantages	Limitations
- SC relies on two simple inputs: the number of animal detections at each camera station and the locations of those camera stations (Chandler and Royle 2013). There is no need to collect or measure any other information. - As with SCR, treating a population as a collection of activity centres defines the sampling frame: the total area sampled is the area within which the activity centres of all individuals detected during a study are contained (Sollmann 2018). Density is thus the number of activity centres within the area encompassing all activity centres (Sollmann 2018). - Cameras can be deployed on roads and trails or baited to increase the number of (re)captures.	- SC density estimates tend to be quite imprecise (Chandler and Royle 2013, Morin et al. 2022, Royle et al. 2014). - The precision of SC density estimates decreases as the number of individuals detected at given a camera station increases (Morin et al. 2022). Thus, the more individuals' home ranges overlap, the less precise the density estimate (Augustine et al. 2019). - The model can fail to work for very low-density populations or elusive species, as (re)captures are too few to confidently infer the number and location of activity centres (Burgar et al. 2018). - Likewise, the model can fail to work for very high-density populations with evenly-spaced activity centres (Burgar, personal communication), since trap-specific counts will be too similar across the camera network – muddling activity centre inference and often leading to non-converging models. - SC models are ill-suited to populations that exhibit group-travelling behaviour (Sun et al. 2022).

- SC models are sensitive to sampling design; trap layout can dramatically affect the accuracy and precision of density estimates (Sollmann 2018).

- Camera stations must be spaced close enough together that animals are detected at multiple camera stations (Chandler and Royle 2013). SC is therefore challenging to implement at large scales, as many cameras are needed.

Simulations and Field Studies

The relatively few studies that have tested SC models suggest that they tend to produce fairly accurate but imprecise density estimates.

- A study on fishers showed that, compared to genetic SCR, SC underestimated density and estimates were less precise (Burgar et al. 2018).
- Evans and Rittenhouse (2018) found that SC yielded accurate but less precise estimates of black bear density than camera trap SCR.
- Another study compared estimates of caribou density from SC with estimates from the spatial partial identity model (SPIM; see *2.3.2 Spatial Partial Identity Model*). In this system, SC likely underestimated density compared with SPIM – perhaps because the model interpreted captures of many individuals as recaptures of a few individuals – and was less precise and more variable year-to-year (Sun et al. 2022).
- SC was used to estimate the densities of caribou, moose, wolf, coyote and black bear populations in the oil sands region of Alberta (Burgar et al. 2019). Estimates for all species were imprecise; some had confidence intervals with upper and lower bounds that differed more than 10-fold. The authors note, however, that other density estimation methods used in the region (e.g., aerial surveys) are not more precise than SC (Burgar et al. 2019). The researchers also simulated their data, finding that SC tended to underestimate density when the number of captures and spatial recaptures (i.e., spatially-correlated detections between cameras) were low.

Box 1. The unmarked models that follow estimate density within the collective viewshed area (i.e., the combined fields-of-view of all cameras in a network) and assume that this estimate applies to the larger study area (Gilbert et al. 2021). This is in contrast to spatial capture-recapture (SCR; see *2.1.2 Spatial Capture-Recapture*) models and derivatives – including spatial count (SC; see *2.2.1 Spatial Count*), spatial mark-resight (SMR; see *2.3.1 Spatial Mark-Resight*) and the spatial partial identity model (SPIM; see *2.3.2 Spatial Partial Identity Model*) – which estimate density over a defined area.

2.2.2 Distance Sampling (or Camera Trap Distance Sampling)

Howe et al. (2017)	
Assumptions	**Data Needed**
1) cameras deployed independently of animal distribution 2) animals perfectly detected at distance 0 3) distances measured exactly 4) animals detected at initial location	☐ number of detections ☐ viewshed angle ☐ distance between camera and animal's centre

How the Model Works

Distance sampling (DS) theory was developed in the early 1990s to estimate density from line- or point-transect surveys, including aerial surveys (e.g., Alberta Environment and Parks 2016; Buckland et al. 1993). The novelty of the DS approach is in its capacity to correct for imperfect detection (i.e., not observing animals that are present) by measuring the distance between survey lines or points and animals (Morin et al. 2022). t (Buckland et al. 2015, Gilbert et al. 2021).

The DS model was adapted for use with camera trap data by Howe et al. (2017). Camera trap DS capitalizes on the similarities between camera trap surveys and human-observer point transect surveys – for example, both cameras and people tabulate the number of animals seen in a "snapshot" moment from a point in space (Buckland 2006). There are, however, important differences to account for. For one: in human-observer studies, a point is sampled for an instant, and only one or a few times total; a camera, in contrast, samples the same point for a long period of time (Palencia et al. 2021). For another: human observers can pivot 360º around a point to count animals, while cameras are fixed in place and sample only
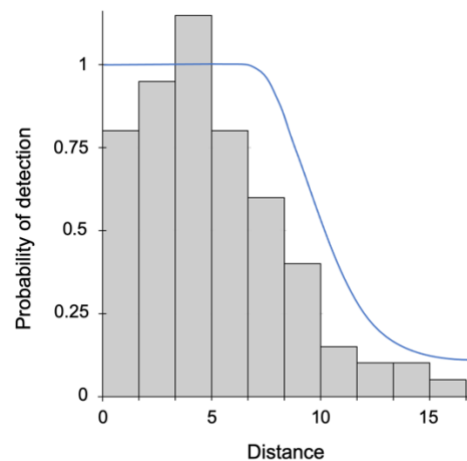
Figure 6. An example detection function. The probability of detecting an animal decreases with increasing distance from the observer.

a fraction of a circle (Howe et al. 2017). Camera trap DS must therefore include inputs of time and viewshed angle. The equation derived by Howe et al. (2017) is:

$$D = \frac{Y}{\pi w^2 ep}$$

where Y is the number of detection events, w is the truncation distance (i.e., the distance beyond which animal-camera distances are no longer considered), e is the sampling effort, and p is the probability of capturing an image of an animal within distance w (Howe et al. 2017).

To calculate sampling effort e: let us first consider temporal effort. At a given camera, temporal effort is a function of the camera's total sampling time H and a predetermined interval t units of time apart, at which the distance between camera and animal(s) is measured, such that temporal effort at the camera is H/t (Howe et al. 2017). If that same camera has a viewshed angle of θ radians, the fraction of a circle it samples is $\frac{\theta}{2\pi}$. Taken together, sampling effort can therefore be expressed as:

$$e = \frac{\theta H}{2\pi t}.$$

To estimate the probability of capturing an animal p: practitioners must estimate the horizontal distance r between a camera and the centre of every animal detected, at each snapshot moment t intervals apart, for as long as animals are within the viewshed (Howe et al. 2017). Howe et al. (2017) recommend a t of 0.25 to 3 seconds; if the focal species is fast-moving or rare, and/or cameras have fast trigger speeds, practitioners should use a smaller t. Measurements of r can then be inputted into a detection function, $f(r)$, which describes the probability an animal at distance r is detected given $0 \leq r \leq w$ – producing an estimate of p (Buckland et al. 2015).

Options for measuring camera-animal distance r include: 1) comparing images of animals to reference images of field crew or objects at known distances from the camera (manually or automated; Hauke et al. 2022, Howe et al. 2017); 2) placing

permanent reference objects at known distances from the camera so they are visible in every capture (Palencia et al. 2021); 3) physically measuring out camera-animal distances in the field, using animal images as references (Rowcliffe et al. 2011); and 4) a recently-developed, fully-automated approach (https://github.com/PJ-cs/DistanceEstimationTracking) which does not require reference images or objects (Johanns et al. 2022).

If the species of interest is regularly and predictably inactive (e.g., rests at night), estimates of density must be corrected for activity level to minimize bias (Howe et al. 2017, Palencia et al. 2021). Practitioners may choose to set total sampling time H as the time the study population was active and available for detection; another option is to correct density D for the proportion of time animals are active, such that:

$$D_C = D \times \frac{1}{a}$$

where D_C is the corrected density estimate and a is activity level (Howe et al. 2017, Palencia et al. 2021). Activity level is determined as per Rowcliffe et al. (2014).

Assumptions

1) Camera placement is independent of animal distribution. Said differently: cameras should not target places animals are known to prefer or avoid (Howe et al. 2017). When sampling designs are representative (i.e., random or systematic random placement of cameras), this assumption is met (Buckland et al. 2015, Howe et al. 2017). Note that this assumption extends to camera orientations – cameras should point either in random directions or in one consistent direction (Howe et al. 2017).

2) Perfect detection at distance 0. In mathematical terms: the probability of detecting an animal at distance $r = 0$ is 100% (i.e., $f(0) = 1$; Buckland et al. 2015). In practical terms: animals are always detected when directly in front of the camera. This assumption is violated when an animal passes the camera at distance 0, but: 1) is above or below the viewshed, 2) is not identifiable (e.g., only

a part of the animal is captured), or 3) the camera is not triggered (Howe et al. 2017). Failure to detect animals at distance 0 results in underestimates of density (Buckland et al. 1993). Violations can be minimized by deploying cameras at the correct height for the species of interest; cameras can also be deployed in pairs and facing each other to catch causes of violation (Howe et al. 2017).

3) Distances are measured exactly. Incorrectly measuring the distance between cameras and animals impacts the detection function, and thus estimates of density (Buckland et al. 2015).

4) Animals are detected at their initial locations. This assumption is violated when animals move prior to detection – either away from or towards the observer (Buckland et al. 1993). Either is possible in a camera trapping context, as some animals may deviate their "normal" course in response to cameras and/or reference objects, whether to avoid or investigate. Violations of assumption 4 are difficult to detect and account for (Buckland et al. 1996, Palencia et al. 2021).

Advantages and Limitations

Advantages	Limitations
- Animal movement does not bias density estimates since camera-animal distance are measured at instants in time (intervals of duration t apart; Howe et al. 2017). - There is some evidence the DS model can be applied to low-density populations (Palencia et al. 2021).	- DS is best-suited to larger animals. The smaller the focal species, the lower camera traps must be set, which reduces the depth of the viewshed, and thus sampling size and the flexibility of the model (Howe et al. 2017). - The DS model does not accommodate spatial variation in density (Gilbert et al. 2021). - Calculating camera-animal distances can be labour-intensive and time-consuming. However, recently developed techniques (e.g., Johanns et al. 2022) show promise for simplifying and automating the tedious process of camera-animal distance measurement. - Practitioners must have a good understanding of focal populations' activity patterns. Density estimates can be biased when regular periods of inactivity are not accounted for (Howe et al. 2017, Palencia et al. 2021).

Simulations and Field Studies

Howe et al. (2017) ran simulations of "complex" animal movement patterns (i.e., animals moved with variable speeds, meandered, and rested periodically), and found that, when periods of rest were excluded from analyses, the DS model produced unbiased and precise estimates of density (CV $\cong$ 0.10). When periods of rest were included, in contrast, DS performed poorly and inconsistently – whether animals rested within the viewshed or outside of the viewshed (i.e., were not detected). Animal activity patterns should therefore be considered when implementing the DS model; practitioners should have a strong understanding of when their species of interest is active versus inactive. Note that population and camera trap densities were both quite high in this simulation – 10 animals/km^2 and 6.25 camera traps/km^2 (Howe et al. 2017).

In northwestern Africa, camera trap DS produced higher estimates of duiker density than line-transect surveys – a method generally thought to underestimate the densities of forest-dwelling ungulates (Howe et al. 2017). The researchers collected video data.

Another study in northwestern Africa found that the DS model performed variably for different species (Cappelle et al. 2021). DS density estimates of a common ungulate – duiker – were comparable to previous estimates (line-transect surveys and Howe et al.'s (2017) camera trap DS study), and similarly precise. For semi-arboreal chimpanzees, DS-derived density estimates were biased low and depended greatly on measures of activity level (i.e., the proportion of the day chimpanzees were on the ground and available for detection). Compared with other studies:

- DS performed inferiorly to spatial capture-recapture (SCR; see section *2.1.2 Spatial Capture Recapture*) with individual identification (Després-Einspenner et al. 2017, Cappelle et al. 2019).
- DS estimates were, however, comparable to labour-intensive line-transect nest surveys.

The DS model performed inconsistently for rare species in this system, producing reasonable estimates of leopard density but questionable estimates of elephant density.

DS-derived leopard density was similar to a previous study combining collar, camera and track data (Cappelle et al. 2021, Jenny 1996). DS-derived elephant density was nearly double that from previous line-transect surveys and extremely imprecise (0.60 < CV < 2.00; Cappelle et al. 2021). As per Howe et al. (2017), videos were also used for this study.

Palencia et al. (2021) used DS to estimate the densities of red deer and boar. They found that the model performed similarly to the random encounter model (REM; see *2.2.3 Random Encounter Model*) and the random encounter and staying time model (REST; see *2.2.4 Random Encounter and Staying Time*) for both species. Compared to independent density estimates (line-transect distance sampling for red deer, drive counts for boar): DS yielded a comparable density for deer but underestimated density for boar, perhaps due to slow camera recovery times (Palencia et al. 2021). Precision of camera trap DS was quite low, with an average CV of 0.42. Still images were used.

Bessone et al. (2020) used camera trap DS to estimate the densities of 14 vertebrate species, finding that low population density and reactivity to cameras were major sources of bias, and that the model applied best to evenly-distributed (versus clumpily-distributed) populations. Precision was highest for common, high-density species, but satisfactory (i.e., CV < 0.35) for rare-but-widely-distributed species.

Finally, another density methods comparison study showed that camera trap DS was more precise than genetic mark-recapture, live capture-recapture, REM, and spatial count (SC; see section *2.2.1 Spatial Count*) for pine marten (CV = 0.34; Twining et al. 2022). While all methods produced densities within accepted ranges, DS tended to underestimate density (Twining et al. 2022).

2.2.3 Random Encounter Model

Rowcliffe et al. (2008)	
Assumptions	**Data Needed**
1) population closure	☐ number of images per unit time
2) independence of detections	☐ animal movement speed
3) cameras deployed representatively	☐ radius and angle of detection zone
4) animals behave like ideal gas particles	☐ average group size

How the Model Works

The random encounter model (REM) treats animals like ideal gas particles – that is, like randomly moving entities which are neither attracted to nor repelled by one another or landscape features (Gilbert et al. 2021, Rowcliffe et al. 2008). If animals behave like ideal gas particles, the rate at which they "bump into" and trigger camera traps is a function of animal movement, population density and the area within which cameras detect animals (Nakashima et al. 2018). So, the more animals move, the more animals in a population, or the larger the viewshed – the more images will be captured (Palencia 2022). This relationship can be used to estimate density, such that:

$$D = \frac{Y}{T} \times \frac{\pi}{vr(2 + \theta)}$$

where Y is the number of detection events, T is the total sampling time and v is animal movement speed (or the distance travelled by an individual in a day); and r and θ, the mean radius and angle of the detection zone (i.e., the area within which animals are detected with certainty) are used to calculate the area of the detection zone (Nakashima et al. 2018, Pettigrew et al. 2021, Rowcliffe et al. 2008).

Independent estimates of v can be sourced from telemetric studies, estimated from intensive observation or calculated using camera trap data (Nakashima et al. 2018, Rowcliffe et al. 2008, Rowcliffe et al. 2016). To calculate v using camera traps: for each observation, practitioners should determine how long it took the animal to pass through

the viewshed (i.e., time between first and last image in a sequence), then measure the distance the animal travelled by either a) retracing their path in the field using photos as a guide or b) estimating their movement image-to-image during photo processing using markers (Pfeffer et al. 2018, Rowcliffe et al. 2016).

r and θ can be measured in a few different ways. The first is by field trial: the detection zone is delineated by approaching the camera trap from different angles and at different speeds, recording where the sensor is triggered (Figure 7; Rowcliffe et al. 2008). The second is using a distance sampling method described in Rowcliffe et al. (2011). The third is by setting a focal area of standard size and shape (i.e., of known r and θ), within which detection is assumed to be perfect; only animals captured within the focal area are considered for analyses (Nakashima et al. 2018). θ may also be specified by the manufacturer (Pettigrew et al. 2021).
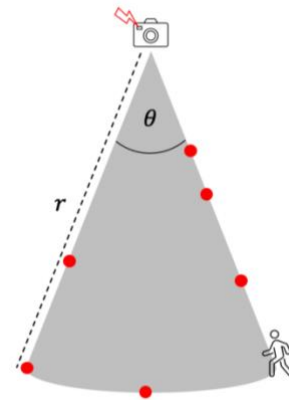
Figure 7. Measuring r and θ by field trial. The perimeter of the detection zone is determined by approaching the camera from different angles and at different speeds, and noting where the camera's sensor (red flash) detects motion (red dots).

When the species of interest travels in packs or herds, density as calculated per the equation above represents group density (i.e., the number of groups per unit area; Rowcliffe et al. 2008). To convert group density to individual density, D must be multiplied by an independent estimate of average group size (Rowcliffe et al. 2008).

Assumptions

1) Population closure. The size of the focal population should not change over the course of the study; that is, there should be no births, deaths, immigration or emigration. To meet this assumption, practitioners should set relatively short sampling periods that fall outside of major breeding, mortality and migration events (Rowcliffe et al. 2008). Note, however, that sampling periods must also be long enough to collect at least 10 events per focal species per camera station

(Rowcliffe et al. 2008). Roughly 100 to 1,000 camera trap days are needed for most carnivores and ungulates (Rowcliffe et al. 2008). If population size changes during a survey, the REM will provide a density estimate averaged across the trend (Rowcliffe et al. 2008).

2) Detections are independent. It is assumed that detection events are bounded and separate – that is, that animals (or groups of animals) clearly enter and then exit the viewshed area (Rowcliffe et al. 2008). Animals that linger in front of the camera violate assumption 2; this can be an issue, given the ubiquity of investigative behaviour at cameras. At the image processing stage, practitioners should examine image series to distinguish independent detection events (Rowcliffe et al. 2008).

3) Cameras are deployed representatively. They should not target roads, trails, water bodies or other features where detection probability might be particularly high, nor should they be preferentially placed near animal sign (Rowcliffe et al. 2008). One way to achieve a representative sampling design is to deploy cameras in a random configuration. Failure to meet this assumption results in biased density estimates (e.g., Cusack et al. 2015).

4) Animals behave like ideal gas particles. This assumption will never be met in actual populations; animals simply do not move completely randomly and independently (because of inter- and intraspecific interactions, grouping behaviour, complex landscapes, etc.). Nevertheless, the REM appears to be robust to "typical" (i.e., non-random, non-independent) patterns of animal movement (Rowcliffe et al. 2008). Attraction to or avoidance of camera traps (e.g., baiting, luring, trap shyness) will, however, bias density estimates (Rowcliffe et al. 2008).

Advantages and Limitations

Advantages	Limitations
- Sampling design is not influenced by home range size (Rowcliffe et al. 2008). No prior knowledge of home range size is required.	- The REM is sensitive to animal movement speed. Inputting biased movement data into the model produces misleading density

estimates – particularly for slow-moving species (Morin et al. 2022, Pettigrew et al. 2021). Ideally, movement speed should be measured for the population and period of interest – preferably using multiple methods (Jensen et al. 2022, Morin et al. 2022, Pettigrew et al. 2021). When this is not possible, the movement rates of several similar populations (i.e., same species, occupying comparable habitats) should be used (Pettigrew et al. 2021). Telemetry data should be collected at high fix rate (i.e., GPS points taken often throughout the day) and corrected for tortuosity (Jensen et al. 2022, Pettigrew et al. 2021).

- Where no movement data is available: collaring, intensively observing or using camera data to estimate movement speed is challenging, costly and tedious (Gilbert et al. 2021, Nakashima et al. 2018).

- Detection zone area varies with species, habitat and camera placement, so must be calculated for each station and calibrated to animals of different sizes (Gilbert et al. 2021).

- Because the REM assumes that animals move randomly and independently across the landscape, it cannot be used to make inferences about spatial variation in density (Gilbert et al. 2021).

- Cameras cannot be targeted, baited or lured to maximize detections; the REM may therefore be ill-suited to low-density and elusive species (Morin et al. 2022).

- When most detections occur at a small subset of camera stations, the precision of the REM decreases (Loonam et al. 2021a).

Simulations and Field Studies

Of all the unmarked density models, the REM has undergone the most empirical testing (Palencia et al. 2021). Rowcliffe et al. (2008) piloted the model in an enclosed animal park housing populations of known sizes, and found that the REM produced accurate density estimates for three out of four target species (two cervids and a marsupial). The model underestimated the density of the fourth species (a large rodent) because

cameras were deployed in habitats it did not frequent – a violation of assumption 3 (Rowcliffe et al. 2008).

The REM has proven robust in many study systems. Examples include:

- Palencia et al. (2021) found that the REM yielded similar density estimates as two non-camera methods, line-transect sampling and drive counts, for red deer and wild boar, respectively. The researchers also compared the REM to two other camera methods (random encounter and staying time (REST) and distance sampling (DS) models) – of the three, the REM was the most consistent (Palencia et al. 2021). In this study, animal movement speed v was determined using camera trap data.
- REM-derived density estimates of a mountain ungulate were highly consistent with visual count survey results (Kavčić et al. 2021). Animal movement speed was measured using camera trap data (Kavčić et al. 2021).
- A study on black bears in Québec found that the REM produced comparable results to DNA mark-recapture using hair samples, but that REM estimates were less precise (Pettigrew et al. 2021). The researchers estimated animal movement speed by averaging 19 years of telemetry data from four neighbouring black bear populations (Pettigrew et al. 2021).
- In the boreal forest of Washington state, REM and live-trapping spatial capture-recapture (SCR) produced similar density estimates for snowshoe hare (Jensen et al. 2022). The REM and the REST performed identically in this system; both models outperformed the time-to-event (TTE) model (Jensen et al. 2022). Measures of animal movement speed v were pulled from camera data and combined with telemetry data from a study in the Yukon.
- The REM yielded similar density estimates as, and was more precise than, live-trapping SCR at almost 90% of sampling sites in a study of hedgehogs (Shaus et al. 2020). Moreover, the REM was powerful enough to detect a 25% population change in this system (Schaus et al. 2020). Animal movement speed was estimated from camera trap images.

The REM has also significantly over and underestimated the densities of natural populations. In Africa, for example, estimates of lioness density using the REM were significantly higher than from pride censuses (Cusack et al. 2015). REM-derived densities skewed high because cameras were placed under shady trees, which attracted lions in the daytime (a violation of assumption 3), inflating the number of detection events Y (Cusack et al. 2015). When only nighttime detections were considered, however, REM-derived densities did not differ significantly from census-derived densities (Cusack et al. 2015). v, animal movement speed, was determined via intensive observation. A study comparing the REM with fecal DNA mark-recapture found that the REM underestimated marten density by 60% or more (Balestrieri et al. 2016). Animal movement speed v may have biased density low; the researchers estimated v from studies of pine marten occupying a different kind of habitat, where individuals may have moved more (Balestrieri et al. 2016).

Simulations suggest that, to achieve adequate precision using the REM, a minimum of 20 to 40 camera stations should be deployed for as long as needed to collect at least 10 to 20 image sets (Rowcliffe et al. 2008). For populations with variable detection: about 100 cameras are needed to obtain a level of precision appropriate for wildlife management (coefficient of variation (CV) of 0.20 or less; Palencia et al. 2021, Williams et al. 2002). To collect 10 to 20 image sets takes approximately 100 to 1,000 camera trap days for most mammal species; for rare species, cameras may need to be deployed for 1,000 camera trap days or more (Rowcliffe et al. 2008).

2.2.4 Random Encounter and Staying Time

Nakashima et al. (2018)	
Assumptions	**Data Needed**
1) population closure	☐ number of detections
2) independence of detections	☐ camera focal area
3) cameras deployed randomly relative to animal distribution	☐ time individuals spend in focal area
4) perfect detection within focal area	☐ total sampling time
5) movement of animals not affected by cameras	☐ proportion of time animals spend active
6) staying time representative of animal movement	
7) staying time parametrically distributed	

How the Model Works

The random encounter and staying time (REST) model is an extension of the random encounter model (REM; Gilbert et al. 2021). Like the REM, the REST treats animals like ideal gas particles (i.e., like randomly and independently moving entities); unlike the REM, the REST does not require measures of animal movement speed. Instead, the model uses the time animals spend in the camera viewshed (i.e., their "staying time") as a proxy for animal movement speed, since the two measures are inversely proportional (Nakashima et al. 2018).

The REST equation is a modified version of the REM equation which substitutes staying time for movement speed, and a detection area of set size for detection zone radius and angle, such that:

$$D = \frac{YT}{sH}$$

where Y is the number of detections, T is the staying time, s is the area within which all individuals are certain to be detected (hereafter, focal area), and H is the total research

period (i.e., the total sampling time; Nakashima et al. 2018). This equation produces an estimate of density D at a single camera; to determine population density for the study area, density estimates must be averaged across camera stations.

To implement the REST model, practitioners must first establish the focal area s. Methods at practitioners' disposal include testing focal areas of different sizes under controlled conditions (e.g., using domestic animals) and determining detection probabilities (Nakashima et al. 2018, Rowcliffe et al. 2011), or using distance sampling (DS) functions to delineate the zone of certain detection (as described in Hofmeester et al. 2017 and implemented in Palencia et al. 2021). Although it can be any shape, a triangular focal area maximizes the number of usable detections (fewer captures fall outside of the focal area; Nakashima et al. 2018).

Once established, the focal area is staked out in front of every camera in the field (e.g., using ropes and pegs), a reference image is taken, and any staking equipment is removed before the camera is left to collect images or videos (Nakashima et al. 2018, Palencia et al. 2021, 中島啓裕 2021). During image processing, captures of animals are overlaid on reference images (Figure 8A; 中島啓裕 2021). Alternatively, the focal area can be superimposed on captures of animals as in Figure 8B. Markers (e.g., stones) placed at known distances from the camera are used as a guide for placing the focal area (Palencia et al. 2021). Staying time T is the time an animal spends in the focal area; it is
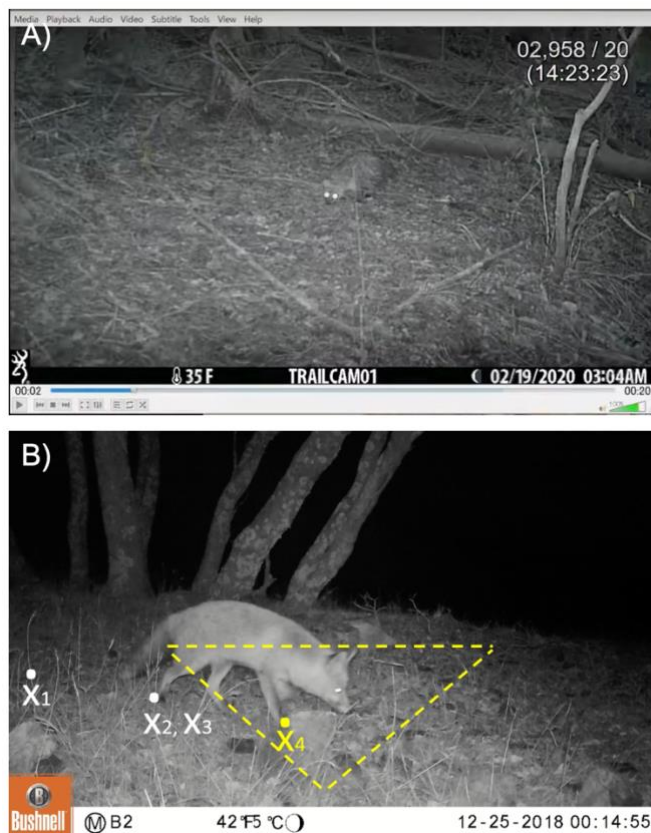
Figure 8. A) Still from 中島啓裕's (2021) video series. Example of overlaying a video recording of an animal on a reference image of the focal area (faint triangle) to determine staying time T. B) Still from Appendix S2 from Palencia et al. (2021). Example of superimposing the focal area on an image capture.

measured from the moment an animal's hind leg enters the focal area until it exits (i.e., $T_{exit} - T_{enter}$).

Importantly, estimates of density D must be corrected for activity level – that is, the proportion of time animals are active – such that:

$$\widehat{D} = D \times \frac{1}{a}$$

where $\widehat{D}$ is the corrected density estimate and a is the activity level (Palencia et al. 2021, Rowcliffe et al. 2014). Activity level is determined as per Rowcliffe et al. (2014).

Assumptions

1) Population closure. In contrast to models like the REM, immigration, emigration, births and deaths are permissible under the REST – so long as the population is balanced over the course of the study period (Garland et al. 2020). If population size does change over the course of a survey, the REST will produce an average density estimate for the survey period (Palencia et al. 2021).

2) Detections are independent. In other words, captures should not be correlated in space or time (Amburgey et al. 2021). To mitigate breaches of this assumption, practitioners should minimize spatial autocorrelation (i.e., the tendency for sites that are close together to have similar detection records) by spacing cameras far enough apart (Nakashima et al. 2018).

3) Cameras are deployed randomly relative to animal distribution. Camera cannot be baited or lured, nor can they be deployed in areas animals are known to prefer (Garland et al. 2020).

4) Detection is perfect within the focal area. This assumption is violated when detections are missed because of environmental factors (e.g., obstructions, poor weather conditions), camera specifics (e.g., cameras are set to become inactive after capturing images or video, slow trigger and media-storing speeds) or other reasons (Nakashima et al. 2018). To minimize violations of assumption 5, practitioners should program cameras to remain active after detection (i.e., no

delay period), choose camera models with fast trigger and storing speeds, test detection probability within the focal area, and deploy cameras at an appropriate height for the species of interest (Nakashima et al. 2018, Palencia et al. 2021).

5) Cameras should not affect animal movement. Individuals should not be attracted to or repelled by cameras; the former inflates staying time while the latter depresses it, resulting in over and underestimates of density, respectively (Palencia et al. 2021). Palencia et al. (2021) recommend discarding captures of animals investigating equipment when measuring staying time.

6) Staying times are representative of animal movement. Said differently, detection events should reflect the activity level of the population: when animals are active, they should be captured moving across the focal area (short staying times); when animals are inactive, they should be captured resting in the focal area (long staying times). It is, however, unlikely that randomly deployed camera traps will capture animals during periods of inactivity (Nakashima et al. 2018). Any such captures should therefore be excluded from analyses, and density estimates corrected for activity level (i.e., the proportion of time animals spend active; Nakashima et al. 2018, Palencia et al. 2021, Rowcliffe et al. 2014). Activity level is calculated as per Rowcliffe et al. (2014).

7) Staying times are parametrically distributed. A normal distribution (i.e., a bell curve) is an example of a parametric distribution (Chin and Lee 2008). Detections of animals resting or lingering within the focal area will skew the distribution of staying times right – a violation of assumption 7 (Amburgey et al. 2021). Such detections should therefore be excluded from analyses (Nakashima et al. 2018).

Advantages and Limitations

Advantages	Limitations
- Unlike the REM, the REST does not require independent estimates of animal movement speed (e.g., from telemetric studies; Gilbert et al. 2021). - Spatial variation in density can be modelled using the REST – another improvement over	- Only detections within the focal area are considered for analysis – a condition that may exclude many captures, and could limit the model's applicability to low-density species (Nakashima et al. 2018, Palencia et al. 2021). - Because the REST produces density estimates by camera station, and these

40

the REM (Gilbert et al. 2021, Nakashima et al. 2020).

- The model can be applied to group-travelling species (Brownlee at al. 2022, Garland et al. 2020). When multiple individuals pass through the camera viewshed at a time, practitioners must simply determine the staying time of each individual (Garland et al. 2020).

- The model can also be applied to territorial and non-territorial species, so long as cameras are placed randomly (Garland et al. 2020).

- The REST is robust to variation in movement speed, home range size and population size (Garland et al. 2020).

- Even relatively low camera coverage (e.g., 1% of total study area sampled) can result in accurate REST-based density estimates (Garland et al. 2020, Nakashima et al. 2018).

estimates must be averaged across stations to determine population density: estimates of error represent the differences in density among cameras, rather than a truly probabilistic estimate of density precision (Fisher, personal communication).

- Rowcliffe et al.'s (2014) method for estimating activity level relies on the assumption that all individuals in a population are active during peak periods. When this assumption is not met – that is, when some individuals are not active during peak times – activity level is overestimated, and thus density is underestimated (Nakashima et al. 2018).

- The REST model was developed for video data (Becker et al. 2022, Brownlee et al. 2022, Nakashima et al. 2018). Videos tend to fill SD cards and drain batteries faster than still images (Granados 2021, Proctor et al. 2022); compared to similar models, then, the REST is more memory- and energy-consumptive (Nakashima et al. 2018). Still image data can be used if cameras are set to take photos continuously upon sensing motion, with minimal lag between triggers (see Jensen et al. 2022, Palencia et al. 2021). Note, however, than Palencia et al. (2021) found that image-based density estimates were insignificantly lower than video-based estimates – further investigation may be necessary to establish the effects of image versus image data on the REST.

Simulations and Field Studies

Nakashima et al. (2018) ran random walk simulations to test the REST's performance. In its simplest form, a random walk models the series of steps an animal (the "walker") takes – each in a completely arbitrary direction, or in a pattern informed by behaviour, ecology and environment (Codling et al. 2008). Nakashima et al.'s (2018) simulations showed that the REST model was robust to grouping behaviour and variation in animal movement speed. More specifically, the REST produced accurate estimates of density when animals travelled in pairs, and when animals covered different distances during the sampling period (Nakashima et al. 2018). The model produced biased results, however, when captures of animals resting in the focal area were included in staying times (Nakashima et al. 2018). To minimize bias: 1) any detections with exceedingly

long staying times (i.e., right outliers) should be discarded; and 2) density estimates should be corrected for activity level a using the method outlined in Rowcliffe et al. (2014; Nakashima et al. 2018).

Garland et al. (2020) ran a "real life" simulation of the REST using human volunteers. The researchers found that the model produced accurate density estimates, even when home range size, population size and movement patterns varied – but that scenarios in which people moved at a constant rate yielded more precise estimates than those in which people rested periodically (Garland et al. 2020). Larger populations were also associated with lower-precision estimates (i.e., the bigger the population, the less precise the density estimate) – as population size increases, so too does the variation in staying times, reducing the overall precision of REST estimates (Garland et al. 2020). Note than humans were fully agnostic to detectors – an assumption often violated by animals (Caravaggi et al. 2020).

Both Garland et al. (2020) and Nakashima et al. (2018) tested the effect of sampling effort on the REST; both concluded that the model can yield accurate results, even when effort is relatively small (1% of study area sampled or 10 cameras deployed for 10 days, respectively). Note, however, that these results pertain to very high-density populations – animal density was 125 to 750 individuals per km^2 in Garland et al. (2020) and 10 individuals per km^2 in Nakashima et al. (2018) – and likely do not apply to average-to-low density populations. Low sampling effort was also linked to imprecision – the fewer cameras deployed, the less precise the density estimate (Garland et al. 2020, Nakashima et al. 2018). Thus, although little sampling effort is needed to produce accurate density estimates for very dense populations, considerable sampling effort will be necessary for most populations, and to produce precise estimates.

In the field:

- The REST was initially validated by Nakashima et al. (2018), who compared density estimates of forest-dwelling antelopes from the camera data-based model and line-transect surveys (see *2.2.2 Distance Sampling*). In this system,

both methods produced similar estimates of antelope density, with similar precision (Nakashima et al. 2018). A follow-up study in the same area further demonstrated that the model can produce unbiased estimates of density (Nakashima et al. 2020).

- The model produced estimates of snowshoe hare density comparable to live-trapping SCR in the boreal forest of the northwestern United States (Jensen et al. 2022). REST- and REM-based estimates were also consistent with each other, and both models outperformed the time-to-event model (TTE; see *2.2.6 Time-to-Event Model*; Jensen et al. 2022).

- Palencia et al. (2021) found that REST-derived density estimates were consistent with line-transect surveys of deer, but not with drive-count surveys of boar; the REST underestimated density compared to the latter. The model was, however, highly consistent with the REM and camera trap distance sampling (DS; Palencia et al. 2021). Furthermore, the REST was more precise than the other two camera models – although not significantly (Palencia et al. 2021).

Practitioners should be aware that population densities were quite high in the studies listed above (about 1 to 160 animals per km^2; Jensen et al. 2022, Nakashima et al. 2018). Thus, while the REST model applies well to very dense populations, it may not be appropriate for average-to-low density populations (e.g., wildlife populations in BC, with densities often <1 animal/km^2); further investigation is needed (Morin et al. 2022). The precision of the REST is also inversely related to population size – the smaller the population, the less precise the density estimate (Morin et al. 2022).

2.2.5 Time in Front of the Camera

Becker et al. (2022)	
Assumptions	**Data Needed**
1) cameras deployed representatively (e.g., random, stratified random) at landscape and micro-habitat scales 2) perfect detection within 5 m of camera 3) movement of animals not affected by cameras or equipment	☐ counts of individuals in images ☐ time individuals spend in viewshed ☐ viewshed divided into distance bins ☐ total camera operating time

How the Model Works

The time in front of the camera (TIFC) model is based on quadrat sampling. Typically, quadrats are used to sample slow- or non-moving organisms at a moment in time; as a simple example, a researcher lays a quadrat on the ground, counts the number of mussels in it and divides the count by the quadrat area. TIFC treats the camera viewshed like a vertical quadrat (Becker et al. 2022, Dickie 2022). Unlike a conventional quadrat, however, the camera viewshed samples highly mobile organisms in a relatively small sliver of space and over long periods time (Becker et al. 2022, Dickie 2022). The count of animals in the camera viewshed "quadrat," then, can be thought of in "animal-time" and the area covered by the quadrat in "area-time," such that:

$$D = \frac{\Sigma(N \times T_V)}{A_V \times T_O}$$

where the numerator, animal-time, is the number of animals N multiplied by the time those animals spend in the viewshed T_V, summed over all detections; and the denominator, area-time, is the area of the viewshed A_V multiplied by the total camera operating time T_O (Becker et al. 2022). Using this equation, density must be calculated for each species at each camera station, then averaged across the camera network.
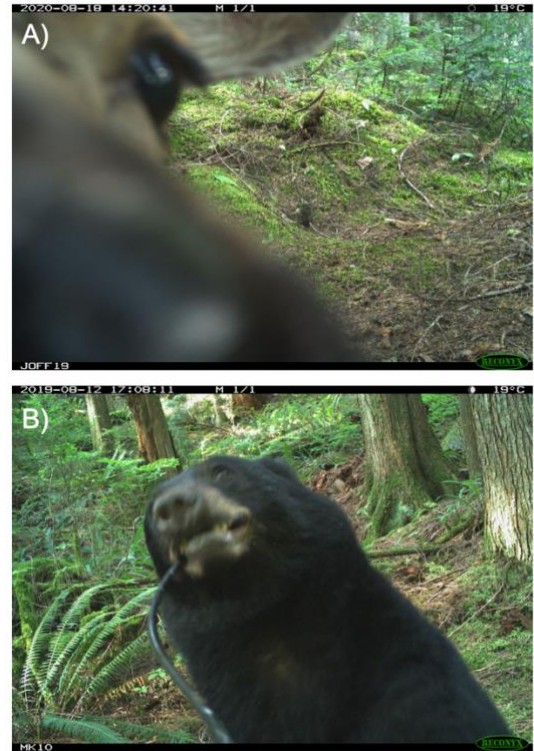
To calculate A_V in the field, markers (e.g., poles) must be placed at known distances from the camera to divide the viewshed into distance bins; during analysis, the

proportion of detections in each bin is determined (Becker et al. 2022). The camera angle of view – which varies with make and model – is also needed to solve for A_V. In most cases, T_O will be the time from initial camera deployment to final camera collection (Becker et al. 2022). In case of displacement, damage or failure, cameras should be programmed to take time-lapse images, so end-of-operation time can be traced back to a specific day or hour (Becker et al. 2022).

Assumptions

1) Cameras are deployed representatively at both the landscape and micro-habitat scales. At the landscape level, assumption 1 can be satisfied by deploying cameras in a random or stratified random configuration (Becker et al. 2022). Meeting this assumption at the micro-habitat level is more challenging – and often impractical. For example: it is common practice to set camera traps to face habitat openings, where they can collect clear, useful images of animals. Targeting habitat openings, however, can bias TIFC density estimates if focal species prefer or avoid open spaces (Becker et al. 2022). One possible work-around is to use remote-sensing or other geospatial tools to break down the study landscape and correct for non-representative placement – although this is still an active area of research (Becker et al. 2022).

2) Animal movement is not affected by camera traps or other field equipment. In other words, the time animals spend in front of the camera should not be influenced by the presence of the camera station (Brownlee et al. 2022). Avoidance of or attraction to cameras, distance stakes or other implements impacts the amount of time animals spend in the camera viewshed (T_v), which can bias density estimates (Dickie 2022). For example: when animals investigate equipment, the time they spend in front of the camera increases, inflating density (Figure 9; Becker et al. 2022). Becker et al. (2022) found that analyses that included images of investigative behaviour doubled or tripled average moose density (depending on the

Figure 9. Examples of behaviours that increase time in the viewshed (T_v). A) A mule deer inspects a camera trap. © Cole Burton, Wildlife Coexistence Lab. B) A black bear pulls on the lock securing a camera trap to a tree. © Michael Procko, Wildlife Coexistence Lab.

criteria used to define investigative behaviour) compared to analyses that excluded such images (i.e., the "true" density of moose based on natural movement in front of the camera). Excluding the time animals spend interacting with equipment is one way of addressing violations of assumption 2 (Becker et al. 2022), but requires practitioners to decide what they consider interactive/investigative behaviour (i.e., direct interaction with equipment only? walking to/from equipment after investigating? lingering near equipment?).

3) Perfect detection within 5 m of the camera. Whether this assumption holds depends on camera make and model, animal body size and movement patterns, and a host of environmental variables, such as snow cover, vegetation and temperature (Becker et al. 2022). Practitioners should consider testing this assumption for their species and landscape of interest.

Advantages and Limitations

Advantages	Limitations
- TIFC was designed to be approachable and easy-to-use. Little-to-no coding is required; wildlife managers with an understanding of the statistical software R (https://www.r-project.org/) can use the workflow and code developed by Becker et al. (2022) that is publicly available on GitHub (https://github.com/mabecker89/tifc-method/tree/v1.0.1).	- TIFC tends not to produce highly precise density estimates, although precision increases with deployment and network size (Dickie, personal communication). - Given adequate sampling design (i.e., many cameras deployed representatively), the TIFC model will produce robust estimates of high-density species; as with many other unmarked models, however, TIFC is ill-suited to rare and elusive species (Dickie, personal communication). - The proportion of detections in each distance bin changes with species, season, and habitat, and must therefore be calculated for each combination of these (Becker et al. 2022).

Simulations and Field Studies

The TIFC model has been field-tested on several different species. For moose, TIFC produced similar density estimates as aerial distance sampling (DS) after TIFC-derived estimates were corrected for the time animals spent investigating equipment (camera and 5 m pole; Becker et al. 2022). This study used image data collected in Alberta at 2,990 camera stations over the course of 6 years; despite the large sample size and long study duration, estimates were not very precise.

A study of five ungulate species (moose, bison, elk, mule and white-tailed deer) in two enclosed parks in Alberta found that TIFC- and aerial survey-derived density estimates were similar for moose and bison, but that TIFC significantly overestimated elk density compared with aerial surveys (Foca 2021). Two potential reasons for the discrepancy in elk density are: 1) that aerial surveys underestimated density, since elk in the study area occupy forested habitats, do not form large herds during the survey period, and estimates were not corrected for sightability; and 2) cameras may have been disproportionately set in areas elk prefer (Foca 2021). Group travelling behaviour may also have affected elk TIFC estimates, since detection probability and time in the viewshed (T_V) can change with group size (Foca 2021). Estimates of mule and white-

tailed deer densities could not be compared with aerial survey results, since deer are not surveyed by air in this area. Foca's (2021) TIFC analyses produced the first density estimates for deer in both parks.

In Uganda, TIFC-derived estimates of antelope were comparable to results from camera trap spatial capture-recapture (SCR; Brownlee et al. 2022, Warbington and Boyce 2020). The model performed inconsistently for black bears, caribou, white-tailed deer and other species, however, compared to camera-based spatial count (SC), DNA mark-recapture and aerial survey methods (Fisher et al. in review).

2.2.6 Time-To-Event, Space-to-Event and Instantaneous Sampling Models

Time-to-Event

Moeller et al. (2018)	
Assumptions	**Data Needed**
1) population closure	☐ time until individual(s) detected
2) independent detections	☐ animal movement speed
3) random camera placement	☐ viewshed area
4) perfect detection	
5) animals Poisson distributed	

How the Model Works

Time-to-event (TTE) analysis is used in many disciplines to estimate the rate at which an event occurs, by repeatedly measuring the time that elapses before said event takes place (Loonam et al. 2021b). A TTE model might be used in medicine, for example, to approximate time from diagnosis until remission or death (Clark et al. 2003). Moeller et al. (2018) developed an extension of the TTE framework to estimate animal density using camera trap data, where the "event" of interest is an animal detection, and the rate of interest is animals per viewshed area – density (Loonam et al. 2021b). Their version capitalizes on the fact that, at a randomly deployed motion-triggered camera, the time it takes to capture an image of an animal is a function of animal movement speed, detection probability and population size (Jennelle et al. 2002, Moeller et al. 2018, Parsons et al. 2017). When movement speed is known and detection probability is perfect, population size can be estimated by measuring the time from an arbitrary starting point until an image of an animal is captured (Lukacs 2021, Moeller et al. 2018). The equation for camera data-based density estimation using TTE is:

$$D = \frac{\lambda}{a}$$

where λ is the average number of animals in the viewshed, given the time until an animal is detected, and a is the average viewshed area. a is calculated using the equation:

$$a = \pi r^2 \frac{\theta}{360}$$

where r is the trigger distance (i.e., the maximum distance from which an animal can reliably trigger a camera's motion sensor), and θ is the angle of the camera lens in degrees (Moeller et al. 2018).

To illustrate how λ is calculated, let's take a simple example. We begin by dividing the total time cameras are active into sampling occasions, then sampling periods (Figure 10; Moeller et al. 2018). We might choose to define a sampling occasion as a day, and a sampling period as one of 24 one-hour intervals in a day (Moeller et al. 2018). The images collected at a camera station can now be grouped by occasion and period to generate a detection history, and the number of sampling periods (i.e., k out of 24) until an image of an animal is encountered can be determined for each sampling occasion (Moeller et al. 2018). The detection history at a given camera after 7 days might look something like {NA, NA, 7, NA, 22, 1, NA}, where NA indicates no animal detections for that day. Inputting this information into a likelihood equation generates the average number of animals in the viewshed, λ (Moeller et al. 2018).
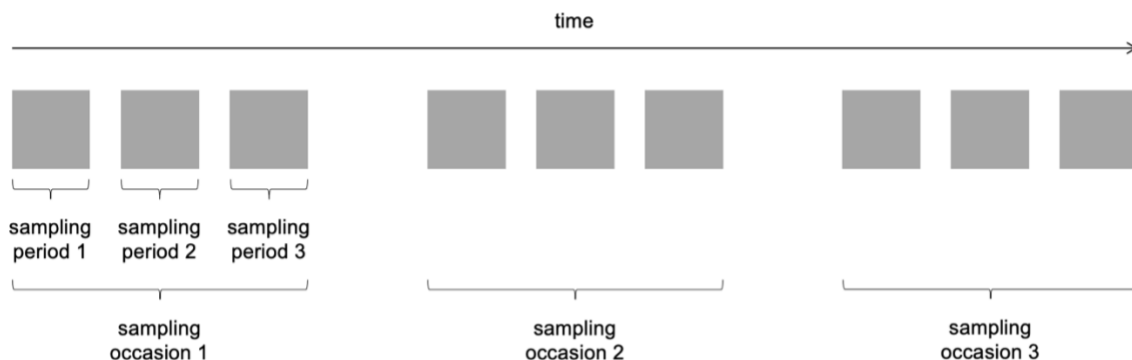
Figure 10. Adapted from Moeller et al. (2018). Visualization of how total sampling time at a camera station is broken down into sampling occasions and then sampling periods.

To account for movement, the sampling period is set as the average time animals take to pass through the camera viewshed (Moeller et al. 2018). Thus, practitioners need measures of animal movement speed.

Assumptions

1) Population closure. The TTE model assumes that populations do not experience any births, deaths, immigration or emigration during the study (Moeller et al. 2018). To meet this assumption, practitioners are advised to choose a sampling area and period for which this is essentially "true" – that is, a shorter study period, outside of mating, mortality or migration events (Morin et al. 2022). When this assumption is not met, the TTE produces an estimate of average density across the study period (Loonam et al. 2021b).

2) Detections are independent. At the level of the camera network: an animal that is captured at one camera station should not be any more or less likely to be captured at a neighbouring camera station (Gilbert et al. 2021). When cameras are deployed randomly (see assumption 3), this likely to hold (Moeller et al. 2018). At the level of a single camera: a sampling occasion should be long enough that animals have the chance to spread out across the landscape (Moeller et al. 2018). At the animal level: individuals should move independently of one another, although the model appears robust to pairing and occasional detections of large groups (e.g., 40 individuals or more; Moeller et al. 2018). Detections should also be independent in time, meaning animals do not linger in the camera viewshed (Gilbert et al. 2021).

3) Cameras are deployed randomly across the study landscape. Often, camera trap researchers will set units on roads or trails to maximize animal detections; such sampling designs are a violation of this assumption. Assumption 3 is also violated by baiting and luring cameras, as animals should not be drawn to (or driven away by) cameras (Moeller et al. 2018). In homogenous landscapes where animals move freely, this assumption can be relaxed, and cameras can be set to maximize animal detections at

4) Perfect detection. This assumption will rarely be met when camera traps are set to take motion-triggered pictures. The likelihood an animal will activate a camera's motion sensor and trigger an image to be taken will vary with vegetation cover, weather conditions, animal body size, grouping of individuals, and camera make, model and settings, among other factors (Burton et al. 2015). Detection probability also decreases with increasing distance from the camera (Rowcliffe et al. 2011). Moeller et al. (2018) provide a model extension to account for imperfect detection, but suggest further research. In the interim, practitioners can choose to analyze images of animals in close proximity to the camera, where detection probability can more reasonably be considered "perfect," and exclude other images from analysis (Moeller et al. 2018).

5) Animals are Poisson distributed across the study area. Individuals are equally likely to be anywhere on the landscape, and are neither attracted to nor repelled by one another (Whitlock and Schluter 2020). Overly-dispersed (i.e., territorial behaviour) or clumped distributions (i.e., grouping behaviour) are examples of violations of assumption 4 – but simulations show the model may be robust to such violations (Figure 11; Loonam et al. 2021b). If animals congregate in response to landscape topography (e.g., resources clumpily distributed), covariates (i.e., known confounding variables) can also be included in the model (Moeller et al. 2018).

Figure 11. Simple diagrams showing dispersed, clumped and Poisson-distributed animals (red dots) in space.

Advantages and Limitations

Advantages	Limitations
- The TTE model requires less image processing effort than many other models. Practitioners need only "draw" images until an animal is first in frame; any further images do not need to be processed (Moeller et al. 2018).	- The TTE requires accurate measures of animal movement speed to set the sampling period (Loonam et al. 2021a, Moeller et al. 2018, Morin et al. 2022). Obtaining movement information can be costly and labour-intensive.
- Weather, travelling and investigative behaviour, obstructions, camera malfunctions, and other factors can affect image quality, making it difficult to accurately count the number of individuals in some images (Moeller et al. 2018). The TTE does not rely on counts of animals in images – it simply relies on whether an individual was within frame during each sampling period (Moeller et al. 2018).	- The TTE model is sensitive to animal movement speed. Misrepresentative or incorrect values of movement speed bias density estimates (Loonam et al. 2021b). Ideally, movement should be measured using GPS collars for the study population and period of interest (Loonam et al. 2021b).
- The TTE can account for spatial variation in density (Moeller et al. 2018). A model extension is available which compares densities at different camera stations as a result of habitat covariates (Loonam et al. 2021b).	- Randomly-placed cameras may not collect enough images of rare or elusive species. The TTE model is therefore best suited to relatively common, high-density species (Moeller et al. 2018, Morin et al. 2022).
- TTE studies are simple to scale up or down, since the number of cameras – not camera density or coverage – determines the precision of estimates (Loonam et al. 2021a). 100 cameras can be used to estimate density in a large area just as effectively as a small area (Loonam et al. 2021a).	

Simulations and Field Studies

Simulations show that:

- The TTE model tends to underestimate population density. In both walk (Loonam 2019) and random walk simulations (Moeller et al. 2018), the TTE yielded density estimates below the true value, whether populations were large or small, or animals moved quickly or slowly. Estimates were, however, particularly low for slow-moving species.

- The TTE is sensitive to movement speed. Indeed, Loonam et al.'s (2021b) simulations showed that over- or underestimating movement rate biases density estimates. For example: a 50% underestimation of movement speed resulted in a

density estimate 40% lower than the true density; overestimating movement speed by 200% resulted in density estimates that were over 85% higher than actual (Loonam et al. 2021b). Taken together, these results suggest that the integrity of TTE estimates depends on the movement behaviour of the focal species, and obtaining accurate measures of animal movement speed.

- The TTE model performs best when cameras are deployed randomly on the landscape. Setting cameras to maximize detections (i.e., targeted deployment) resulted in considerable over- or underestimates of density in walk simulations (Loonam et al. 2021b). Of the sampling designs tested in Grosklos' (in preparation) simulations, random camera placement produced the best results. Thus, practitioners using the TTE model are advised to deploy their camera networks randomly to minimize model bias.

- The TTE is robust to population openness and territoriality. Population openness is a violation of assumption 1 (population closure); territoriality is a violation of assumption 5 (animals are Poisson distributed across the landscape; Moeller et al. 2018). Neither appeared to impact TTE estimates – indicating that the model applies well to actual populations, which often violate these assumptions (Loonam et al. 2021b).

It is worth noting that in all of Loonam et al.'s (2021b) simulations, the precision of TTE estimates was inflated – that is, estimates were calculated to be more precise than they actually were. Practitioners should keep this in mind when evaluating reported values of precision, as they may be artificially high.

In the field: the TTE has produced density estimates similar to established censusing techniques. Moeller et al. (2018) piloted the TTE on a population of elk in Idaho, and found that the model produced a density estimate comparable to an aerial survey of the same area – even though cameras were not deployed randomly. In this system, the TTE produced higher estimates of population density than either of its sister models (space-to-event (STE) and instantaneous sampling (IS); see below). For cougars – a low-density species – TTE-based estimates were actually more precise than both genetic mark-recapture and random encounter model (REM; see *2.2.3 Random*

Encounter Model) estimates, and similarly or more consistent across years, respectively (Loonam et al. 2021a). Density estimates could have been biased and misleadingly precise, however, because of non-random camera placement (Loonam et al. 2021a, Morin et al. 2022).

The TTE has also performed poorly in natural populations. A study on snowshoe hare found that the TTE tended to overestimate density compared with the REM and the random encounter and staying time model (REST; see *2.2.4 Random Encounter and Staying Time*; Jensen et al. 2022). Out of the three camera-based models, the TTE was also the least consistent with live-trapping spatial capture-recapture (SCR; see *2.1.2 Spatial Capture-Recapture*; Jensen et al. 2022).

Space-to-Event

Moeller et al. (2018)	
Assumptions	**Data Needed**
1) population closure 2) independent detections 3) random camera placement 4) perfect detection 5) animals Poisson distributed	☐ number of cameras until individual(s) detected ☐ viewshed area

How the Model Works

The space-to-event model (STE) is an extension of the time-to-event model (TTE; see above) that measures the area, instead of the time, sampled before an image of an animal is observed (Moeller et al. 2018). The conceptual underpinnings of the STE are the same as those of the TTE, with the exception that sampling occasions are collapsed into instantaneous samples using time-lapse images – photographs taken at predetermined periods of the day or night (e.g., every hour, every day at noon), regardless of whether animals are within frame (Figure 12; Granados 2021, Moeller et al. 2018). Because they are collapsed into instants in time, there is no need to break sampling occasions down into sampling periods – and no need for measures of animal movement speed. The STE is therefore an alternative to the TTE that requires no additional non-camera data.

Figure 12. One of many time-lapse images taken at a camera station at noon. Notice, the camera trap captures an image at a predetermined time (12:00), regardless of whether an animal is within frame.

The STE model is based on the simple logic that, as population density increases, the number of animal images captured by the cameras in a network increases, and thus the number of cameras that capture images increases – so, at a moment in time, the number of cameras from which images need to be "drawn" until an image of an animal is picked decreases (Lukacs 2021). To visualize how to model works: say an array of camera traps is deployed randomly across a study landscape, and set to take images every hour, on the hour (i.e., hourly sampling occasion). After image collection, for each occasion, images are "drawn" from cameras in random order, until an image of an animal is picked (Moeller et al. 2018). An example encounter history after 7 sampling occasions (e.g., 7 hours), for which the average viewshed area a is 20 m^2, might look like: {NA, 40 m^2, NA, NA, 1180 m^2, NA, 800 m^2}, where 40 m^2 indicates that images from 2 cameras had to be drawn before observing an animal, 1180 m^2 indicates images from 59 cameras had to be drawn, and so on; and NA indicates no animal detections for that occasion. This encounter history – which summarizes the space until detections – can then be plugged into a modified TTE equation to produce a density estimate (Moeller et al. 2018).

As with the TTE, the average area of a camera viewshed is calculated using the equation:

$$a = \pi r^2 \frac{\theta}{360}$$

where r is detection distance and θ is the angle of the camera lens in degrees (Moeller et al. 2018). r – instead of being the maximum distance at which an animal can trigger a camera's motion sensor, however, as it is for the TTE – is simply the maximum distance at which an animal is identifiable, and is measured using landmarks as references (Gilbert et al. 2021, Moeller et al. 2018).

Assumptions

The STE model makes the same assumptions as the TTE model (see above). Note, however, that assumption 4 – perfect detection – is much more likely to be met when

using the STE, since the model uses time-lapse instead of motion-triggered images. When camera viewsheds are clear and open, animals will be detected with reasonable certainty using the time-lapse function (Moeller et al. 2018).

Advantages and Limitations

Advantages	Limitations
- The STE model does not require measurements of animal movement speed (Moeller et al. 2018). Instead, sampling occasions are collapsed into instants in time using camera traps' time-lapse function. - The STE is not biased by animal movement speed (i.e., animals travelling slow vs fast). This contrasts with the TTE, which is sensitive to animal movement speed (i.e., more reliable when animals move quickly; Moeller et al. 2018). - Like the TTE, the STE does not rely on counts of animals in images; practitioners need only record whether any animals were in the viewshed at each camera during a sampling occasion (Moeller et al. 2018). Thus, the model is unaffected by weather, travelling and investigative behaviour, obstructions, camera malfunctions and other factors that make accurately counting the number of individuals challenging (Moeller et al. 2018). - The STE uses time-lapse images. Unlike motion-triggered images, there is essentially no uncertainty in detection probability when using time-lapse images (Moeller et al. 2018). - As with the TTE, STE studies are simple to scale up or down. The number of cameras – and not camera density – determines the precision of estimates (Loonam et al. 2021a). 100 cameras can be used to estimate density in a large area just as effectively as a small area (Loonam et al. 2021a).	- The model does not apply well to very rare species, as detections of animals from randomly-placed cameras in time-lapse images can be too few to draw meaningful conclusions (Loonam et al. 2021b, Moeller et al. 2018). Population density must be sufficiently high to ensure an adequate number of animal detections – although deploying more cameras can also increase the number of detections (Loonam et al. 2021a, Moeller et al. 2018). - Because animal movement speed is not an input, the STE is less precise than the TTE (Loonam et al. 2021a, Moeller et al. 2018). - Depending on the time-lapse interval chosen, the STE can produce a lot of images (Morin et al. 2022). For example: Loonam et al. (2021a) captured time-lapse images every 5 minutes at about 70 cameras for two-to-three winters, resulting in hundreds of thousands of images. - Unlike the TTE, the STE cannot can account for spatial variation in density (Gilbert et al. 2021).

Simulations and Field Studies

Random walk simulations show that the STE – unlike the TTE – is insensitive to movement speed (Moeller et al. 2018). This means that the model produces unbiased estimates of density, whether animals move slowly or quickly.

The STE has been field-tested on high-density ungulates and low-density carnivores in Idaho:

- In Idaho, the STE produced an estimate of elk density comparable to an aerial survey and the TTE (Moeller et al. 2018). The precision of STE and TTE estimates was similar in this system.

- For wolves – a low-density, social species – the STE yielded densities close to those from a parallel DNA mark-recapture study (Ausband et al. 2022). STE-derived results were less precise, however. Density was also significantly overestimated during one survey period (before data transformation) because of high detection rates at a single camera (Ausband et al. 2022). The researchers recommended bootstrapping (i.e., resampling a data set with replacement) to correct estimates when a camera collects too few or too many images.

- The model performed comparatively poorly for low-density, solitary cougars; STE estimates were less precise and more variable than those from genetic mark-recapture and the random encounter model (REM; see *2.2.3 Random Encounter Model*; Loonam et al. 2021a). Small sample sizes (i.e., few occasions with images of cougars) contributed to the STE's inconsistency (Loonam et al, 2021a). It is worth noting, however, that genetic mark-recapture-based estimates were also fairly inconsistent, and density was not calculable during some surveys due to a lack of recaptures, despite considerable field effort (Loonam et al. 2021a). The STE may therefore still be an efficient alternative to DNA mark-recapture.

Instantaneous Sampling

Moeller et al. (2018)	
Assumptions	**Data Needed**
1) population closure	☐ counts of individuals in images
2) independent detections	☐ viewshed area
3) random camera placement	
4) perfect detection	

How the Model Works

The instantaneous sampling model (IS) is an extension of the space-to-event model (STE; see above) that uses counts of animals in time-lapse images – instead of the area until an animal is first detected – to estimate density (Moeller et al. 2018). As with the STE, all cameras in a randomly-deployed array are programmed to take time-lapse images at predefined intervals (e.g., every hour) to get instantaneous "snapshot" samples of the study area. During image processing, the number of animals in each photograph is recorded. Thus, the IS is essentially a series of fixed-area point counts (Moeller et al. 2018): camera traps act as "standing observers" tabulating the number of individuals seen within a set area and time.

The IS equation is as follows:

$$D = \frac{1}{JM} \times \sum_{j=1}^{J} \sum_{m=1}^{M} \frac{n_{mj}}{a_{mj}}$$

where J is the total number of sampling occasions, M is the total number of camera stations, and n_{mj} is the count of animals in the viewshed and a_{mj} is the area of the viewshed at station m on sampling occasion j (Moeller et al. 2018).

Assumptions

The first four assumptions of the time-to-event (TTE; see above) and STE models – 1) the study population is closed, 2) detections are independent, 3) cameras are deployed randomly on the landscape and 4) detection is perfect – also apply to the IS model. Unlike its sister models, however, the IS does not assume that animals are Poisson distributed across the landscape. Thus, the relative "clumpiness" (i.e., grouping) or "evenness" (i.e., territoriality) of animals does not impact the model's performance, making the IS more flexible than the TTE and STE (Moeller et al. 2018).

Advantages and Limitations

Advantages	Limitations
- The IS model does not require measurements of animal movement speed, since sampling occasions are collapsed into moments in time (Moeller et al. 2018). - As with the STE – and in contrast to the TTE – the IS is not biased by animal movement speed (Moeller et al. 2018). It is similarly robust, whether animals move slowly or quickly. - Like the STE, the IS uses time-lapse images, for which there is essentially no uncertainty in detection probability (Moeller et al. 2018). - IS studies – like TTE and STE studies – are simple to scale up or down. The number of cameras, not camera density, determines the precision of estimates (Loonam et al. 2021a). 100 cameras can be used to estimate density in a large area as effectively as in a small area (Loonam et al. 2021a). - The IS does not make assumptions about animal distribution. Both the TTE and the STE assume animals are Poisson-distributed across the study landscape; clumped or overly-dispersed spatial patterns violate this assumption. The IS does not assume animals are Poisson-distributed, so is more flexible than its sister models (Moeller et al. 2018).	- The IS requires counts of animals. Accurately counting animals in camera trap photos can be challenging; weather, animal behaviour, obstructions and camera malfunctions – among other factors – can impact visibility and clarity, and thus image processors' ability to effectively count individuals (Moeller et al. 2018). - Because it relies on time-lapse images at randomly-placed cameras, from which detections can be sparse, the model does not apply well to very rare species (Loonam et al. 2021b, Moeller et al. 2018). Practitioners can, however, deploy more cameras to bolster the number of detections (Loonam et al. 2021a, Moeller et al. 2018). - Setting cameras to take time-lapse images at frequent intervals (e.g., every 5 minutes) can produce an immense amount of data to process (Loonam et al. 2021a, Morin et al. 2022). - The IS cannot account for spatial variation in density (Gilbert et al. 2021). - The IS is the least precise of its sister models (Moeller et al. 2018).

Simulations and Field Studies

The IS is relatively untested opposite its sister models. Simulations have shown that the IS is unbiased to animal movement speed or population size, so is applicable to slow- and fast-moving animals and to low- and high-density populations (Moeller et al. 2018). When tested on a population of elk in Idaho, the IS produced a similar density estimate as an aerial survey, but which was less precise than both TTE- and STE-derived estimates (Moeller et al. 2018).

2.2.7 Site-Structured Models

Royle (2004), Royle and Nichols (2003)	
Assumptions	**Data Needed**
1) population closure 2) independence of detections 3) cameras have discrete effective sampling areas 4) equal detection probability across individuals 5) no double-counting or misidentification of animals	☐ counts of individuals in images during each survey occasion (Royle-Nichols) ☐ detections-nondetections of animals during each survey occasion (N-mixture)

How the Models Work

Site-structured models were initially developed for abundance estimation from human-observer point count surveys, but can also be used to estimate density from camera trap studies. Unlike most other camera-based density models, which sample one population using many cameras, site-structured models treat each camera as though it samples its own distinct population within a larger meta-population (Burton, personal communication). And because the "population" of animals at each camera station moves beyond the sliver of area sampled in the camera viewshed, the total area each camera samples (i.e., its effective sampling area) is some larger area around the viewshed (Figure 13; Gilbert et al. 2021). Thus, site-structured models estimate density by measuring abundance at each
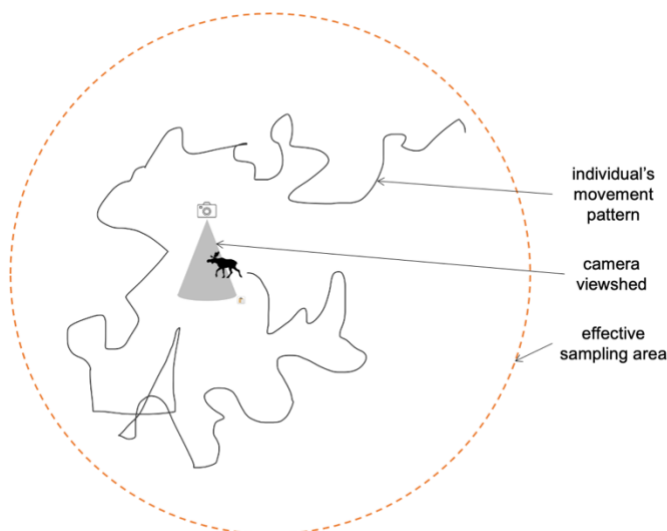

Figure 13. The effective sampling area of a camera station extends beyond its viewshed to encompass the area used by the "population" it samples. Effective sampling area is thus a function of animal movement (and study duration; Gilbert et al. 2021).

camera trap, dividing these camera-specific abundances by each camera's effective sampling area, and extrapolating estimates to the total study area (i.e., the sampling frame; Figure 14). Effectively, density is extrapolated twice: once from the level of the viewshed to the level of the effective sampling area, and once from the level of the effective sampling area to the level of the sampling frame.
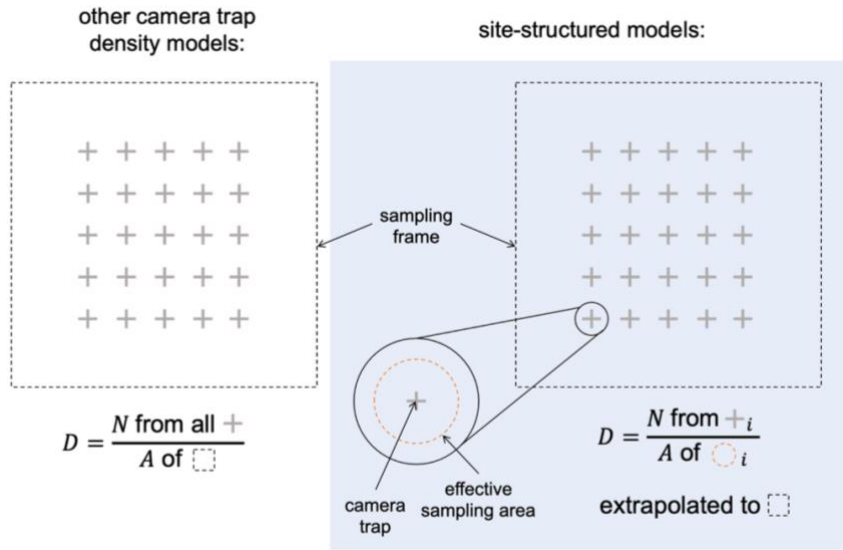
Figure 14. Comparative illustration of site-structured density models. On the left: camera-based models typically measure abundance N using data from all cameras (grey crosses) in a network, and divide N by the area of the sampling frame A to obtain a density estimate. On the right: site-structured models estimate density for every camera station, using site-specific abundance and effective sampling area. These density estimates are then extrapolated to the entire sampling frame. The subscript i refers to camera location i.

There are two classes of site-structured models: Royle-Nichols (RN) and N-mixture (NM) models. An RN model uses binary detection-nondetection data (i.e., 1s and 0s) to estimate site-specific density (Royle and Nichols 2003). An N-mixture (NM) model uses count data to estimate site-specific density (Royle 2004).

Assumptions

1) Population closure. A study population should not experience any births, deaths, immigration or emigration during the study period (Royle 2004, Royle and Nichols 2003). This assumption is critical for NM models. Practitioners must balance the need for population closure with study duration, as longer studies can improve estimates but are also more likely to violate assumption 1.
2) Detections are independent. An animal detected during one survey occasion should not be any more or less likely to be detected during subsequent occasions (Gilbert et al. 2021).

3) The effective sampling area of each camera is discrete. Camera stations should therefore be spaced far enough apart that effective sampling areas do not overlap, so animals are not detected at more than one camera station (Gilbert et al. 2021).

4) All animals are equally likely to be detected. Detection probability should not be biased towards certain individuals or demographics.

5) Individuals are not misidentified or miscounted. In other words: repeat detections of one individual are not misinterpreted as singular detections of many different individuals (Nakashima 2020). Such errors are sometimes called "false positives," and can inflate population size (and therefore density; Gilbert et al. 2021, Nakashima 2020). Both the RN and the NM appear to be robust to violations of this assumption (Nakashima 2020).

Advantages and Limitations

Advantages	Limitations
- Site-structured models rely on independent animal detections. Camera stations must be spaced far apart (i.e., more than one home range distance from each other) – so large areas can be sampled using relatively few cameras.	- Area is determined *ad hoc* (i.e., not measured explicitly) at two spatial scales. At the camera trap level: the effective sampling area is unknown. Effective sampling area is a function of animal movement and survey length (Figure 13; Gilbert et al. 2021); because animal movement is not measured, detections-nondetections (RN) or counts (NM) at a camera are assumed to represent some vague area several m^2 or km^2 around the camera. Some studies incorporate measures of average home range size (obtained via telemetry) to better estimate effective sampling area. At the study level: the total area sampled by the camera network is never explicitly measured, rendering site-structured density estimates fairly arbitrary.
- Unlike many other unmarked density models, site-structured models allow for non-random camera placement. Cameras can be targeted (e.g., set on trails/roads) and even baited (Gilbert et al. 2021).	
- Site-structured models can be used to estimate density at very large spatial scales, so are well-suited to species with large ranges (Morin et al. 2022).	
- Habitat characteristics that influence spatial variation in density can be estimated directly in site-structured models (Royle 2004, Royle and Nichols 2003).	- Because abundance is estimated per camera station, animals cannot be detected at more than one camera in an array. Overlapping detections result in overestimates of density (Suwanrat et al. 2015).
- RN models are well-suited to low-density populations, like rare and territorial carnivores (Furnas et al. 2017, Royle and Dorazio 2008).	- Site-structured models are sensitive to assumption violations and, when their assumptions are not met, are best viewed as

indices of density (see *2.2.8 Indices of Density*; Gilbert et al. 2021).

- Site-structured models may not be appropriate for medium-to-large mammals at small spatial scales (Morin et al. 2022).

- RN is not suitable for moderate- to high-density populations. At high densities, animals are likely to be captured at many camera stations, rendering detection-nondetection data difficult to interpret (i.e., too many 1s to draw meaningful conclusions; Gilbert et al. 2021).

- NM models should not be used to estimate absolute density unless the assumption of population closure can be met (Morin et al. 2022, Royle 2004).

- NM is only appropriate for solitary, territorial species (Morin et al. 2022).

Simulations and Field Studies

Camera-based site-structured models have not been extensively tested on medium-to-large mammals. There are, however, some examples of camera trap RN and NM for bird and small mammal density estimation:

- Camera trap RN and NM were found to produce density estimates comparable to spot-mapping – a well-established methods of measuring bird density – for ground-dwelling fowl. RN- and NM-derived density estimates were more accurate and precise than line-transect distance sampling (DS; see *2.2.2 Distance Sampling*; Suwanrat et al. 2015). Effective sampling area was estimated using data from a simultaneous telemetry study, and defined as the circular area around a camera trap with radius equal to the diameter of an average home range (Suwanrat et al. 2015).

- For fisher in the northwestern United States, the RN model yielded density estimates similar to independent estimates using other techniques (Furnas et al. 2017). The researchers estimated effective sampling area by pooling home range size estimates from telemetry and trapping studies previously carried out in their focal area, modelling how home range size changed with sex and distance

inland, and considering home range size for the research period (autumn; Furnas et al. 2017).

2.3 Partially Marked Populations

2.3.1 Spatial Mark-Resight

Chandler and Royle (2013), Sollmann et al. (2013a)	
Assumptions	**Data Needed**
1) population closure	☐ individual detection histories
2) no loss or misidentification of marks	☐ camera-specific counts of animals
3) inability to identify marked animals is random	☐ camera trap coordinates
4) marked animals are random subset of population (conventional model)	

How the Model Works

We have already discussed spatially-explicit density models for completely marked populations (spatial capture-recapture, SCR; see *2.1.2 Spatial Capture-Recapture*) and completely unmarked populations (spatial count, SC; see *2.2.1 Spatial Count*) – but what about the "intermediate" situation, in which only a fraction of a population carries marks? Spatial mark-resight (SMR) models were developed for such scenarios.

First, let's familiarize ourselves with non-spatial mark-resight models (or simply mark-resight models). Mark-resight models are similar to capture-recapture (CR; see *2.1.1 Capture-Recapture*) models, but relax CR's stipulation that all animals in a study population are individually identifiable – that is, that all animals carry unique natural marks, or that all animals are trapped and tagged (Royle et al. 2014, Sollmann et al. 2013a). Instead, mark-resight models need only a subset of the population to be marked (either naturally or from a single trapping-and-tagging event; Sollmann et al. 2013a). The entire population is then resighted using a "non-invasive" survey technique (i.e., a method that does not require the handling of animals, like an aerial or camera trap survey; Royle et al. 2014, Sollmann et al. 2013a) and population size is calculated using the equation:

$$N = m + \frac{u}{p}$$

where m is the number of marked animals, u is the number of unmarked animals and p is detection probability – the latter of which is determined using data from marked individuals only (Chandler and Royle 2013). Dividing N by the area of the sampling frame A produces an estimate of total population density.

SMR models integrate spatial information into the mark-resight framework. The result is a hybrid model that combines data from the detection histories of marked individuals, as per SCR, with site-specific counts of unmarked individuals, as per SC (Royle et al. 2014). For the remainder of this section, we will discuss camera trap SMR, for which animals are resighted using camera trap arrays.

The first SMR model, developed by Chandler and Royle (2013) and Sollmann et al. (2013a) and now coined "conventional SMR," models the resighting process only (i.e., ignores the marking process; Whittington et al. 2018). In doing so, conventional SMR makes the implicit assumption that marked animals are a random subset of the study population, and thus that 1) marked and unmarked animals are distributed similarly across the landscape, and 2) marked and unmarked animals have equal detection probabilities (Royle et al. 2014, Whittington et al. 2018). Such assumptions can hold – for example, when a random subset of the population carries natural marks, or when a closed population of animals is trapped and tagged at random locations (Sollmann et al. 2013a, Rich et al. 2014, Whittington et al. 2018). These assumptions are violated, however, when animals are trapped and tagged non-randomly (e.g., owing to inaccessibility, rough terrain) before resighting, since the distribution of marked animals will be clustered around trapping-and-tagging sites, and marked animals will have a higher chance of being detected at camera traps near where they were tagged (Whittington et al. 2018).

To ease the assumptions and address the limitations of conventional SMR, Whittington et al. (2018) developed generalized SMR, which models the marking and resighting

processes separately. The marking sub-model describes where animals were trapped and tagged on the study landscape – that is, how marked individuals are distributed in space (Jiménez et al. 2019). Explicitly modelling the marking process allows practitioners to trap and tag animals non-randomly (e.g., using linear or grid trap layouts) without biasing density estimates (Whittington et al. 2018). The resighting sub-model combines marked individuals' detection histories, camera trap-specific counts of unmarked individuals and estimates of detection probability to determine population density (Whittington et al. 2018).

Practitioners should note that the number of marked animals in a population can influence the precision of SMR studies. The general trend in precision, based on previous SMR studies (both conventional and generalized), is: the more marked animals, the more precise the density estimation (see Whittington et al. 2018). Of the four studies compared, only those with 22 or more marked individuals achieved coefficients of variation (CVs) below the accepted threshold for wildlife management (i.e., CV $\leq$ 0.2; Sollmann et al. 2013a, Whittington et al. 2018, Williams et al. 2002).

Assumptions

SMR makes the same assumptions as SCR and SC, plus the following assumptions:

1) No loss or misidentification of unique marks. The former means that marked animals do not "become" unmarked part-way through a study, and thus erroneously lumped in with the unmarked subset of the population. The latter means that animals are correctly identified as either marked or unmarked, and that, for marked individuals, the correct identities are assigned to the correct individual (or they are placed in a separate category, marked but not identifiable; Royle et al. 2014, Sollmann et al. 2013a).
2) Failure to identify marked individuals is random. More specifically, failure to identify marked animals is not linked to any particular demographic or spatial location (Royle et al. 2014).

3) Marked animals are a random subset of the population. For conventional SMR: marked animals should represent both the demographic composition and the spatial distribution of the larger population (Royle et al. 2014). This assumption is violated when certain groups of animals are more likely to be marked (e.g., only males are trapped and tagged), or when marked animals are clustered in particular areas or habitat types (e.g., animals are trapped and tagged only at the centre of the sampling frame; Royle et al. 2014). To avoid the latter, practitioners can trap and mark animals uniformly across the state space, or implement generalized SMR (Whittington et al. 2018).

Advantages and Limitations

Advantages	Limitations
- SMR "bridges the gap" between SCR and SC: it relaxes SCR's requirement that all individuals are marked and uniquely identifiable, but is more precise than SC (Morin et al. 2022). - SMR studies can capitalize on pre-existing tagging or collaring projects, thereby extracting as much information as possible from invasive physical-trapping methodologies (Fennell, personal communication). - An extension of generalized SMR allows images of unmarked, marked and marked-but-unidentifiable individuals to be included in density estimates (Jiménez et al. 2019).	- SMR performs poorly when resightings are few – either because too few animals are marked, or cameras are spaced too far apart (Sollmann et al. 2013a). The number of resightings should be about double the size of the population (Arnason et al. 1991). - Because SMR is an SCR-SC hybrid, it, like SCR and SC, is difficult to scale up. Each animal must be detected at multiple camera stations, which requires high camera density (Ausband et al. 2022, Chandler and Royle 2013, Loonam et al. 2021).

Simulations and Field Experiments

Kane et al. (2015) used conventional SMR to estimate lion density in Senegal, and found that – even with relatively few camera traps – SMR-derived density estimates were more precise than previous track survey- and expert opinion-derived estimates (Henschel et al. 2014). Nine lions were identified using natural features, such as scars, missing tail tips and the condition of the mane (Kane et al. 2015).

SMR models have also been tested in western Canada. In southern BC: generalized SMR produced higher, more precise estimates of mountain goat density than camera

trap SCR (Fennell 2022). Across three years, SMR estimates had a mean CV of 0.20, while SCR estimates had a mean CV of 0.40 and never dipped below 0.20 (Fennell 2022). In this system, 12 goats were marked (Fennell 2022). In Banff National Park: generalized SMR and genetic SCR produced comparable estimates of grizzly bear density, while conventional SMR underestimated density compared to genetic SCR (Whittington et al. 2018). In this system, generalized SMR produced accurate estimates of grizzly bear density, even though marked bears were clustered in certain parts of the landscape (Whittington et al. 2018). 22 bears were marked and individually identifiable (10 females, 12 males).

As a complement to the grizzly bear field study, Whittington et al. (2018) also performed simulations to test the effects of linear, grid and random marking trap configurations. They found that, regardless of trap design, generalized SMR yielded unbiased estimates of density. Conventional SMR, on the other hand, yielded biased estimates when traps were non-randomly dispersed.

2.3.2 Spatial Partial Identity Model

Two-Flank Spatial Partial Identity Model

Augustine et al. (2018)	
Assumptions	**Data Needed**
1) population closure	☐ individual detection histories
2) independence of detections	☐ camera trap coordinates
3) activity centres randomly dispersed	
4) activity centres stationary	
5) activity centres isotropic	
6) both-side, right-side and left-side captures are independent	

How the Model Works

The two-flank spatial partial identity model (2-flank SPIM) is an extension of camera trap spatial capture-recapture (SCR; see *2.1.2 Spatial Capture-Recapture*). Camera trap SCR uses images of uniquely-identifiable animals to infer the number of activity (or home range) centres in a population, and the area bounding these activity centres – or population size N and sampling frame A, respectively (see *How the Model Works* in the SCR section). Oftentimes, individual identities are linked to animals using a paired camera sampling design: two cameras are deployed per station, facing each other, to capture the left and right flanks of a passing animal simultaneously. This design ensures that a single identity is linked to both sides of an individual (i.e., an individual's identity is completely resolved; Augustine et al. 2018). Single-sided captures (e.g., due to unpaired sampling design, camera failure, unclear images, obstructions) cannot be used to resolve an individual's identity with certainty, as separate identities can be erroneously assigned to the left and right sides of the same animal. Single-sided images are therefore partially-identifying, and are often excluded from analyses, resulting in loss of data and compromised density estimates (Augustine et al. 2018).

The 2-flank SPIM draws on the locations of partially-identifying images captures to probabilistically resolve animals' complete identities (Augustine et al. 2018). Partially-identifying captures that are many home ranges apart, for example, are not likely to belong to the same individual; left-and-right flank images captured at the same camera station in quick succession, on the other hand, are likely to belong to the same individual (Augustine et al. 2018). Thus, the 2-flank SPIM is essentially an SCR model augmented with data from partially-identifying images (i.e., "SCR+").

Assumptions

The 2-flank SPIM makes the same assumptions as SCR, but also assumes that left-only, right-only and both-side image capture processes are independent (Augustine et al. 2018). This assumption allows us to model detection probability per outcome – that is, for both-side, right-side and left-side captures – instead of modelling the detection probability for each camera in a pair (since a pair of cameras is meant to trigger at the same time, so detection probability should be the same for both; Augustine et al. 2018).

Advantages and Limitations

Advantages	Limitations
- Partial identification is a common issue with camera trap SCR (Davis et al. 2021). The 2-flank SPIM can resolve individuals' complete identities from partially-identifying images, and can thus improve the precision of density estimates (Davis et al. 2021).	- 2-flank SPIM analyses can be computationally demanding (Augustine et al. 2018).
- The 2-flank SPIM can be applied to camera trap surveys of various designs: paired-camera stations, single-camera stations, and hybrid configurations with both paired- and single-camera stations (Augustine et al. 2018, Davis et al. 2021).	- Increases in precision will be most pronounced in low-density populations (Augustine et al. 2018, Davis et al. 2021).
- Because it can be used with single-camera and hybrid sampling designs, the 2-flank SPIM can be implemented with fewer cameras than standard camera trap SCR (Davis et al. 2021). Alternatively, more area can be covered using the same number of cameras (Davis et al. 2021).	

Simulations and Field Studies

Simulations show that the 2-flank SPIM improves density estimates – especially when populations are small and few individuals can be completely identified (Augustine et al. 2018). Moreover, the 2-flank SPIM performed better when camera stations were regularly spaced and deployed close to one another relative to animals' home range sizes (Augustine et al. 2018).

In the field: Augustine et al. (2018) found that the 2-flank SPIM improved inference (i.e., accuracy and precision of estimates) for both a paired-camera survey of ocelots and a single-camera survey of bobcats. The 2-flank SPIM also produced estimates of leopard and spotted hyaena density that were more precise than SCR (Davis et al. 2021).

Categorical Spatial Partial Identity Model

Augustine et al. (2019)	
Assumptions	**Data Needed**
1) population closure 2) independence of detections 3) activity centres randomly dispersed 4) activity centres stationary 5) activity centres isotropic 6) every individual has a full categorical identity	☐ camera-specific counts of animals ☐ camera trap coordinates ☐ categorical identifiers

How the Model Works

The categorical spatial partial identity model (catSPIM) is an extension of the spatial count (SC; see *2.2.1 Spatial Count*) model. It was originally developed for use with genetic capture-recapture studies, but can also be applied to camera trap studies (Augustine et al. 2019). Here, we will discuss the camera trap catSPIM.

Camera trap SC uses the number and location of unmarked animal detections to infer the number and location of activity (or home range) centres, which can then be used to infer population density (see *How the Model Works* in the SC section). With SC, individual identities are not known and cannot be resolved with any certainty. The catSPIM incorporates categorical information (i.e., information that can be divided into distinct groups) into the SC model to partially-resolve unmarked animals' identities. Said differently: instead of viewing animals as completely unidentifiable and relying exclusively on model parameters to tease individuals apart, as SC does, the catSPIM uses model parameters and suites of traits to help distinguish animals – even if incompletely (Sun et al. 2022). Thus, catSPIM can be thought of as "SC+": an SC model augmented with categorical identifiers.

Examples of categorical identifiers include sex, age class, colour type, markings and antler point count (Augustine et al. 2019, Sun et al. 2022). Each categorical identifier

(e.g., sex) has a fixed number of possibilities (e.g., male/female). Every animal detection is assigned a "full categorical identity," or a set of traits given all categorical identifiers and possibilities (Augustine et al. 2019).

Categorical identifiers are used to partially-distinguish unmarked animals in three ways:

1) Deterministic identity exclusion. This means that animals that differ in one or more categories cannot be the same individual (Augustine et al. 2019). This makes intuitive sense: an adult, female, brown animal cannot be the same individual as an adult, female, black animal, for example.

2) Categorical probabilistic identity association. This means that animals that share categorical identifiers are more likely to be the same individual (Augustine et al. 2019). The catSPIM's power to resolve individuals' identities increases with the number of categorical identifiers in a full categorical identity and the number of possibilities per categorical identifier, since individuals become increasingly unique (Sun et al. 2022).

3) Spatial probabilistic identity association. The spatial pattern of detections and the size of animals' home ranges limit which detections can be assigned to the same individuals (Augustine et al. 2019). As a simple example: an adult, female, collared elk is detected at two camera traps, many home ranges apart. We can deduce that the elk captured at one camera is not likely to be the same as the elk captured at the other camera, since it is improbable an individual elk would travel that far.

Assumptions

The catSPIM makes the same assumptions as SC, plus one additional assumption: that each individual has a full categorical identity (Augustine et al. 2019). The model likewise assumes that we know every possibility for every categorical identifier, and that possibilities occur with predictable probabilities (Augustine et al. 2019, Sun et al. 2022). These assumptions allow us to assign identities to animal detections.

Advantages and Limitations

Advantages	Limitations
- The catSPIM has the potential to produce density estimates that are nearly as precise as SCR, with less information (Augustine et al. 2019).	- The catSPIM is sensitive to group-travelling behaviour – a violation of the assumption of detection independence (Sun et al. 2022). (Sun et al. 2022). The model may be most appropriate for solitary species (Sun et al 2022).
	- To properly identify and link detections to individuals: practitioners must use enough categorical identifiers with enough possibilities (Sun et al. 2022). Too few identifiers/possibilities can lead to identity misassignments and overestimations of population density (Sun et al. 2022).
	- The catSPIM may work best for low-density populations (Agustine et al. 2019, Sun et al. 2022).

Simulations and Field Studies

Sun et al. (2022) tested the catSPIM on two caribou populations in the Alberta oil sands region. They found that, compared to SC, the catSPIM was more precise and consistent year-to-year – but that it was still fairly imprecise. The catSPIM may also have produced overestimates of density in this system. Any overestimates would likely have been caused by misassigning identities (more specifically, by assigning identities to individuals that didn't exist – that is, individuals that were in the augmented population M but not the actual population N; see *How the Model Works* in the SC section) and could be mitigated by increasing the number of categorical identifiers used (Sun et al. 2022). The researchers used three categorical identifiers for this study: sex (male/female), presence of collars (collared/not collared) and antler point count (0 to 17), which they suggest is too few (Sun et al. 2022).

Field data-based simulations showed that the catSPIM was less biased and more precise than SC (Sun et al. 2022).

Box 2. Note the distinction between SPIMs and spatial mark-resight (SMR; see *2.3.1 Spatial Mark-Resight*) models: SPIMs are for partially-identifying sets of images (two-flank SPIMs) or individuals that are themselves partially-marked, whereas SMR deals with partially-marked populations in which some animals are uniquely marked and identifiable and others are unmarked and unidentifiable.

2.4 Indices of Density

An index is a value that is assumed to be related to a measure of interest (Thompson et al. 1998). For example: unemployment levels are used an index of economic state (Cambridge Dictionary 2022); an unemployment rate of 20% might signal a poorer economy than an unemployment rate of 5%. In wildlife ecology, practitioners may choose to measure indices of density if estimates of absolute density are not needed – for example, if the focus of a study is on relative differences across space (e.g., habitats, parks), time or species – or if density estimation study is not feasible (O'Brien 2011, Sollmann et al. 2013b).

Note: in the sections below, we will mainly refer to abundance – and not density – as the indices discussed are used to make inferences about abundance. Such measures can be converted to density by dividing by the area of the sampling frame. As with many of the models mentioned in this review, however, the sampling frame is often arbitrarily defined.

2.4.1 Relative Abundance

In ecology, relative abundance (RA) is any count of animals or animal sign (e.g., number of deer sighted, number of bird vocalizations per unit time, number of moose tracks per kilometer of transect) that is assumed to correlate with absolute abundance (O'Brien 2011). RA is a controversial index for two reasons: 1) there is often no documented relationship between the number of animals or signs observed and population size (i.e., index validation), and 2) detection probability is assumed to be constant between the areas, times or species being compared (O'Brien 2011, Thompson et al. 1998).

To the first point: the relationship between the number of animals or signs and abundance is rarely established (Burton et al. 2015). Researchers often assume that counts and population size scale linearly – but many other kinds of relationships are possible. When the assumed relationship between counts and abundance diverges from the actual relationship, inferences from RA are not very meaningful (Thompson et

al. 1998). Validating a count-abundance relationship requires comparison with a robust, accurate estimate of absolute density (e.g., Krebs et al. 1987, Rovero and Marshall 2009, Villette et al. 2016).

To the second point: consider the canonical equation,

$$N = \frac{C}{p}$$

where N is population size, C is the count of animals or signs and p is detection probability (Anderson 2001, Brennan 2019). This equation underlies many estimators of abundance, including capture-recapture (CR; see *2.1.1 Capture-Recapture*) and distance sampling (DS; see *2.2.2 Distance Sampling*) methods (O'Brien 2011). RA comparisons assume that detection probability p is constant across space, time or species, and can therefore be ignored (Anderson 2001, O'Brien 2011, Sollmann et al. 2013b), such that:

$$N \cong C$$

so count essentially becomes a surrogate for population size.

Assuming constant detection probability p is problematic, since the likelihood an animal or sign is counted during a survey will vary with observational, environmental, and habitat- and species-specific factors, which in turn can vary with time (Anderson 2001). For example: at site A, animals may be difficult to spot in dense vegetation, while at site B, animals may be easy to spot in open grassland; and the effects of vegetation on observability may differ seasonally. If the effects of vegetation on detectability are not accounted for, how can we be sure that differences in animal counts at site A and B are due to true differences in abundance, and not simply artefacts of detection bias (Sollmann et al. 2013b)?

In a camera trapping context, RA is the comparison of detection rates across space, time or species – where detection rates are typically reported as the number of images per 100 trap days, but can also be reported in terms of the total number of detections,

other units of effort (e.g., camera trap hours), proportion of stations with detections, etc. (Burton et al. 2015). As with other kinds of RA surveys, comparisons of camera trap detection rates can confound abundance with animal behaviour and observability (Anderson 2001, Burton et al. 2015).

RA has been criticized as an abundance estimator. Anderson (2001) condemned the index as "unprofessional," while O'Brien (2011) called it a "metric of last resort." Sollmann et al. (2013b) used simulations to determine that camera trap RA analyses did not detect changes in big cat density, and called use of the index for wildlife management "alarming." Nevertheless, some researchers have had success with the method and/or have argued for its conceptual and practical advantages (e.g., Carbone et al. 2001, Johnson 2008, Palmer et al. 2018, Rovero and Marshall 2009). Broadley et al. (2019) used simulations to show that RA could be sensitive to density-dependent movement, but generally tracked abundance well. Banks-Leite (2014) emphasized the importance of careful sampling design and protocols to control for variation in detectability, arguing that researchers should not solely rely on statistical corrections. Ultimately, there is no "silver bullet" and researchers must carefully consider their inferential objectives and potential sources of sampling and estimation bias when choosing response variables and modelling frameworks for camera trap data.

2.4.2 Occupancy

Occupancy models describe spatial patterns of animal occurrence (Sollmann 2018) and have been proposed as a proxy for abundance (Noon et al. 2012). They ask: what proportion of a study area is inhabited by a population – that is, at how many camera sites do one or more individuals of a species occur (MacKenzie et al. 2017)? The basic equation for occupancy is:

$$\psi = \frac{\hat{x}}{s}$$

where ψ is the probability a site is occupied, $\hat{x}$ is the estimated number of occupied sites (i.e., the count of sites where animals were detected, corrected for detection probability)

and s is the total number of sites surveyed (MacKenzie et al. 2017). Unlike simple measures of presence-absence, occupancy models account for imperfect detection (Sollmann 2018). They attempt to differentiate between absence – animals truly not present – and nondetection – animals present but not detected – by repeatedly sampling sites over time. The central assumption of basic occupancy models is that repeated samples occur during a period in which the site is closed to changes in occupancy (i.e., occupancy status – present or absent – does not change during the sampling period). Thus if a species is detected during one of three sampling occasions, it is assumed that it was present during all three occasions but undetected during two.

In theory, occupancy and abundance share a predictable relationship. As population size increases, the number of sites occupied by members of that population should also increase (until all sites are occupied); likewise, a decrease in population size should lead to a decrease in the number of sites used (Gaston et al. 2000, Royle and Dorazio 2008). This is called an occupancy-abundance relationship, and – because of it – occupancy can be used as an index of abundance.

Advantages of occupancy as an index of abundance include:

- Occupancy studies may be easier to implement than some abundance or density estimators (Noon et al. 2012, Sollmann 2018).
- Occupancy-abundance relationships appear to be robust to territoriality, group-travelling behaviour and other biological traits (Steenweg et al. 2018).
- Occupancy can be modelled as a function of site- and sampling-specific covariates to better understand which factors predict animal occurrence (Sollmann 2018).

However, many researchers have cautioned against the use occupancy as an index. As with relative abundance (RA; see above), there is no consistent, long-term relationship between occupancy and abundance (Efford and Dawson 2012). Occupancy can change with abundance, but also with survey duration, species home range size, animal movement, etc., muddling occupancy-abundance relationships and thus inferences

about population size (Neilson et al. 2018, Steenweg et al. 2018). While occupancy is a powerful stand-alone metric, Sollmann (2018) says it should not be "misinterpreted" as an index of abundance.

Despite its widespread use, occupancy may be particularly problematic for camera trap studies due to the violation of the closure assumption. Burton et al (2015) highlighted that many camera trap studies using occupancy do not explicitly define the "site," although is often implicitly given as some larger area around a camera trap. Since camera trap studies typically target mammal species with relatively large home ranges, the site closure assumption is almost certainly violated in most cases. Many camera trappers therefore assume that "occupancy" is in fact "use" of a site (i.e., the site is not closed), and that detection probability also includes availability for detection. Mackenzie et al. (2017) suggested that estimates should be unbiased if movements in and out of a site are random, but this assumption is rarely tested. And where occupancy estimates have been tested using realistic mammal movements, they have generally performed poorly (Neilson et al 2018, Stewart et al. 2018).

3. Recommendations and Decision-Making Tools

3.1 Recommendations

Camera traps are a viable tool to collect detection data that can be fit to density models.

Given the novelty of many camera trap density estimation models and the uncertainties (in sampling design, consistency, applicability, etc.) that remain, it is not possible to recommend one estimation model over another. Many models have yet to be rigorously and repeatedly validated; the effects of assumption violations and sampling design (e.g., trap configuration, trap spacing, number of cameras, study duration) on density estimates are not well understood for all models; and many models have yet to be extensively tested in landscapes and on species characteristic of BC (Gilbert et al. 2021, Jensen et al. 2022). Future work will need to address these knowledge gaps to provide practitioners with clearer guidelines. We do therefore recommend additional investment in field and simulation tests of camera trap density estimation models.

When practitioners choose to estimate population density with camera traps, they should start by asking themselves:

1) *Are density estimates needed?* Can project goals be achieved by measuring other, less-intensive metrics (e.g., relative abundance, occupancy)? Does the absolute number of individuals need to be known? Can variation in detection probability be reasonably well controlled by sampling design and protocol?
2) *Are camera traps the most appropriate tool/technique for density estimation?* Consider the study species, landscape and goals:
   a) are animals rare or common?
   b) how accessible is the study area?
   c) how big is the study area?
   d) are very precise estimates needed?
   e) etc.?

3) *Do the potential outcomes of camera trap data-based density estimation justify the cost and effort of implementation?*

If the answer to all questions is "yes," practitioners can select the model(s) best-suited to their particular study using the decision-making tools below (Figure 15 and Table 1) and by reading over the appropriate model overview sections and looking into key references.

While we do not recommend replacing existing monitoring and inventorying programs with camera trap density studies outright, we have identified several situations in which camera trap density estimation could be useful:

1) Camera surveys can complement infrequent inventories using other methods. Take, for example, the years-long gaps between aerial surveys in some wildlife management units (WMUs): camera arrays deployed in such WMUs could help fill temporal gaps in aerial survey data, improving the quality of inferences made from sporadic flights. Cameras could also be used to guide aerial survey priorities: management units with camera-derived densities falling below a certain threshold would be moved to the top of the list for the following year's aerial surveys ("two-stage adaptive management"; Becker et al. 2019, Conroy et al. 2008, Morin et al. 2022).

2) Camera surveys can provide density estimates for species which cannot be inventoried practically or reliably by other means. Cameras can provide baseline density data for rare and elusive carnivores, for example (Green et al. 2020). They may also be useful for censusing species like coastal black-tailed deer (look for report out of South Coast), which occupy densely forested habitats and thus cannot be surveyed from the air (BC Ministry of Sustainable Resource Management 2002).

3) Camera traps can also be used to estimate the densities of multiple species simultaneously (Burgar et al. 2019).

4) Camera-based density data can contribute valuable information to integrated population models – especially for areas or species with little data (Vander

Vennen, personal communication). Even imprecise estimates can be usefully incorporated.

Regardless of the extent of surveys or the analytical methods used, practitioners implementing camera trap density models should conduct simulations and power analyses. Before deployment: simulations and power analyses can help practitioners decide whether their planned study designs and sampling efforts are appropriate (Green et al. 2020, Morin et al. 2022). After data collection: simulations derived from field data can help us asses the robustness of our empirical studies and understand what might be limiting our ability to accurately and precisely estimate density (e.g., study duration, number of cameras, choice of density model, etc.; Burgar, personal communication). Simulations and power analyses should become standard practice.

When reporting results, practitioners should also specify what study design they chose and why, what assumptions were made, and the precision of estimates (Burton et al. 2015).

3.2 Decision-Making Tools
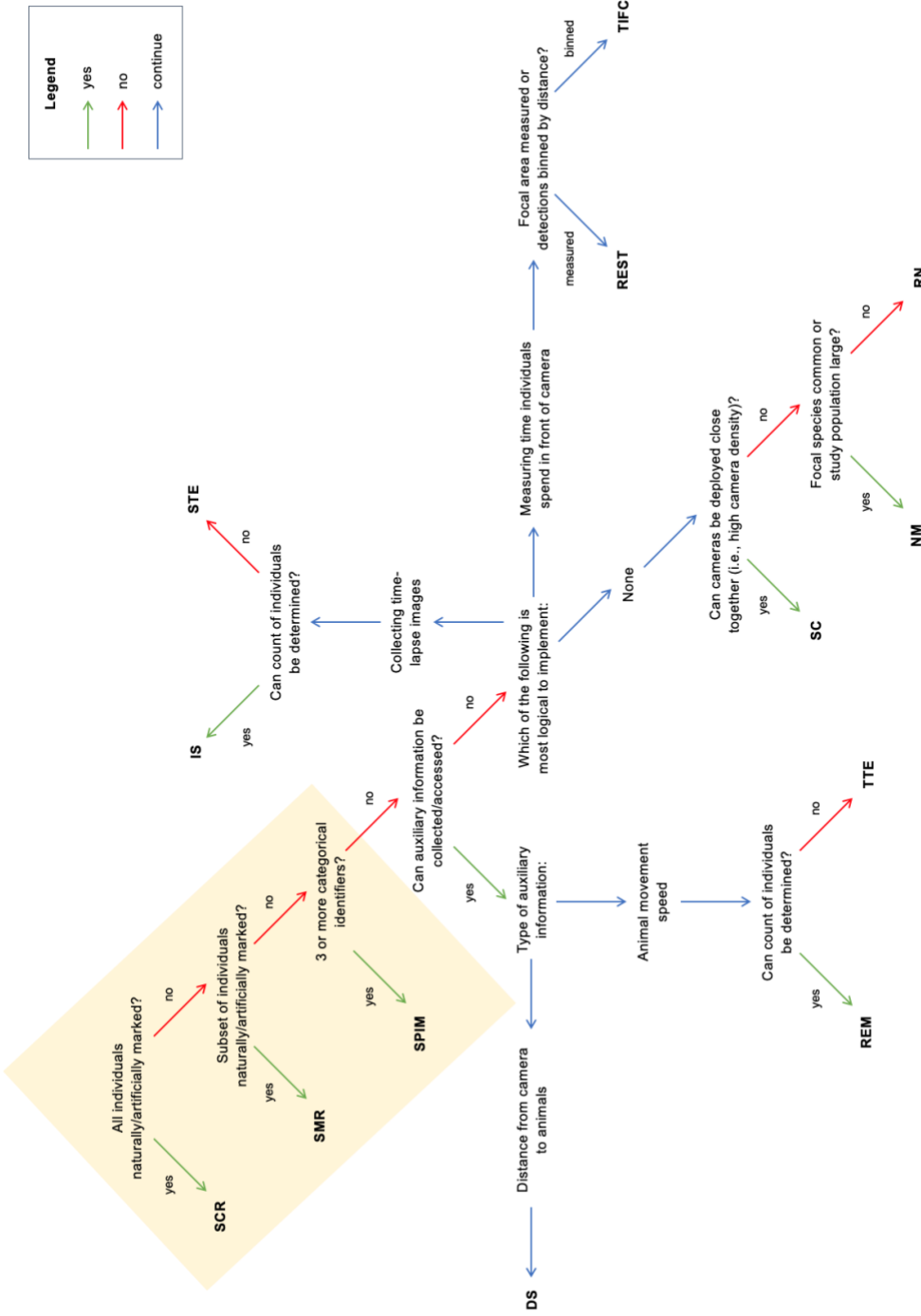
Figure 15. Adapted from Gilbert et al. (2021) and Sun (unpublished). Decision tree for selecting camera trap density models. The models in the yellow rectangle are for marked and partially-marked populations; the remaining models are for unmarked populations. Note, the models in this decision tree are not necessarily ordered from strongest to weakest, but rather are organized by key features.

Table 2. Quick-reference summary table of sampling design and population requirements, as well as available R packages/code, for camera trap density estimation models. Three dashes (---) signify that field is not applicable for the model.

MODEL	CAMERA CONFIGURATION	CAMERA SPACING	TARGET FEATURES?	SOLITARY OR GROUP-TRAVELLING SPECIES?	HIGH- OR LOW-DENSITY POPULATIONS?	R CODE
SCR	grid/clustered	close	yes	both	any	secr, oSCR packages, any Bayesian framework
SC	grid/clustered	close	yes	solitary	moderate	any Bayesian framework
DS	representative	---	no	---	any	Distance R package
REM	representative	---	no	both	moderate to high	https://github.com/timcdlucas/RandEM
REST	representative	far	no	both	---	Nakashima et al. (2018) – Appendix S1
TIFC	representative	---	no	---	high	https://github.com/mabecker89/tifc-method
TTE	representative	---	no	both	moderate to high	https://github.com/annam21/spaceNtime
STE	representative	---	no	both	moderate to high	https://github.com/annam21/spaceNtime
IS	representative	---	no	both	moderate to high	https://github.com/annam21/spaceNtime
RN	---	far	yes	---	low	unmarked package
NM	---	far	yes	solitary	moderate to high	unmarked package
SMR	grid/clustered	close	yes	solitary	---	https://github.com/benaug/Spatial-Mark-Resight
2-flank SPIM	grid/clustered	close	yes	---	---	https://github.com/benaug/SPIM
catSPIM	grid/clustered	close	yes	solitary	low	https://github.com/benaug/SPIM

4. Conclusion

Camera traps can be used to estimate the densities of marked, unmarked and partially-marked animal populations, with 17+ different models to choose from. This report provides examples of density estimators fit to camera detection data that perform well (i.e., accurately, precisely, consistently, as well or better than traditional density estimation methods, such as minimum count aerial surveys and genetic mark-recapture. This is consistent with other research that found ground-based surveys had less observation error than aerial-based surveys (Ahrestani et al, 2013). We have also shown that camera-based density estimation remains challenging. Every model discussed in this review has important advantages and limitations and makes critical assumptions; no method constitutes a "silver bullet."

Critics may point to the labour-intensiveness and cost of camera trap-based density estimation. We do not disagree – estimating density using camera traps can be a logistically-challenging, time-consuming and expensive endeavour. Camera trap surveys will not be feasible or efficient in certain landscapes (e.g., very rugged or inaccessible areas), and have significant field and image-processing requirements. Reliable camera trap models can cost over $500 CAD per unit (in 2022), limiting the number of cameras that can be deployed in an array and, therefore, spatial extent and statistical inference. In other scenarios, camera trap density estimation can be very effective and economical, however. In contrast to BC's standard inventorying methods (see *1.2 Provincial Standards for Density Estimation*), which all produce single-species density estimates, camera traps can generate density estimates for multiple species simultaneously (Burgar et al. 2019) – reducing the number of independent surveys that must be conducted, and thus overall cost. As camera traps detect multiple species over a longer time period than standard inventory methods, they also provide value-added information for multiple species that can be used to inform species knowledge (e.g., seasonal distribution patterns, daily activity patterns, habitat use, health, reproductive condition, etc.). Moreover, a cost comparison found that camera trap surveys cost as much or less than yearly aerial surveys (see *Appendix A*).

Critics may also point to the imprecision of camera trap-based density estimation. Unmarked models tend to suffer from imprecision without about 60+ camera stations or the inclusion of secondary data (e.g., telemetry data; Morin et al. 2022, Twining et al. 2021). Concern over precision is warranted: imprecise density estimates can lead to ineffectual or poor management decisions, or, in extreme cases, put populations at risk (Jiménez et al. 2017). But BC's standard density estimation methods are not necessarily more precise than camera-based models. Indeed, many do not account for detection probability and/or do not provide measures of precision (e.g., minimum count) – leaving practitioners to subjectively determine whether estimates are biased, accurate or precise.

We have devoted much of this review to the discussion of model assumptions and the effects of violating them. To produce meaningful density estimates, it is critical to understand the assumptions a model makes, how well a given population and study design might satisfy them, and what happens when they are violated. While assumption breaches should be minimized, it is also important to accept that wildlife populations will almost never meet every model assumption. Violations can, however, be acknowledged, measured and corrected for (Becker et al. 2022), and the robustness of estimates to violations can be transparently reported. The secondary information that cameras collect (e.g., behavioural responses) can help practitioners recognize and remediate biases (Becker et al. 2022).

BC's guidelines for monitoring and inventorying wildlife have guided managers for over two decades. They have been essential in standardizing methods and data and facilitating comparisons and collaborations. These guidelines no longer reflect the tools at wildlife managers' disposal, however. We identified a disconnect between which density estimation models are possible, known and applied by wildlife managers in BC. We sought to summarize and explain camera-based density estimation models, compare those models to one another and to other models/methods (e.g., aerial surveys, DNA mark-recapture), and build tools to help wildlife managers decide which camera trap models to implement on a case-by-case basis. Further work is needed before more general guidelines can be shared with practitioners, and before updates

can be made to BC's Resources Information Standards Committee (RISC) standards for medium-to-large mammal density estimation. We recommend additional field and simulation tests of camera trap density estimation models.

5. Glossary of Terms

Accuracy: How close a measured or estimated value is to the true value.

Camera trap day: 24-hour period during which a camera is functioning (Beirne, personal communication).

Coefficient of variation (CV): The dispersion in a data set, expressed as a percentage of the mean; a measure of precision (Whitlock and Schluter 2020). A high CV indicates more variability relative to the mean, and low precision; a low CV indicates less variability relative to the mean, and high precision.

Bias: Systematic inaccuracy in estimates (Hammond et al. 2021).

Detection probability: The likelihood an animal is captured by a camera trap; for some models, the probability that an animal is captured by a motion-triggered camera, given the animal is in the camera's viewshed (Moeller et al. 2018).

Power: The likelihood an effect is detected, given there is an effect to detect (Cohen 1992).

Precision: Uncertainty in estimates (Hammond et al. 2021).

Sightability: The ability to sight or spot animals.

Variance: The spread of numbers in a dataset compared to the mean of the dataset.

Viewshed: Depending on the method – the area within which an animal can trigger a camera trap to capture an image, or the total area a camera trap photographs (Gilbert et al. 2021). May also be referred to as the camera trap field-of-view.

6. Positionality Statement

The author of this document is a contracted employee of WildCAM, part of the BC Parks Foundation (a charitable organization). Holger Bohm, Provincial Ungulate Specialist with the BC Ministry of Forests, spearheaded this project and obtained funding; the Government of British Columbia has been a partner throughout. The author and collaborators all have backgrounds in camera trapping.

7. Acknowledgements

8. Literature Cited

中島啓裕. *Density Estimation with the REST Model.* Density Estimation with the REST Model, 2021. https://www.youtube.com/watch?v=s-d81K72yWs&list=PLNlLe3RjftYun9Xh2pJOAuisHaTVyEwAB&index=3.

Ahrestani, Farshid S., Mark Hebblewhite, and Eric Post. "The Importance of Observation versus Process Error in Analyses of Global Ungulate Populations." *Scientific Reports* 3, no. 1 (2013): 3125–3125. https://doi.org/10.1038/srep03125.

Alberta Environment and Parks. "Aerial Ungulate Surveys Using Distance Sampling Techniques – Protocol Manual," November 2016. https://open.alberta.ca/dataset/71c53d7b-0802-4800-9f95-0520b64b63c2/resource/ee933caa-bfc7-4334-a4d0-6085ebf198e7/download/aep-aerial-ungulate-surveys-using-distance-sampling-2016.pdf.

Amburgey, S. M., A. A. Yackel Adams, B. Gardner, N. J. Hostetter, S. R. Siers, B. T. McClintock, and S. J. Converse. "Evaluation of Camera Trap-based Abundance Estimators for Unmarked Populations." *Ecological Applications* 31, no. 7 (2021): 1-n/a. https://doi.org/10.1002/eap.2410.

Anderson, David R. "The Need to Get the Basics Right in Wildlife Field Studies." *Wildlife Society Bulletin* 29, no. 4 (2001): 1294–97.

Arandjelovic, Mimi, and Linda Vigilant. "Non-invasive Genetic Censusing and Monitoring of Primate Populations." *American Journal of Primatology* 80, no. 3 (2018): e22743-n/a. https://doi.org/10.1002/ajp.22743.

Augustine, Ben C., J. Andrew Royle, Marcella J. Kelly, Christopher B. Satter, Robert S. Alonso, Erin E. Boydston, and Kevin R. Crooks. "Spatial Capture–Recapture with Partial Identity: An Application to Camera Traps." *The Annals of Applied Statistics* 12, no. 1 (2018). https://doi.org/10.1214/17-AOAS1091.

Augustine, Ben C., J. Andrew Royle, Sean M. Murphy, Richard B. Chandler, John J. Cox, and Marcella J. Kelly. "Spatial Capture–Recapture for Categorically Marked Populations with an Application to Genetic Capture–Recapture." *Ecosphere (Washington, D.C)* 10, no. 4 (2019): e02627-n/a. https://doi.org/10.1002/ecs2.2627.

Ausband, David E., Paul M. Lukacs, Mark Hurley, Shane Roberts, Kaitlyn Strickfaden, and Anna K. Moeller. "Estimating Wolf Abundance from Cameras." *Ecosphere* 13, no. 2 (2022): e3933. https://doi.org/10.1002/ecs2.3933.

Baddeley, Adrian. "Spatial Point Processes and Their Applications." School of Mathematics & Statistics, University of Western Australia, no date.

Balestrieri, Alessandro, Aritz Ruiz-González, Maria Vergara, Enrica Capelli, Pietro Tirozzi, Sara Alfino, Gianmarco Minuti, Claudio Prigioni, and Nicola Saino. "Pine Marten Density in Lowland Riparian Woods: A Test of the Random Encounter Model Based on Genetic Data." *Mammalian Biology* 81, no. 5 (September 1, 2016): 439–46. https://doi.org/10.1016/j.mambio.2016.05.005.

Banks-Leite, Cristina, Renata Pardini, Danilo Boscolo, Camila Righetto Cassano, Thomas Püttker, Camila Santos Barros, Jos Barlow, and Jason Matthiopoulos. "Assessing the Utility of Statistical Adjustments for Imperfect Detection in Tropical Conservation Science." Edited by Jason

Matthiopoulos. *The Journal of Applied Ecology* 51, no. 4 (2014): 849–59. https://doi.org/10.1111/1365-2664.12272.

Becker, Marcus, Erin Bayne, Peter Solymos, and Eric Neilson. "Moose (*Alces alces*) in Alberta's Oil Sands Region," 2019.

Becker, Marcus, David J. Huggard, Melanie Dickie, Camille Warbington, Jim Schieck, Emily Herdman, Robert Serrouya, and Stan Boutin. "Applying and Testing a Novel Method to Estimate Animal Density from Motion-triggered Cameras." *Ecosphere (Washington, D.C)* 13, no. 4 (2022): n/a-n/a. https://doi.org/10.1002/ecs2.4005.

Bessone, Mattia, Hjalmar S. Kühl, Gottfried Hohmann, Ilka Herbinger, Kouame Paul N'Goran, Papy Asanzi, Pedro B. Da Costa, et al. "Drawn out of the Shadows: Surveying Secretive Forest Species with Camera Trap Distance Sampling." Edited by Fernanda Michalski. *The Journal of Applied Ecology* 57, no. 5 (2020): 963–74. https://doi.org/10.1111/1365-2664.13602.

Bischof, Richard, Pierre Dupont, Cyril Milleret, Joseph Chipperfield, and J. Andrew Royle. "Consequences of Ignoring Group Association in Spatial Capture–Recapture Analysis." *Wildlife Biology* 2020, no. 1 (2020): 1–10. https://doi.org/10.2981/wlb.00649.

Blanc, Laetitia, Eric Marboutin, Sylvain Gatti, and Olivier Gimenez. "Abundance of Rare and Elusive Species: Empirical Investigation of Closed versus Spatially Explicit Capture-Recapture Models with Lynx as a Case Study." *The Journal of Wildlife Management* 77, no. 2 (2013): 372–78. https://doi.org/10.1002/jwmg.453.

Borchers, D. L., and M. G. Efford. "Spatially Explicit Maximum Likelihood Methods for Capture-Recapture Studies." Biometrics 64, no. 2 (2008): 377–85. https://doi.org/10.1111/j.1541-0420.2007.00927.x.

Brennan, Leonard A. *Quantitative Analyses in Wildlife Science.* Book, Whole. Baltimore: Johns Hopkins University Press, 2019.

British Columbia Ministry of Environment, Lands and Parks. *Inventory Methods for Bears.* Version 2.0.--. Vol. no. 21.;no. 21; Book, Whole. Victoria, B.C: Resources Inventory Committee, 1998. https://www2.gov.bc.ca/assets/gov/environment/natural-resource-stewardship/nr-laws-policy/risc/bearml20.pdf.

British Columbia Ministry of Environment, Lands and Parks. *Inventory Methods for Medium-Sized Territorial Carnivores: Coyote, Red Fox, Lynx, Bobcat, Wolverine, Fisher & Badger.* Version 2.0.--. Vol. no. 25;no. 25.; Book, Whole. Victoria, B.C: Resources Inventory Committee, 1998. https://www2.gov.bc.ca/assets/gov/environment/natural-resource-stewardship/nr-laws-policy/risc/mstc.pdf.

British Columbia Ministry of Environment, Lands and Parks. *Inventory Methods for Wolf and Cougar.* Version 2.0.--. Vol. no. 34;no. 34.; Book, Whole. Victoria, B.C: Resources Inventory Committee, 1998. https://www2.gov.bc.ca/assets/gov/environment/natural-resource-stewardship/nr-laws-policy/risc/wolf.pdf.

British Columbia Ministry of Sustainable Resource Management. *Aerial-Based Inventory Techniques for Selected Ungulates: Bison, Mountain Goat, Mountain Sheep, Moose, Elk, Deer and Caribou.* Version 2.0--. Vol. no. 32.;no. 32; Book, Whole. Victoria, B.C.: Resources Inventory Committee, 2002. https://go.exlibris.link/L4htVzB3.

Broadley, Kate, A. Cole Burton, Tal Avgar, and Stan Boutin. "Density-dependent Space Use Affects Interpretation of Camera Trap Detection Rates." *Ecology and Evolution* 9, no. 24 (2019): 14031–41. https://doi.org/10.1002/ece3.5840.

Brownlee, Megan, Camille Warbington, and Mark Boyce. "Monitoring Sitatunga (Tragelaphus Spekii) Populations Using Camera Traps," no. Generic (2022). https://go.exlibris.link/L2gRGPb3.

Bruns, Jennifer. "Why Aerial Surveys Are Important to Managing Big Game in Idaho," December 30, 2019. https://idfg.idaho.gov/blog/2019/12/why-aerial-surveys-are-important-managing-big-game-idaho.

Buckland, S. T., D.R. Anderson, K.P. Burnham, and J.L. Laake. Distance Sampling: Estimating Abundance of Biological Populations. 1st ed. Book, Whole. London;New York; Chapman & Hall, 1993. https://doi.org/10.1007/978-94-011-1574-2.

Buckland, S. T., E. A. Rexstad, T. A. Marques, C. S. Oedekoven, SpringerLink (Online service), and SpringerLINK ebooks - Mathematics and Statistics. Distance Sampling: Methods and Applications. Book, Whole. Cham: Springer International Publishing, 2015. https://doi.org/10.1007/978-3-319-19219-2.

Buckland, Stephen T. "Point-Transect Surveys for Songbirds: Robust Methodologies." Edited by C. M. Handel. The Auk 123, no. 2 (2006): 345–57. https://doi.org/10.1642/0004-8038(2006)123[345:PSFSRM]2.0.CO;2.

Burgar, Joanna M., A. Cole Burton, and Jason T. Fisher. "The Importance of Considering Multiple Interacting Species for Conservation of Species at Risk." *Conservation Biology* 33, no. 3 (2019): 709–15. https://doi.org/10.1111/cobi.13233.

Burgar, Joanna M., Frances E. C. Stewart, John P. Volpe, Jason T. Fisher, and A. Cole Burton. "Estimating Density for Species Conservation: Comparing Camera Trap Spatial Count Models to Genetic Spatial Capture-Recapture Models." *Global Ecology and Conservation* 15, no. Journal Article (2018): e00411. https://doi.org/10.1016/j.gecco.2018.e00411.

Burton, A. Cole, Eric Neilson, Dario Moreira, Andrew Ladle, Robin Steenweg, Jason T. Fisher, Erin Bayne, Stan Boutin, and Phil Stephens. "Wildlife Camera Trapping: A Review and Recommendations for Linking Surveys to Ecological Processes." *The Journal of Applied Ecology* 52, no. 3 (2015): 675–85. https://doi.org/10.1111/1365-2664.12432.

Cambridge Dictionary. Cambridge University Press, 2022. https://dictionary.cambridge.org/dictionary/english/index.

Cappelle, Noémie, Marie-Lyne Després-Einspenner, Eric J. Howe, Christophe Boesch, and Hjalmar S. Kühl. "Validating Camera Trap Distance Sampling for Chimpanzees." American Journal of Primatology 81, no. 3 (2019): e22962-n/a. https://doi.org/10.1002/ajp.22962.

Cappelle, Noémie, Eric J. Howe, Christophe Boesch, and Hjalmar S. Kühl. "Estimating Animal Abundance and Effort–Precision Relationship with Camera Trap Distance Sampling." Ecosphere (Washington, D.C) 12, no. 1 (2021): n/a-n/a. https://doi.org/10.1002/ecs2.3299.

Caravaggi, Anthony, A. Cole Burton, Douglas A. Clark, Jason T. Fisher, Amelia Grass, Sian Green, Catherine Hobaiter, et al. "A Review of Factors to Consider When Using Camera Traps to Study Animal Behavior to Inform Wildlife Ecology and Conservation." *Conservation Science and Practice* 2, no. 8 (2020): n/a-n/a. https://doi.org/10.1111/csp2.239.

Carbone, C., S. Christie, K. Conforti, T. Coulson, N. Franklin, J. R. Ginsberg, M. Griffiths, et al. "The Use of Photographic Rates to Estimate Densities of Tigers and Other Cryptic Mammals." *Animal Conservation* 4, no. 1 (2001): 75–79. https://doi.org/10.1017/S1367943001001081.

Chandler, Richard B., and J. Andrew Royle. "Spatially Explicit Models for Inference about Density in Unmarked or Partially Marked Populations." *The Annals of Applied Statistics* 7, no. 2 (2013): 936–54. https://doi.org/10.1214/12-AOAS610.

Chin, Richard, and Bruce Y. Lee. "Chapter 15 - Analysis of Data." In *Principles and Practice of Clinical Trial Medicine*, edited by Richard Chin and Bruce Y. Lee, 325–59. New York: Academic Press, 2008. https://doi.org/10.1016/B978-0-12-373695-6.00015-6.

Clark, T. G., M. J. Bradburn, S. B. Love, and D. G. Altman. "Survival Analysis Part I: Basic Concepts and First Analyses." *British Journal of Cancer* 89, no. 2 (2003): 232–38. https://doi.org/10.1038/sj.bjc.6601118.

Clarke, Jamie. "BC Camera Trap Project Database," Unpublished.

Codling, Edward A., Michael J. Plank, and Simon Benhamou. "Random Walk Models in Biology." *Journal of the Royal Society Interface* 5, no. 25 (2008): 813–34. https://doi.org/10.1098/rsif.2008.0014.

Cohen, Jacob. "A Power Primer." *Psychological Bulletin* 112, no. 1 (1992): 155–59. https://doi.org/10.1037/0033-2909.112.1.155.

Conroy, Michael J., Jonathan P. Runge, Richard J. Barker, Matthew R. Schofield, and Christopher J. Fonnesbeck. "Efficient Estimation Of Abundance For Patchily Distributed Populations Via Two-Phase, Adaptive Sampling." *Ecology (Durham)* 89, no. 12 (2008): 3362–70. https://doi.org/10.1890/07-2145.1.

Côté, Steeve D., Sandra Hamel, Antoine St-Louis, and Julien Mainguy. "Do Mountain Goats Habituate to Helicopter Disturbance?" *The Journal of Wildlife Management* 77, no. 6 (2013): 1244–1244. https://doi.org/10.1002/jwmg.565.

Crupi, Anthony P., David P. Gregovich, and Kevin S. White. "Steep and Deep: Terrain and Climate Factors Explain Brown Bear (Ursus Arctos) Alpine Den Site Selection to Guide Heli-Skiing Management." *PloS One* 15, no. 9 (2020): e0238711–e0238711. https://doi.org/10.1371/journal.pone.0238711.

Cusack, Jeremy J., Alexandra Swanson, Tim Coulson, Craig Packer, Chris Carbone, Amy J. Dickman, Margaret Kosmala, Chris Lintott, and J. Marcus Rowcliffe. "Applying a Random Encounter Model to Estimate Lion Density from Camera Traps in Serengeti National Park, Tanzania." *The Journal of Wildlife Management* 79, no. 6 (2015): 1014–21. https://doi.org/10.1002/jwmg.902.

Davis, R. S., E. L. Stone, L. K. Gentle, W. O. Mgoola, A. Uzal, and R. W. Yarnell. "Spatial Partial Identity Model Reveals Low Densities of Leopard and Spotted Hyaena in a Miombo Woodland." *Journal of Zoology (1987)* 313, no. 1 (2021): 43–53. https://doi.org/10.1111/jzo.12838.

Delisle, Zackary J., Elizabeth A. Flaherty, Mackenzie R. Nobbe, Cole M. Wzientek, and Robert K. Swihart. "Next-Generation Camera Trapping: Systematic Review of Historic Trends Suggests Keys to Expanded Research Applications in Ecology and Conservation." *Frontiers in Ecology and Evolution* 9, no. Journal Article (2021). https://doi.org/10.3389/fevo.2021.617996.

Dertien, Jeremy S., Paul F. Doherty, Calvin F. Bagley, John A. Haddix, Aleya R. Brinkman, and Elizabeth S. Neipert. "Evaluating Dall's Sheep Habitat Use via Camera Traps." *The Journal of Wildlife Management* 81, no. 8 (2017): 1457–67. https://doi.org/10.1002/jwmg.21308.

Després-Einspenner, Marie-Lyne, Eric J. Howe, Pierre Drapeau, and Hjalmar S. Kühl. "An Empirical Evaluation of Camera Trapping and Spatially Explicit Capture-recapture Models for Estimating Chimpanzee Density." American Journal of Primatology 79, no. 7 (2017): e22647-n/a. https://doi.org/10.1002/ajp.22647.

Dickie, Melanie. "NEW PAPER ALERT!" Tweet. *@MelanieDickie*, April 19, 2022. https://twitter.com/MelanieDickie/status/1516432277009403904.

Dupont, Gates, J. Andrew Royle, Muhammad Ali Nawaz, and Chris Sutherland. "Optimal Sampling Design for Spatial Capture–Recapture." *Ecology (Durham)* 102, no. 3 (2021): e03262-n/a. https://doi.org/10.1002/ecy.3262.

Efford, Murray G., and Deanna K. Dawson. "Occupancy in Continuous Habitat." *Ecosphere (Washington, D.C)* 3, no. 4 (2012): art32-15. https://doi.org/10.1890/ES11-00308.1.

Evans, Michael J., and Tracy A. G. Rittenhouse. "Evaluating Spatially Explicit Density Estimates of Unmarked Wildlife Detected by Remote Cameras." *The Journal of Applied Ecology* 55, no. 6 (2018): 2565–74. https://doi.org/10.1111/1365-2664.13194.

Fisher, Jason, Joanna Burgar, Melanie Dickie, Cole Burton, and Rob Serrouya. "Density Estimates of Unmarked Large Mammals at Camera Traps Vary among Models, Species, and Years, Signalling Importance of Model Assumptions," In review. https://doi.org/10.22541/au.163768980.02146968/v1.

Fleming, Jill, Evan H. Campbell Grant, Sean C. Sterrett, and Chris Sutherland. "Experimental Evaluation of Spatial Capture–Recapture Study Design." *Ecological Applications* 31, no. 7 (2021): 1-n/a. https://doi.org/10.1002/eap.2419.

Foca, Jennifer M. "Camera Traps for Evaluating Ungulate Densities and Interspecific Interactions in the Beaver Hills Region of Alberta." University of Alberta, 2021.

Frid, Alejandro. "Dall's Sheep Responses to Overflights by Helicopter and Fixed-Wing Aircraft." *Biological Conservation* 110, no. 3 (2003): 387–99. https://doi.org/10.1016/S0006-3207(02)00236-7.

Fuller, Angela K., Chris S. Sutherland, J. Andrew Royle, and Matthew P. Hare. "Estimating Population Density and Connectivity of American Mink Using Spatial Capture—Recapture." *Ecological Applications* 26, no. 4 (2016): 1125–35. https://doi.org/10.1890/15-0315.

Furnas, B. J., R. H. Landers, R. L. Callas, and S. M. Matthews. "Estimating Population Size of Fishers (Pekania Pennanti) Using Camera Stations and Auxiliary Data on Home Range Size." *Ecosphere (Washington, D.C)* 8, no. 3 (2017): e01747-n/a. https://doi.org/10.1002/ecs2.1747.

Gardner, Beth, Juan Reppucci, Mauro Lucherini, and J. Andrew Royle. "Spatially Explicit Inference for Open Populations: Estimating Demographic Parameters from Camera-Trap Studies." Edited by KB Newman. *Ecology (Durham)* 91, no. 11 (2010): 3376–83. https://doi.org/10.1890/09-0804.1.

Gardner, Beth, J. Andrew Royle, Michael T. Wegan, Raymond E. Rainbolt, and Paul D. Curtis. "Estimating Black Bear Density Using DNA Data From Hair Snares." *The Journal of Wildlife Management* 74, no. 2 (2010): 318–25. https://doi.org/10.2193/2009-101.

Gardner, Beth, Rahel Sollmann, N. Samba Kumar, Devcharan Jathanna, and K. Ullas Karanth. "State Space and Movement Specification in Open Population Spatial Capture–Recapture Models." *Ecology and Evolution* 8, no. 20 (2018): 10336–44. https://doi.org/10.1002/ece3.4509.

Garland, Laura, Eric Neilson, Tal Avgar, Erin Bayne, and Stan Boutin. "Random Encounter and Staying Time Model Testing with Human Volunteers." *The Journal of Wildlife Management* 84, no. 6 (2020): 1179–84. https://doi.org/10.1002/jwmg.21879.

Gaston, Kevin J., Tim M. Blackburn, Jeremy J. D. Greenwood, Richard D. Gregory, Rachel M. Quinn, and John H. Lawton. "Abundance-Occupancy Relationships." *The Journal of Applied Ecology* 37, no. s1 (2000): 39–59. https://doi.org/10.1046/j.1365-2664.2000.00485.x.

Gerber, Brian D., Sarah M. Karpanty, and Marcella J. Kelly. "Evaluating the Potential Biases in Carnivore Capture–Recapture Studies Associated with the Use of Lure and Varying Density Estimation Techniques Using Photographic-Sampling Data of the Malagasy Civet." *Population Ecology* 54, no. 1 (2012 2011): 43–54. https://doi.org/10.1007/s10144-011-0276-3.

Gilbert, Neil A., John D. J. Clare, Jennifer L. Stenglein, and Benjamin Zuckerberg. "Abundance Estimation of Unmarked Animals Based on Camera-trap Data." *Conservation Biology* 35, no. 1 (2021): 88–100. https://doi.org/10.1111/cobi.13517.

Granados, Alys. "WildCAM Guide to Camera Trap Set Up." WildCAM, 2021. https://wildcams.ca/site/assets/files/1148/wildcam_guide_to_camera_trap_set_up_feb2021.pdf.

Green, Austin M., Mark W. Chynoweth, Çağan Hakkı Şekercioğlu, and Çağan Hakkı Şekercioğlu. "Spatially Explicit Capture-Recapture Through Camera Trapping: A Review of Benchmark Analyses for Wildlife Density Estimation." *Frontiers in Ecology and Evolution* 8, no. Journal Article (2020). https://doi.org/10.3389/fevo.2020.563477.

Grosklos, Guen, in preparation.

Government of British Columbia. "2020-2022 Hunting and Trapping Regulations Synopsis," 2020. https://www2.gov.bc.ca/assets/gov/sports-recreation-arts-and-culture/outdoor-recreation/fishing-and-hunting/hunting/regulations/2020-2022/hunting-trapping-synopsis-2020-2022.pdf.

Hammond, Philip S., Tessa B. Francis, Dennis Heinemann, Kristy J. Long, Jeffrey E. Moore, André E. Punt, Randall R. Reeves, et al. "Estimating the Abundance of Marine Mammal Populations." *Frontiers in Marine Science* 8, no. Journal Article (2021). https://doi.org/10.3389/fmars.2021.735770.

Haucke, Timm, Hjalmar S. Kühl, Jacqueline Hoyer, and Volker Steinhage. "Overcoming the Distance Estimation Bottleneck in Estimating Animal Abundance with Camera Traps." Ecological Informatics 68, no. Journal Article (2021 2022): 101536. https://doi.org/10.1016/j.ecoinf.2021.101536.

Hayes, R.D., A. M. Baer, and D. G. Larsen. "Population Dynamics and Prey Relationships of an Exploited and Recovering Wolf Population in the Southern Yukon," July 1991. https://emrlibrary.gov.yk.ca/environment/population-dynamics-and-prey-relationships-of-an-exploited-and-recovering-wolf-population.pdf.

Hedwig, Daniela, Ivonne Kienast, Matthieu Bonnet, Bryan K. Curran, Amos Courage, Christophe Boesch, Hjalmar S. Kühl, and Tony King. "A Camera Trap Assessment of the Forest Mammal Community within the Transitional Savannah-forest Mosaic of the Batéké Plateau National Park, Gabon." *African Journal of Ecology* 56, no. 4 (2018): 777–90. https://doi.org/10.1111/aje.12497.

Hessami, Mateen A. "Estimating Juvenile Recruitment of Elk in an Occupancy Modeling Framework," 2019. https://scholarworks.umt.edu/utpp/252/.

Hines, J. E., J. D. Nichols, J. A. Royle, D. I. MacKenzie, A. M. Gopalaswamy, N. Samba Kumar, and K. U. Karanth. "Tigers on Trails: Occupancy Modeling for Cluster Sampling." *Ecological Applications* 20, no. 5 (2010): 1456–66. https://doi.org/10.1890/09-0321.1.

Hofmeester, Tim R., J. M. Rowcliffe, and Patrick A. Jansen. "A Simple Method for Estimating the Effective Detection Distance of Camera Traps." Edited by Rob Williams and Natalie Kelly. *Remote Sensing in Ecology and Conservation* 3, no. 2 (2017): 81–89. https://doi.org/10.1002/rse2.25.

Howe, Eric J., Stephen T. Buckland, Marie-Lyne Després-Einspenner, Hjalmar S. Kühl, and Jason Matthiopoulos. "Distance Sampling with Camera Traps." Edited by Jason Matthiopoulos. Methods in Ecology and Evolution 8, no. 11 (2017): 1558–65. https://doi.org/10.1111/2041-210X.12790.

Jennelle, Christopher S., Michael C. Runge, and Darryl I. MacKenzie. "The Use of Photographic Rates to Estimate Densities of Tigers and Other Cryptic Mammals: A Comment on Misleading Conclusions." *Animal Conservation* 5, no. 2 (2002): 119–20. https://doi.org/10.1017/S1367943002002160.

Jenny, David. "Spatial Organization of Leopards Panthera Pardus in Taï National Park, Ivory Coast: Is Rainforest Habitat a 'Tropical Haven'?" Journal of Zoology (1987) 240, no. 3 (1996): 427–40. https://doi.org/10.1111/j.1469-7998.1996.tb05296.x.

Jensen, Paul O, Aaron J Wirsing, and Daniel H Thornton. "Using Camera Traps to Estimate Density of Snowshoe Hare (Lepus Americanus): A Keystone Boreal Forest Herbivore." *Journal of Mammalogy*, March 3, 2022, gyac009. https://doi.org/10.1093/jmammal/gyac009.

Jiménez, José, Juan Carlos Nuñez-Arjona, Carmen Rueda, Luis Mariano González, Francisco García-Domínguez, Jaime Muñoz-Igualada, and José Vicente López-Bao. "Estimating Carnivore Community Structures." Scientific Reports 7, no. 1 (2017): 41036–41036. https://doi.org/10.1038/srep41036.

Johanns, Peter, Timm Haucke, and Volker Steinhage. "Distance Estimation and Animal Tracking for Wildlife Camera Trapping," no. Journal Article (2022). https://go.exlibris.link/Gj2q2Q3Y.

Johansson, Örjan, Shannon Kachel, and Byron Weckworth. "Guidelines for Telemetry Studies on Snow Leopards." *Animals (Basel)* 12, no. 13 (2022): 1663. https://doi.org/10.3390/ani12131663.

Johnson, Douglas H. "In Defense of Indices: The Case of Bird Surveys." *The Journal of Wildlife Management* 72, no. 4 (2008): 857–68. https://doi.org/10.2193/2007-294.

Kavčić, Krešimir, Pablo Palencia, Marco Apollonio, Joaquín Vicente, and Nikica Šprem. "Random Encounter Model to Estimate Density of Mountain-Dwelling Ungulate." *European Journal of Wildlife Research* 67, no. 5 (2021). https://doi.org/10.1007/s10344-021-01530-1.

Krebs, Charles J., B. Scott Gilbert, S. Boutin, and R. Boonstra. "Estimation of Snowshoe Hare Population Density from Turd Transects." *Canadian Journal of Zoology* 65, no. 3 (1987): 565–67. https://doi.org/10.1139/z87-087.

Kucera, Thomas E., and Reginald H. Barrett. "A History of Camera Trapping." In *Camera Traps in Animal Ecology*, 9–26. Tokyo: Springer Japan, 2011. https://doi.org/10.1007/978-4-431-99495-4_2.

Lamb, Clayton T., Adam T. Ford, Michael F. Proctor, J. Andrew Royle, Garth Mowat, and Stan Boutin. "Genetic Tagging in the Anthropocene: Scaling Ecology from Alleles to Ecosystems." *Ecological Applications* 29, no. 4 (2019): e01876-n/a. https://doi.org/10.1002/eap.1876.

Le Cren, E. D. "A Note on the History of Mark-Recapture Population Estimates." *The Journal of Animal Ecology* 34, no. 2 (1965): 453–54. https://doi.org/10.2307/2661.

Loonam, Kenneth E., David E. Ausband, Paul M. Lukacs, Michael S. Mitchell, and Hugh S. Robinson. "Estimating Abundance of an Unmarked, Low-Density Species Using Cameras." *The Journal of Wildlife Management* 85, no. 1 (2021): 87–96. https://doi.org/10.1002/jwmg.21950.

Loonam, Kenneth E., Paul M. Lukacs, David E. Ausband, Michael S. Mitchell, and Hugh S. Robinson. "Assessing the Robustness of Time-to-event Models for Estimating Unmarked Wildlife Abundance Using Remote Cameras." *Ecological Applications* 31, no. 6 (2021): 1-n/a. https://doi.org/10.1002/eap.2388.

Lukacs, Paul M. "Animal Abundance from Camera Data:Pipe Dream to Main Stream." Presented at the FCFC Seminar, October 26, 2021. https://umontana.zoom.us/rec/play/eY6_CAjDNUjCAfFrmRvJH8NtrL4J38-I46T5idY4gO3i1YHqxBnDUrDeufvgAps-D-aFJFJ_F9AMuE6k.VjerQ5kRpa5HsybV.

Mace, Georgina M., Nigel J. Collar, Kevin J. Gaston, Craig Hilton-Taylor, H. Resit Akçakaya, Nigel Leader-Williams, E. J. Milner-Gulland, and Simon N. Stuart. "Quantification of Extinction Risk: IUCN's System for Classifying Threatened Species." *Conservation Biology* 22, no. 6 (2008): 1424–42. https://doi.org/10.1111/j.1523-1739.2008.01044.x.

MacKenzie, Darryl I., James D. Nichols, J. Andrew Royle, Kenneth H. Pollock, Larissa L. Bailey, James E. Hines, eBook - Environmental Science 2017 [EBCES17], and Elsevier All Access Books. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. 2nd ed. Book, Whole. San Diego: Academic Press [Imprint], 2017. https://go.exlibris.link/NmXF2yQ3.

McFarlane, Samantha, Micheline Manseau, Robin Steenweg, Dave Hervieux, Troy Hegel, Simon Slater, and Paul J. Wilson. "An Assessment of Sampling Designs Using SCR Analyses to Estimate Abundance of Boreal Caribou." *Ecology and Evolution* 10, no. 20 (2020): 11631–42. https://doi.org/10.1002/ece3.6797.

McLellan, Bruce N. "Dynamics of a Grizzly Bear Population during a Period of Industrial Resource Extraction. I. Density and Age-Sex Composition." *Canadian Journal of Zoology* 67, no. 8 (1989): 1856–60. https://doi.org/10.1139/z89-264.

Miller, Sterling D. "Detection of Differences in Brown Bear Density and Population Composition Caused by Hunting." *Bears, Their Biology and Management* 8, no. Journal Article (1990): 393–404. https://doi.org/10.2307/3872943.

Miller, Sterling D., Gary C. White, Richard A. Sellers, Harry V. Reynolds, John W. Schoen, Kimberly Titus, Victor G. Barnes, et al. "Brown and Black Bear Density Estimation in Alaska Using Radiotelemetry and Replicated Mark-Resight Techniques." *Wildlife Monographs*, no. 133 (1997): 3–55.

Moeller, Anna K., Paul M. Lukacs, and Jon S. Horne. "Three Novel Methods to Estimate Abundance of Unmarked Animals Using Remote Cameras." *Ecosphere (Washington, D.C)* 9, no. 8 (2018): e02331-n/a. https://doi.org/10.1002/ecs2.2331.

Morin, Dana J., John Boulanger, Richard Bischof, David C. Lee, Dusit Ngoprasert, Angela K. Fuller, Bruce McLellan, et al. "Comparison of Methods for Estimating Density and Population Trends for Low-Density Asian Bears." *Global Ecology and Conservation*, no. Journal Article (2022). https://doi.org/10.1016/j.gecco.2022.e02058.

Murray, Maureen H., Mason Fidino, Elizabeth W. Lehrer, Juniper L. Simonis, and Seth B. Magle. "A Multi-state Occupancy Model to Non-invasively Monitor Visible Signs of Wildlife Health with Camera Traps That Accounts for Image Quality." *The Journal of Animal Ecology* 90, no. 8 (2021): 1973–84. https://doi.org/10.1111/1365-2656.13515.

Nakashima, Yoshihiro. "Potentiality and Limitations of N-mixture and Royle-Nichols Models to Estimate Animal Abundance Based on Noninstantaneous Point Surveys." *Population Ecology* 62, no. 1 (2020): 151–57. https://doi.org/10.1002/1438-390X.12028.

Nakashima, Yoshihiro, Keita Fukasawa, Hiromitsu Samejima, and Philip Stephens. "Estimating Animal Density without Individual Recognition Using Information Derivable Exclusively from Camera Traps." Edited by Philip Stephens. *The Journal of Applied Ecology* 55, no. 2 (2018): 735–44. https://doi.org/10.1111/1365-2664.13059.

Nakashima, Yoshihiro, Shun Hongo, and Etienne François Akomo-Okoue. "Landscape-Scale Estimation of Forest Ungulate Density and Biomass Using Camera Traps: Applying the REST Model." *Biological Conservation* 241, no. Journal Article (2020): 108381. https://doi.org/10.1016/j.biocon.2019.108381.

Nawaz, Muhammad Ali, Barkat Ullah Khan, Amer Mahmood, Muhammad Younas, Jaffar ud Din, and Chris Sutherland. "An Empirical Demonstration of the Effect of Study Design on Density Estimations." *Scientific Reports* 11, no. 1 (2021): 13104–13104. https://doi.org/10.1038/s41598-021-92361-2.

Neilson, Eric W., Tal Avgar, A. Cole Burton, Kate Broadley, and Stan Boutin. "Animal Movement Affects Interpretation of Occupancy Models from Camera-trap Surveys of Unmarked Animals." *Ecosphere (Washington, D.C)* 9, no. 1 (2018): n/a-n/a. https://doi.org/10.1002/ecs2.2092.

Noon, Barry R., Larissa L. Bailey, Thomas D. Sisk, and Kevin S. McKelvey. "Efficient Species-Level Monitoring at the Landscape Scale." *Conservation Biology* 26, no. 3 (2012): 432–41. https://doi.org/10.1111/j.1523-1739.2012.01855.x.

O'Brien, Timothy G. "Abundance, Density and Relative Abundance: A Conceptual Framework." In *Camera Traps in Animal Ecology*, 71–96. Tokyo: Springer Japan, 2011. https://doi.org/10.1007/978-4-431-99495-4_6.

Obbard, Martyn E., Eric J. Howe, and Christopher J. Kyle. "Empirical Comparison of Density Estimators for Large Carnivores." *The Journal of Applied Ecology* 47, no. 1 (2010): 76–84. https://doi.org/10.1111/j.1365-2664.2009.01758.x.

Otis, David L., Kenneth P. Burnham, Gary C. White, and David R. Anderson. "Statistical Inference from Capture Data on Closed Animal Populations." Wildlife Monographs, no. 62 (1978): 3–135. Palencia, Pablo. *Camera Trap Methods for Density Estimation*. Project ENETWILD, 2022. https://www.youtube.com/watch?v=NUW4oLGeQwk.

Palencia, Pablo, J. Marcus Rowcliffe, Joaquín Vicente, and Pelayo Acevedo. "Assessing the Camera Trap Methodologies Used to Estimate Density of Unmarked Populations." *The Journal of Applied Ecology* 58, no. 8 (2021): 1583–92. https://doi.org/10.1111/1365-2664.13913.

Palmer, Meredith S., Alexandra Swanson, Margaret Kosmala, Todd Arnold, and Craig Packer. "Evaluating Relative Abundance Indices for Terrestrial Herbivores from Large-scale Camera Trap Surveys." *African Journal of Ecology* 56, no. 4 (2018): 791–803. https://doi.org/10.1111/aje.12566.

Parsons, Arielle Waldstein, Tavis Forrester, William J. McShea, Megan C. Baker-Whatton, Joshua J. Millspaugh, and Roland Kays. "Do Occupancy or Detection Rates from Camera Traps Reflect Deer Density?" *Journal of Mammalogy* 98, no. 6 (2017): 1547–57. https://doi.org/10.1093/jmammal/gyx128.

Pettigrew, Pascal, Daniel Sigouin, and Martin-Hugues St-Laurent. "Testing the Precision and Sensitivity of Density Estimates Obtained with a Camera-trap Method Revealed Limitations and Opportunities." *Ecology and Evolution* 11, no. 12 (2021): 7879–89. https://doi.org/10.1002/ece3.7619.

Pfeffer, Sabine E., Robert Spitzer, Anew M. Allen, Tim R. Hofmeester, Göran Ericsson, Freik Widemo, Navinder J. Singh, Joris P. G. M. Cromsigt, and Sveriges lantbruksuniversitet. "Pictures or Pellets? Comparing Camera Trapping and Dung Counts as Methods for Estimating Population Densities of Ungulates." Edited by Marcus Rowcliffe and Timothy O'Brien. *Remote Sensing in Ecology and Conservation* 4, no. 2 (2018): 173–83. https://doi.org/10.1002/rse2.67.

Proctor, Michael F., David L. Garshelis, Prachi Thatte, Robert Steinmetz, Brian Crudge, Bruce N. McLellan, William J. McShea, et al. "Review of Field Methods for Monitoring Asian Bears." *Global Ecology and Conservation* 35, no. Journal Article (2022): e02080. https://doi.org/10.1016/j.gecco.2022.e02080.

Ransom, Jason I. "Detection Probability in Aerial Surveys of Feral Horses: Aerial Survey Detection Probability." *The Journal of Wildlife Management* 76, no. 2 (2012): 299–307. https://doi.org/10.1002/jwmg.204.

Rich, Lindsey N., Marcella J. Kelly, Rahel Sollmann, Andrew J. Noss, Leonardo Maffei, Rosario L. Arispe, Agustin Paviolo, Carlos D. De Angelo, Yamil E. Di Blanco, and Mario S. Di Bitetti. "Comparing Capture–Recapture, Mark–Resight, and Spatial Mark–Resight Models for Estimating Puma Densities via Camera Traps." *Journal of Mammalogy* 95, no. 2 (2014): 382–91. https://doi.org/10.1644/13-MAMM-A-126.

Romairone, Juan, José Jiménez, Juan José Luque-Larena, and François Mougeot. "Spatial Capture-Recapture Design and Modelling for the Study of Small Mammals." Edited by Antoni Margalida. *PloS One* 13, no. 6 (2018): e0198766–e0198766. https://doi.org/10.1371/journal.pone.0198766.

Rönnegård, Lars, Håkan Sand, Henrik Andrén, Johan Månsson, and Åke Pehrson. "Evaluation of Four Methods Used to Estimate Population Density of Moose Alces Alces." *Wildlife Biology* 14, no. 3 (2008): 358–71. https://doi.org/10.2981/0909-6396(2008)14[358:EOFMUT]2.0.CO;2.

Rovero, Francesco, and Andrew R. Marshall. "Camera Trapping Photographic Rate as an Index of Density in Forest Ungulates." *The Journal of Applied Ecology* 46, no. 5 (2009): 1011–17. https://doi.org/10.1111/j.1365-2664.2009.01705.x.

Rowcliffe, J. M., R. Kays, B. Kranstauber, C. Carbone, and P. A. Jansen. "Quantifying Levels of Animal Activity Using Camera Trap Data." Edited by Diana Fisher. *Methods in Ecology and Evolution* 5, no. 11 (2014): 1170–79. https://doi.org/10.1111/2041-210X.12278.

Rowcliffe, J. Marcus, Chris Carbone, Patrick A. Jansen, Roland Kays, and Bart Kranstauber. "Quantifying the Sensitivity of Camera Traps: An Adapted Distance Sampling Approach:

Quantifying Camera Trap Sensitivity." *Methods in Ecology and Evolution* 2, no. 5 (2011): 464–76. https://doi.org/10.1111/j.2041-210X.2011.00094.x.

Rowcliffe, J. Marcus, Juliet Field, Samuel T. Turvey, and Chris Carbone. "Estimating Animal Density Using Camera Traps without the Need for Individual Recognition." *The Journal of Applied Ecology* 45, no. 4 (2008): 1228–36. https://doi.org/10.1111/j.1365-2664.2008.01473.x.

Rowcliffe, J. Marcus, Patrick A. Jansen, Roland Kays, Bart Kranstauber, Chris Carbone, and Nathalie Pettorelli. "Wildlife Speed Cameras: Measuring Animal Travel Speed and Day Range Using Camera Traps." Edited by Nathalie Pettorelli. *Remote Sensing in Ecology and Conservation* 2, no. 2 (2016): 84–94. https://doi.org/10.1002/rse2.17.

Royle, J. Andrew. "N-Mixture Models for Estimating Population Size from Spatially Replicated Counts." *Biometrics* 60, no. 1 (2004): 108–15. https://doi.org/10.1111/j.0006-341X.2004.00142.x.

Royle, J. Andrew. *"Spatial Capture-Recapture Modeling."* CompSustNet, 2016. https://www.youtube.com/watch?v=4HKFimATq9E.

Royle, J. Andrew. *Introduction to Spatial Capture-Recapture*. oSCR Package, 2020. https://www.youtube.com/watch?v=yRRDi07FtPg.

Royle, J. Andrew, and Robert M. Dorazio. *Hierarchical Modeling and Inference in Ecology: The Analysis of Data from Populations, Metapopulations and Communities*. 1st ed. Book, Whole. Amsterdam;Boston; Academic, 2008.

Royle, J. Andrew, and Robert M. Dorazio. "Parameter-Expanded Data Augmentation for Bayesian Analysis of Capture–Recapture Models." *Journal of Ornithology* 152, no. Suppl 2 (2012): 521–37. https://doi.org/10.1007/s10336-010-0619-4.

Royle, J. Andrew, Angela K. Fuller, and Chris Sutherland. "Spatial Capture–Recapture Models Allowing Markovian Transience or Dispersal." *Population Ecology* 58, no. 1 (2016): 53–62. https://doi.org/10.1007/s10144-015-0524-z.

Royle, J. Andrew, Audrey J. Magoun, Beth Gardner, Patrick Valkenburg, and Richard E. Lowell. "Density Estimation in a Wolverine Population Using Spatial Capture-Recapture Models." *The Journal of Wildlife Management* 75, no. 3 (2011): 604–11. https://doi.org/10.1002/jwmg.79.

Royle, J. Andrew, and James D. Nichols. "Estimating Abundance from Repeated Presence-Absence Data or Point Counts." *Ecology (Durham)* 84, no. 3 (2003): 777–90. https://doi.org/10.1890/0012-9658(2003)084[0777:EAFRPA]2.0.CO;2.

Royle, J. Andrew, and Kevin V. Young. "A Hierarchical Model for Spatial Capture-Recapture Data." Ecology (Durham) 89, no. 8 (2008): 2281–89. https://doi.org/10.1890/07-0601.1.

Sashika, Mariko, Michito Shimozuru, Toshio Tsubota, Masanao Nakanishi, Mina Jimbo, Yuri Shirane, Fumihiko Mori, Tsuyoshi Ishinazaka, Tsutomu Mano, and Masami Yamanaka. "Development of a Noninvasive Photograph-Based Method for the Evaluation of Body Condition in Free-Ranging Brown Bears." *PeerJ (San Francisco, CA)* 8, no. Journal Article (2020): e9982–e9982. https://doi.org/10.7717/peerj.9982.

Sasse, D. Blake. "Job-Related Mortality of Wildlife Workers in the United States, 1937-2000." *Wildlife Society Bulletin* 31, no. 4 (2003): 1015–20.

Sawaya, Michael A., Toni K. Ruth, Scott Creel, Jay J. Rotella, Jeffrey B. Stetz, Howard B. Quigley, and Steven T. Kalinowski. "Evaluation of Noninvasive Genetic Sampling Methods for Cougars in Yellowstone National Park." *The Journal of Wildlife Management* 75, no. 3 (2011): 612–22. https://doi.org/10.1002/jwmg.92.

Schaub, Michael, J. Andrew Royle, and Richard Barker. "Estimating True Instead of Apparent Survival Using Spatial Cormack–Jolly–Seber Models." Edited by Richard Barker. *Methods in Ecology and Evolution* 5, no. 12 (2014): 1316–26. https://doi.org/10.1111/2041-210X.12134.

Schaus, Jessica, Antonio Uzal, Louise K. Gentle, Philip J. Baker, Lucy Bearman-Brown, Simone Bullion, Abigail Gazzard, et al. "Application of the Random Encounter Model in Citizen Science Projects to Monitor Animal Densities." *Remote Sensing in Ecology and Conservation* 6, no. 4 (2020): 514–28. https://doi.org/10.1002/rse2.153.

Schoenecker, Kathryn A., Sarah R. B. King, L. Stefan Ekernas, and Sara J. Oyler-McCance. "Using Fecal DNA and Closed-Capture Models to Estimate Feral Horse Population Size." *The Journal of Wildlife Management* 85, no. 6 (2021): 1150–61. https://doi.org/10.1002/jwmg.22056.

Simpson, Keith, Eliot Terry, and British Columbia. Wildlife Branch. *Impacts of Backcountry Recreation Activities on Mountain Caribou : Management Concerns, Interim Management Guidelines and Research Needs.* Book, Whole. Victoria: Ministry of Environment, Lands & Parks, Wildlife Branch, 2000. https://go.exlibris.link/CySR2Q3T.

Sinclair, A. R. E., John M. Fryxell, and Graeme Caughley. *Wildlife Ecology, Conservation, and Management.* 2nd ed. Book, Whole. Malden, Mass: Blackwell, 2006.

Smith, J. A., J. P. Suraci, J. S. Hunter, K. M. Gaynor, C. B. Keller, M. S. Palmer, J. L. Atkins, et al. "Zooming in on Mechanistic Predator-Prey Ecology: Integrating Camera Traps with Experimental Methods to Reveal the Drivers of Ecological Interactions." Edited by Ben Dantzer. *The Journal of Animal Ecology* 89, no. 9 (2020): 1997–2012. https://doi.org/10.1111/1365-2656.13264.

Solberg, Knut Håkon, Eva Bellemain, Ola-Mattis Drageset, Pierre Taberlet, and Jon E. Swenson. "An Evaluation of Field and Non-Invasive Genetic Methods to Estimate Brown Bear (Ursus Arctos) Population Size." *Biological Conservation* 128, no. 2 (2006): 158–68. https://doi.org/10.1016/j.biocon.2005.09.025.

Sollmann, Rahel. "A Gentle Introduction to Camera-trap Data Analysis." *African Journal of Ecology* 56, no. 4 (2018): 740–49. https://doi.org/10.1111/aje.12557.

Sollmann, Rahel, Mariana Malzoni Furtado, Beth Gardner, Heribert Hofer, Anah T. A. Jácomo, Natália Mundim Tôrres, and Leandro Silveira. "Improving Density Estimates for Elusive Carnivores: Accounting for Sex-Specific Detection and Movements Using Spatial Capture–Recapture Models for Jaguars in Central Brazil." *Biological Conservation* 144, no. 3 (2011): 1017–24. https://doi.org/10.1016/j.biocon.2010.12.011.

Sollmann, Rahel, Beth Gardner, and Jerrold L. Belant. "How Does Spatial Study Design Influence Density Estimates from Spatial Capture-Recapture Models?" Edited by Jane M. Waterman. *PloS One* 7, no. 4 (2012): e34575–e34575. https://doi.org/10.1371/journal.pone.0034575.

Sollmann, Rahel, Beth Gardner, Arielle W. Parsons, Jessica J. Stocking, Brett T. McClintock, Theodore R. Simons, Kenneth H. Pollock, and Allan F. O'Connell. "A Spatial Mark-Resight Model Augmented with Telemetry Data." *Ecology (Durham)* 94, no. 3 (2013): 553–59. https://doi.org/10.1890/12-1256.1.

Sollmann, Rahel, Azlan Mohamed, Hiromitsu Samejima, and Andreas Wilting. "Risky Business or Simple Solution – Relative Abundance Indices from Camera-Trapping." *Biological Conservation* 159, no. Journal Article (2013): 405–12. https://doi.org/10.1016/j.biocon.2012.12.025.

Steenweg, Robin, Mark Hebblewhite, Jesse Whittington, Paul Lukacs, and Kevin McKelvey. "Sampling Scales Define Occupancy and Underlying Occupancy–Abundance Relationships in Animals." *Ecology (Durham)* 99, no. 1 (2018): 172–83. https://doi.org/10.1002/ecy.2054.

Stewart, Frances E. C. "Forecasting Climate-Sensitive Landscape Change Reveals Habitat Shifts and Population Uncertainty for Northern Boreal Caribou." Presented at the Caribou Ecology and Recovery Webinar Series, May 24, 2022.

Stewart, Frances E. C., Jason T. Fisher, A. Cole Burton, and John P. Volpe. "Species Occurrence Data Reflect the Magnitude of Animal Movements Better than the Proximity of Animal Space Use," no. Generic (2018). https://go.exlibris.link/tRkRhY7c.

Sun, Catherine, Joanna M. Burgar, Jason T. Fisher, and A. Cole Burton. "A Cautionary Tale Comparing Spatial Count and Partial Identity Models for Estimating Densities of Threatened and Unmarked Populations." *Global Ecology and Conservation* 38, no. Journal Article (2022): e02268.

Sun, Catherine C., Angela K. Fuller, and J. Andrew Royle. "Trap Configuration and Spacing Influences Parameter Estimates in Spatial Capture-Recapture Models." Edited by David L. Roberts. *PloS One* 9, no. 2 (2014): e88025–e88025. https://doi.org/10.1371/journal.pone.0088025.

Sutherland, Chris, Angela K. Fuller, J. Andrew Royle, and Olivier Gimenez. "Modelling Non-Euclidean Movement and Landscape Connectivity in Highly Structured Ecological Networks." Edited by Olivier Gimenez. *Methods in Ecology and Evolution* 6, no. 2 (2015): 169–77. https://doi.org/10.1111/2041-210X.12316.

Suwanrat, Saranphat, Dusit Ngoprasert, Christopher Sutherland, Pongthep Suwanwaree, and Tommaso Savini. "Estimating Density of Secretive Terrestrial Birds (Siamese Fireback) in Pristine and Degraded Forest Using Camera Traps and Distance Sampling." *Global Ecology and Conservation* 3, no. C (2015): 596–606. https://doi.org/10.1016/j.gecco.2015.01.010.

Thompson, William L., Gary C. White, and Charles Gowan. "Chapter 3 - Enumeration Methods." In *Monitoring Vertebrate Populations*, edited by William L. Thompson, Gary C. White, and Charles Gowan, 75–121. San Diego: Academic Press, 1998. https://doi.org/10.1016/B978-012688960-4/50003-4.

Twining, Joshua P., Claire McFarlane, Denise O'Meara, Catherine O'Reilly, Marina Reyne, W. Ian Montgomery, Sarah Helyar, David G. Tosh, and Ben C. Augustine. "A Comparison of Density Estimation Methods for Monitoring Marked and Unmarked Animal Populations." *Ecosphere (Washington, D.C)* 13, no. 10 (2022): n/a-n/a. https://doi.org/10.1002/ecs2.4165.

U.S. Energy Information Administration. "Carbon Dioxide Emissions Coefficients By Fuel," 2021. https://www.eia.gov/environment/emissions/co2_vol_mass.php.

Villette, Petra, Charles J. Krebs, Thomas S. Jung, and Rudy Boonstra. "Can Camera Trapping Provide Accurate Estimates of Small Mammal (Myodes Rutilus and Peromyscus Maniculatus) Density in the Boreal Forest?" *Journal of Mammalogy* 97, no. 1 (2016): 32–40. https://doi.org/10.1093/jmammal/gyv150.

Warbington, Camille H., and Mark S. Boyce. "Population Density of Sitatunga in Riverine Wetland Habitats." *Global Ecology and Conservation* 24, no. Journal Article (2020): e01212. https://doi.org/10.1016/j.gecco.2020.e01212.

Whitlock, Michael, and Dolph Schluter. *The Analysis of Biological Data*. Third. Book, Whole. New York;Austin;Plymouth;Boston; Macmillan Learning, 2020.

Williams, Byron K., James D. Nichols, and Michael J. Conroy. *Analysis and Management of Animal Populations: Modeling, Estimation, and Decision Making*. Book, Whole. San Diego: Academic Press, 2002. https://go.exlibris.link/qSfqP9dC.

Windell, Rebecca M., Jesse S. Lewis, Ashley R. Gramza, and Kevin R. Crooks. "Carnivore Carrying Behavior as Documented with Wildlife Camera Traps." *Western North American Naturalist* 79, no. 4 (2019): 471–80. https://doi.org/10.3398/064.079.0401.

Appendix A: Cost Comparison of Aerial vs Camera Trap Surveys

Introduction

How much does it cost to inventory a wildlife population? "Cost" can be a dollar amount, but also a measure of the quality of a population estimate. For example: practitioners who need robust population information to make conservation decisions may find inexpensive tools and/or methods that produce imprecise, biased, or statistically weak results "costly," despite their small price tag (Davis et al. 2020). Cost can therefore be thought of as the money required to undertake a survey effort and/or the relative risk of taking management actions based on survey results.

Direct comparisons of wildlife survey costs should be interpreted with caution – the money needed for different surveys varies, but so, too, do the outcomes of those surveys (Poole and Reynolds 2010). A presence-absence flight does not produce the same results as an intensive aerial survey for density estimation, for instance. The comparisons below are meant to demonstrate the relative costs of aerial and camera trap surveys by way of high- and low-cost example studies; the comparisons are neither exhaustive nor universal.

Methods

Camera trap survey cost estimates were based on actual camera networks deployed in BC. Estimates included the cost of camera equipment, field needs, and image storage and processing. Image processing times were estimated using an average tagging rate of 800 images per hour, based on low-end image tagging rates recorded by members of the Wildlife Coexistence Lab (unpublished). The approximate cost of the aerial surveys was calculated using a helicopter rental fee estimate of $1,400 per hour and a spatial coverage estimate of 20 km^2 per hour (Bohm, personal communication).

The high-cost example study covers a large area (about 1,200 km^2) in a remote, difficult-to-access region. For the camera trap survey: extensive time in the field is

needed (about 2 months), and ATVs/helicopters must be rented to access some camera sites. 190 Reconyx HyperFire cameras – priced at roughly $515 per unit – are required. After the field season, two image taggers working 40 hours per week would need about four months to process the images collected. For the aerial survey: a crew would need about 60 hours of flight time to cover the same area as the camera network.

The low-cost example study covers a smaller area (about 400 km^2) and is more accessible than the high-cost study. For the camera trap survey: approximately 3 weeks of field time are required, and no ATV/helicopter rentals are needed. 65 Browning StrikeForce Pro cameras – priced at roughly $250 per unit – are required. After the field season, one image tagger working 40 hours per week would need about 2 weeks to process the images collected. For the aerial survey: a crew would need about 20 hours of flight time to cover the same area as the camera network.

Results

The cost of a camera trap project will be highest the year that cameras are acquired. For the high-cost example, camera units accounted for 65% of total costs for year one; costs decreased by nearly 73% from the first year to the second year, after cameras had already been purchased (Table 1). An aerial survey that covers the same area as the camera network would cost about half as much as the camera project during year one, but about twice as much as the camera project in year two (Table 1). For the low-cost example, camera units accounted for 35% of total costs for the deployment year; costs decreased by nearly 40% in following years (Table 1). An aerial survey covering the same area as the camera network would cost about 60% of what the camera project cost for the deployment year, and slightly less than the camera project in following years (Table 1).

When camera and aerial surveys are conducted yearly (Figure 1, 2A): high-cost aerial surveys were more expensive than camera trap surveys every year except for the year cameras were purchased, but low-cost aerial surveys were always less expensive.

When camera surveys are conducted yearly aerial surveys are conducted every five year (Figure 1, 2B): aerial surveys were always less expensive.

Table 1. Comparison of high- and low-cost camera trap and aerial surveys. Camera trap and aerial survey costs include a 20% contingency fund.

	Year 1	Year 2	Year 3
High-cost camera survey	$202,007	$54,707	$52,427
Low-cost camera survey	$56,354	$37,478	$36,698
High-cost aerial survey	$109,008	$109,008	$109,008
Low-cost aerial survey	$35,428	$35,428	$35,428

The upfront cost of a camera network will change with trap make and model. For example, a Reconyx HyperFire 2 Professional Covert IR Camera is about $515 CAD per unit; a Browning StrikeForce HD Pro X is about $250 CAD per unit. The make and model most appropriate for an inventorying program will depend on its resources and objectives (for more information on selection camera traps for research, visit https://wildcams.ca/library/choosing-camera-trap-models/).

Discussion

The cost effectiveness of camera trap versus aerial surveys depends on the area of the study, the intensity of the camera trapping field effort and the frequency of aerial resurveys.

When comparing cost estimates, the breadth of information collected using each method should also be considered. Camera traps are passive, non-selective detectors that capture images of a wide variety of terrestrial vertebrates (Kucera and Barrett 2011). As such, they are a useful tool for multi-species monitoring – population metrics can be measured for many species at the same time, by way of a single camera

network (i.e., a single field effort). Aerial surveys, in contrast, are a single-species censusing technique, best-suited to large mammals – typically ungulates – that inhabit relatively open habitats (BC Ministry of Sustainable Resource Management 2002). Multi-species data is collected by repeating flights for different species of interest; repeating flights multiplies costs. The data collected by camera traps can also be used to make inferences about community composition, interactions between animals and their environment, recruitment and survival, habitat selection, prevalence of disease, body condition, behaviour, phenology and plant productivity, and more (Dertien et al. 2017, Hedwig et al. 2018, Hessami 2019, Murray et al. 2021, Sashika et al. 2020, Smith et al. 2020, Sun et al. 2021, Windell et al. 2019). Aerial surveys collect information on the size of the population and its component herds, as well as sex and age ratios (BC Ministry of Sustainable Resource Management 2002).

Depending on the processing software used, the experience of the processing staff, and the content of the images, image tagging rates may be slower or faster than 800 images per hour.
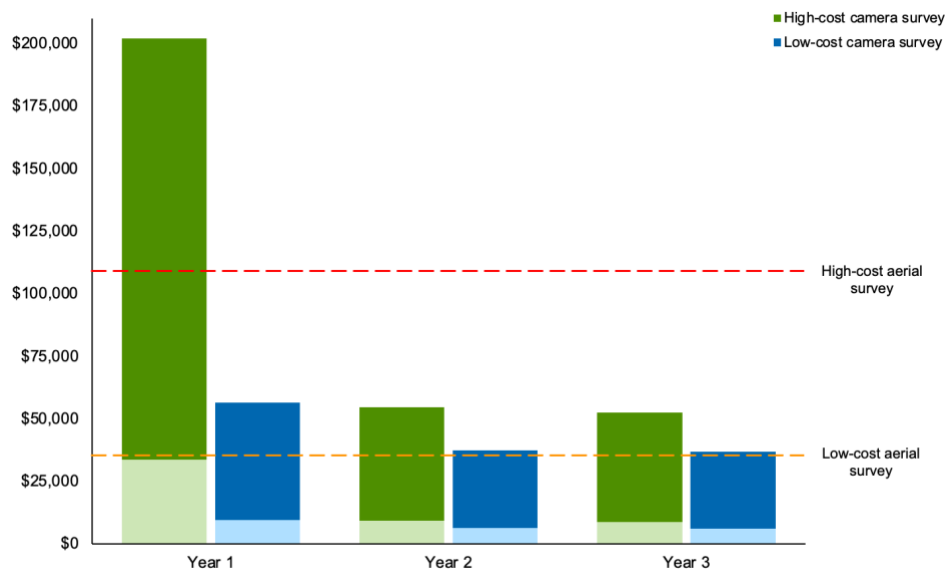
Figure 1. Comparison of high- and low-cost camera and aerial surveys. Dark bars represent the total estimated cost of camera projects, including camera equipment, field needs and image storage/processing; light bars represent an additional 20% contingency fund. Year 1 includes camera units as an expense; subsequent years exclude camera units as an expense. From Year 3 onwards, expenses should remain steady. Dashed lines represent the estimated cost of aerial surveys covering the same areas as the camera trap networks; this cost remains fixed over time (barring inflation, changes to aircraft rental policy, etc.). Aerial survey costs also included a 20% contingency fund.
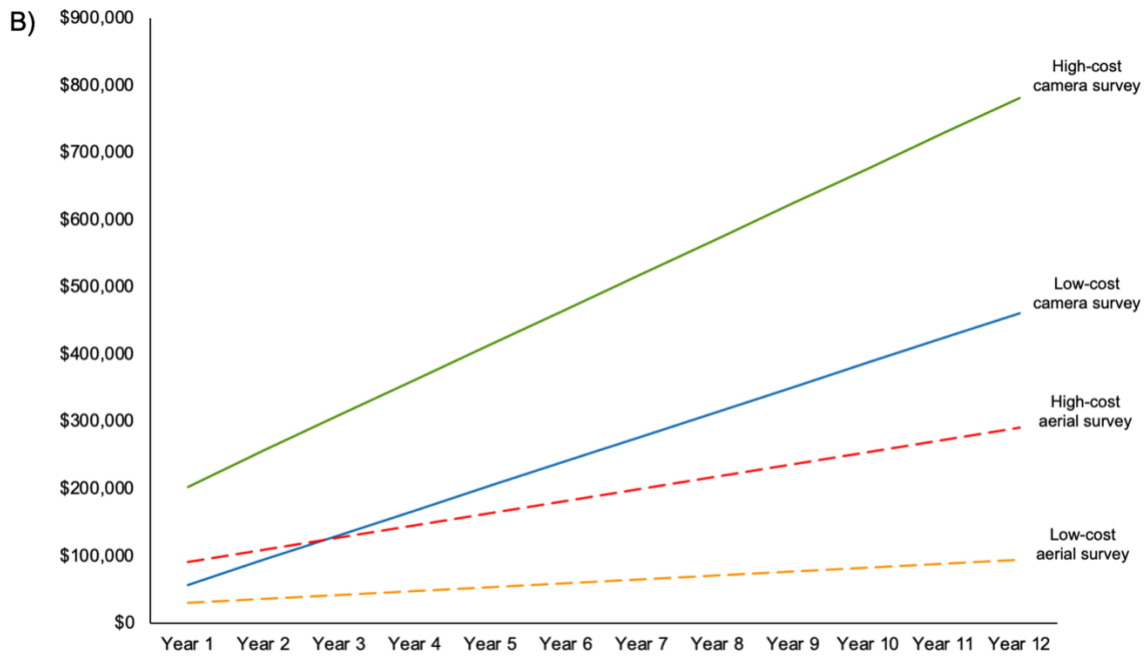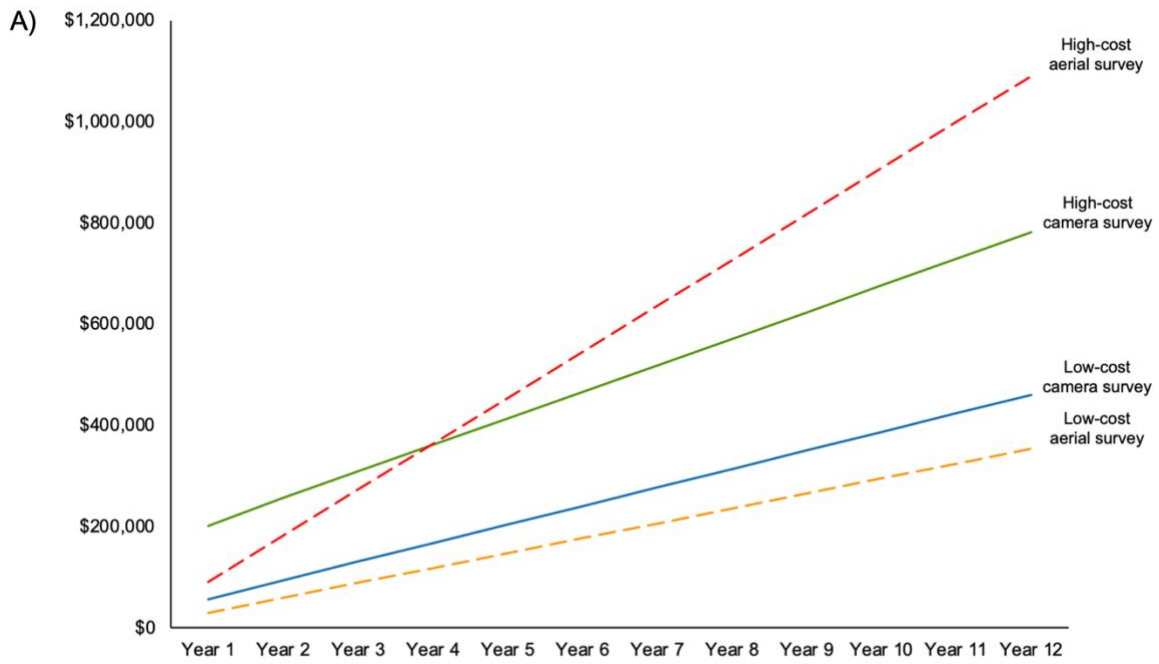
Figure 2. A) Cumulative cost of yearly aerial and camera trap surveys. B) Cumulative costs of yearly camera trap surveys and aerial surveys every 5 years. Camera trap and aerial survey costs include a 20% contingency fund.

Literature Cited

British Columbia Ministry of Sustainable Resource Management. *Aerial-Based Inventory Techniques for Selected Ungulates: Bison, Mountain Goat, Mountain Sheep, Moose, Elk, Deer and Caribou*. Version 2.0--. Vol. no. 32.;no. 32; Book, Whole. Victoria, B.C.: Resources Inventory Committee, 2002. https://go.exlibris.link/L4htVzB3.

Davis, Amy J., David A. Keiter, Elizabeth M. Kierepka, Chris Slootmaker, Antoinette J. Piaggio, James C. Beasley, Kim M. Pepin, and Aiken Savannah River Site (SRS) SC (United States). Savannah River Ecology Lab. (SREL). "A Comparison of Cost and Quality of Three Methods for Estimating Density for Wild Pig (Sus Scrofa)." *Scientific Reports* 10, no. 1 (2020): 2047–2047. https://doi.org/10.1038/s41598-020-58937-0.

Dertien, Jeremy S., Paul F. Doherty, Calvin F. Bagley, John A. Haddix, Aleya R. Brinkman, and Elizabeth S. Neipert. "Evaluating Dall's Sheep Habitat Use via Camera Traps." *The Journal of Wildlife Management* 81, no. 8 (2017): 1457–67. https://doi.org/10.1002/jwmg.21308.

Hedwig, Daniela, Ivonne Kienast, Matthieu Bonnet, Bryan K. Curran, Amos Courage, Christophe Boesch, Hjalmar S. Kühl, and Tony King. "A Camera Trap Assessment of the Forest Mammal Community within the Transitional Savannah-forest Mosaic of the Batéké Plateau National Park, Gabon." *African Journal of Ecology* 56, no. 4 (2018): 777–90. https://doi.org/10.1111/aje.12497.

Hessami, Mateen A. "Estimating Juvenile Recruitment of Elk in an Occupancy Modeling Framework," 2019. https://scholarworks.umt.edu/utpp/252/.

Kucera, Thomas E., and Reginald H. Barrett. "A History of Camera Trapping." In *Camera Traps in Animal Ecology*, 9–26. Tokyo: Springer Japan, 2011. https://doi.org/10.1007/978-4-431-99495-4_2.

Murray, Maureen H., Mason Fidino, Elizabeth W. Lehrer, Juniper L. Simonis, and Seth B. Magle. "A Multi-state Occupancy Model to Non-invasively Monitor Visible Signs of Wildlife Health with Camera Traps That Accounts for Image Quality." *The Journal of Animal Ecology* 90, no. 8 (2021): 1973–84. https://doi.org/10.1111/1365-2656.13515.

Poole, Kim G., and Darryl M. Reynolds. "Mt. Meager Mountain Goat Survey and DNA Census, 2009," March 2010.

Sashika, Mariko, Michito Shimozuru, Toshio Tsubota, Masanao Nakanishi, Mina Jimbo, Yuri Shirane, Fumihiko Mori, Tsuyoshi Ishinazaka, Tsutomu Mano, and Masami Yamanaka. "Development of a Noninvasive Photograph-Based Method for the Evaluation of Body Condition in Free-Ranging Brown Bears." *PeerJ (San Francisco, CA)* 8, no. Journal Article (2020): e9982–e9982. https://doi.org/10.7717/peerj.9982.

Smith, J. A., J. P. Suraci, J. S. Hunter, K. M. Gaynor, C. B. Keller, M. S. Palmer, J. L. Atkins, et al. "Zooming in on Mechanistic Predator-Prey Ecology: Integrating Camera Traps with Experimental Methods to Reveal the Drivers of Ecological Interactions." Edited by Ben Dantzer. *The Journal of Animal Ecology* 89, no. 9 (2020): 1997–2012. https://doi.org/10.1111/1365-2656.13264.

Sun, Catherine, Christopher Beirne, Joanna M. Burgar, Thomas Howey, Jason T. Fisher, A. Cole Burton, Marcus Rowcliffe, and Tim Hofmeester. "Simultaneous Monitoring of Vegetation Dynamics and Wildlife Activity with Camera Traps to Assess Habitat Change." Edited by Marcus Rowcliffe and Tim Hofmeester. *Remote Sensing in Ecology and Conservation* 7, no. 4 (2021): 666–84. https://doi.org/10.1002/rse2.222.

Windell, Rebecca M., Jesse S. Lewis, Ashley R. Gramza, and Kevin R. Crooks. "Carnivore Carrying Behavior as Documented with Wildlife Camera Traps." *Western North American Naturalist* 79, no. 4 (2019): 471–80. https://doi.org/10.3398/064.079.0401.