# 03\_mod\_approach

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# POST-DEMO

## (#i\_mod\_viewshed\_dens\_est)=

# Viewshed density estimators

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| Question: | | | | |
| **Overview**  **Viewshed density estimators:** Methods used to estimate the abundance of unmarked populations from observations of animals that relate animal observations to the space directly sampled by each camera’s viewshed (Moeller\_et\_al\_2023); they result in viewshed density estimates that can be extrapolated to abundance within broader sampling frames (Gilbert\_et\_al\_2020; Moeller\_et\_al\_2023). | | | | |
| **Advanced** | | | | |
| **Figures & Videos** | | | | |
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| **Analytical tools & resources** | | | | |
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| **References**  (Alberta Remote Camera Steering Committee (RCSC)\_et\_al\_2023)  {{ ref\_intext\_clarke\_et\_al\_2023 }} | | | | |

## (#i\_mod\_mr)=

# Mark-resight (MR)

**notes**

* Capture-recapture technique (HIGHER) (<https://www.youtube.com/watch?v=Diq4A7QGknM>)

## (#i\_mod\_smr)=

# Spatial mark-resight (SMR)

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| **Advanced - How the Model Works {{ ref\_intext\_clarke\_et\_al\_2023 }}**  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 markresight 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:  ```{figure} ../03\_images/03\_image\_files/clarke\_et\_al\_2023\_eqn\_smr1.png  :width: 80px  :align: center  ```  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 & 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 submodel 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  0.2; Sollmann\_et\_al\_2013a, Whittington\_et\_al\_2018, Williams\_et\_al\_2002). | | | | | |
| **Assumptions** | | **Pros** | | **Cons** | |
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| **Figures & Videos** | | | | | |
| A diagram of a graph  Description automatically generated with medium confidence  ```{figure} ./03\_images/whittington et al.-2018\_fig1.png  :align: center  ``` | | | A screenshot of a map  Description automatically generated  ```{figure} ./03\_images/SECR\_creemmural.org\_secr.png  :align: center  ``` | | |
| **Analytical tools & resources** | | | | | |
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| **References**  {{ ref\_intext\_clarke\_et\_al\_2023 }}  Sollmann\_et\_al\_2013a, Whittington\_et\_al\_2018, Williams\_et\_al\_2002  Jiménez\_et\_al\_2019) | | | | | |

**notes**

## (#i\_mod\_sc)=

# Spatial count (SC) model / Unmarked spatial capture-recapture

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| **Overview - How the Model Works** | | | | | |
| Advanced - How the Model Works **{{ ref\_intext\_clarke\_et\_al\_2023 }}**  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 trapspecific counts to estimate the number and location of activity centres (Royle\_et\_al\_2014, Sun\_et\_al\_2022). <br>  <br>  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 & 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 & Royle, 2013, Sun\_et\_al\_2022).  To relate trap-specific counts to detection histories, we use the equation:  A black and white math equation  Description automatically generated  clarke\_et\_al\_2023\_eqn\_sc1.png  <br>  where 𝑛𝑗𝑘 is the count of animals at sampling location \*𝑗\* and during sampling period \*𝑘\*; \*𝑁\* is population size; and 𝑦𝑖𝑗𝑘 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 𝑛𝑗𝑘  – 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).  <br>  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:  A black and white math formula  Description automatically generated with medium confidence  clarke\_et\_al\_2023\_eqn\_sc2.png  where 𝑀 ≫ 𝑁 and 𝜔𝑖 is the probability of existence of individual 𝑖 within population 𝑁 (Chandler & Royle, 2013, Sun\_et\_al\_2022). 𝜔𝑖 is Bernoulli distributed – an animal can be present (i.e., 𝜔𝑖 = 1) or absent (i.e., 𝜔𝑖 = 0) – and depends on the number of detections at traps and the distance between traps and individuals’ activity centres (Chandler & Royle, 2013, Sun\_et\_al\_2022).<br>  <br>  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 & Royle, 2013, Royle\_et\_al\_2014). We will refer to camera traps for the remainder of this section. <br>  <br>  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 & 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 & Royle, 2013). Grid or clustered designs may be best (Burgar\_et\_al\_2019, Clark, 2019, Sun\_et\_al\_2014).<br>  **## Simulations and Field Experiments {{ ref\_intext\_clarke\_et\_al\_2023 }}**  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-toyear (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 ({{ ref\_intext\_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-Resigh*t) and the spatial partial identity model (SPIM; see *2.3.2 Spatial Partial Identity Model*) – which estimate density over a defined area. | | | | | |
| **Assumptions** | | **Pros** | | **Cons** | |
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| **Figures & Videos** | | | | | |
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| SC models with the ‘nimble’ package (de Valpine\_et\_al\_2017 |  | |  | |  |
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| **References**  {{ ref\_bib\_clarke\_et\_al\_2023 }}  {{ ref\_bib\_royle\_et\_al\_2014 }}  {{ ref\_bib\_sun\_et\_al\_2022 }}  {{ ref\_bib\_burgar\_et\_al\_2018 }}  {{ ref\_bib\_burgar\_et\_al\_2019 }}  {{ ref\_bib\_chandler\_royle\_2013 }}  {{ ref\_bib\_sollmann\_2018 }}  {{ ref\_bib\_evans\_rittenhouse\_2018 }} | | | | | |

**notes**

## (#i\_mod\_catspim)=

# Categorical partial identity model (catSPIM) (Augustine\_et\_al\_2019; Sun\_et\_al\_2022)

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| **Overview - How the Model Works** | | | |
| **Advanced - How the Model Works {{ ref\_intext\_clarke\_et\_al\_2023 }}**  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.   **## Simulations and Field Experiments {{ ref\_intext\_clarke\_et\_al\_2023 }}**  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. | | | |
| **Analytical tools & resources** | | | |
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| SPIMswith the ‘SPIM’ package (Augustine\_et\_al\_2019) | https://rdrr.io/github/benaug/SPIM/ |  | Models fit: 2-flank SPIM, categorical SPIM, categorical conventional and generalized Spatial Mark Resight |
|  |  |  |  |
| **References**  Augustine\_et\_al\_2019  Sun\_et\_al\_2022  Clarke, J., Bohm, H., Burton, C., & Constantinou, A. (2023). Using Camera Traps to Estimate Medium and Large Mammal Density: Comparison of Methods and Recommendations for Wildlife Managers. <https://doi.org/10.13140/RG.2.2.18364.72320> | | | |

**notes**

## (#i\_mod\_2flankspim)=

# Spatial Partial Identity Model (2-flank SPIM)

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| **Advanced - How the Model Works {{ ref\_intext\_clarke\_et\_al\_2023 }}**  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 **Link**ed 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). Partiallyidentifying 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** | | **Pros** | | | **Cons** | |
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| **Simulations and Field Experiments {{ ref\_intext\_clarke\_et\_al\_2023 }}**  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). | | | | | | |
| **Figures & Videos** | | | | | | |
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**notes**

## (#i\_mod\_ds)=

# Distance sampling (DS)

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| **Advanced - How the Model Works {{ ref\_intext\_clarke\_et\_al\_2023 }}**  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; {{ ref\_intext\_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 ({{ ref\_intext\_morin\_et\_al\_2022 }}). t ({{ ref\_intext\_buckland\_et\_al\_2015 }}; {{ ref\_intext\_gilbert\_et\_al\_2021 }}).  A graph of a number of data  Description automatically generated  ```{figure} .//03\_images/03\_image\_files/clarke\_et\_al\_2023/clarke\_et\_al\_2023\_fig6\_clipped.png  :align: center  ```  Figure 6. An example detection function. The probability of detecting an animal decreases with increasing distance from the observer.  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 ({{ ref\_intext\_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 ({{ ref\_intext\_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 a fraction of a circle ({{ ref\_intext\_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:    ```{figure} .//03\_images/03\_image\_files/clarke\_et\_al\_2023/Clarke\_et\_al\_2023\_eqn\_ds1.png  :align: center  ```  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 ({{ ref\_intext\_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\* ({{ ref\_intext\_howe\_et\_al\_2017 }}). If that same camera has a viewshed angle of 𝜃 radians, the fraction of a circle it samples is  ```{figure} .//03\_images/03\_image\_files/clarke\_et\_al\_2023/Clarke\_et\_al\_2023\_eqn\_ds2.png  :align: center  ```  Taken together, sampling effort can therefore be expressed as:    ```{figure} .//03\_images/03\_image\_files/clarke\_et\_al\_2023/Clarke\_et\_al\_2023\_eqn\_ds3.png  :align: center  ```  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 ({{ ref\_intext\_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 ≤ 𝑟 ≤ 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, {{ ref\_intext\_howe\_et\_al\_2017 }}); 2) placing permanent reference objects at known distances from the camera so they are visible in every capture ({{ ref\_intext\_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/PJcs/DistanceEstimationTracking)](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 ({{ ref\_intext\_howe\_et\_al\_2017 }}; {{ ref\_intext\_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:  A black and white image of a mathematical equation  Description automatically generated  ```{figure} ../03\_images/03\_image\_files/clarke\_et\_al\_2023/clarke\_et\_al\_2023\_eqn\_ds4.png  :align: center  ```  where \*𝐷<sub>𝐶</sub>\* is the corrected density estimate and 𝑎 is activity level ({{ ref\_intext\_howe\_et\_al\_2017 }}; {{ ref\_intext\_palencia\_et\_al\_2021 }}). Activity level is determined as per Rowcliffe\_et\_al\_(2014).  **## Simulations & Field Experiments {{ ref\_intext\_clarke\_et\_al\_2023 }}**  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  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<sup>2</sup> and 6.25 camera traps/km<sup>2</sup> ({{ ref\_intext\_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 ({{ ref\_intext\_howe\_et\_al\_2017 }}). The researchers collected video data.  Another study in northwestern Africa found that the DS model performed variably for different species ({{ ref\_intext\_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, {{ ref\_intext\_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 ({{ ref\_intext\_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; {{ ref\_intext\_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 ({{ ref\_intext\_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 clumpilydistributed) 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; {{ ref\_intext\_Twining\_et\_al\_2022 }}). While all methods produced densities within accepted ranges, DS tended to underestimate density ({{ ref\_intext\_Twining\_et\_al\_2022 }}).  {{ ref\_intext\_Twining\_et\_al\_2022 }}  Després-Einspenner\_et\_al\_2017 |
| **References**  {{ ref\_intext\_clarke\_et\_al\_2023 }}  {{ ref\_intext\_howe\_et\_al\_2017 }}  {{ ref\_bib\_twining\_et\_al\_2022 }}  {{ ref\_intext\_palencia\_et\_al\_2021 }} |

**notes**

## (#i\_mod\_tte)=

# Time-to-event (TTE)

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| **Advanced - How the Model Works {{ ref\_intext\_clarke\_et\_al\_2023 }}**  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 ({{ ref\_intext\_loonam\_et\_al\_2021b }}). A TTE model might be used in medicine, for example, to approximate time from diagnosis until remission or death ({{ ref\_intext\_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 ({{ ref\_intext\_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 ({{ ref\_intext\_jennelle\_et\_al\_2002 }}, {{ ref\_intext\_moeller\_et\_al\_2018 }}, {{ ref\_intext\_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 ({{ ref\_intext\_lukacs\_2021 }}; {{ ref\_intext\_moeller\_et\_al\_2018 }}).  The equation for camera data-based density estimation using TTE is:  ```{figure} ../03\_images/03\_image\_files/clarke\_et\_al\_2023/clarke\_et\_al\_2023\_eqn\_tte1.png  :align: center  ```  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:  ```{figure} .//03\_images/03\_image\_files/clarke\_et\_al\_2023/clarke\_et\_al\_2023\_eqn\_tte2.png  :align: center  ```  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 ({{ ref\_intext\_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; {{ ref\_intext\_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 ({{ ref\_intext\_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 ({{ ref\_intext\_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\* ({{ ref\_intext\_moeller\_et\_al\_2018 }}).  ```{figure} ../03\_images/03\_image\_files/clarke\_et\_al\_2023/clarke\_et\_al\_2023\_fig10\_clipped.png  :align: center  ```  **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 ({{ ref\_intext\_moeller\_et\_al\_2018 }}). Thus, practitioners need measures of animal movement speed. | | | | | | |
| **Assumptions** | | **Pros** | | | **Cons** | |
|  | |  | | |  | |
| **Simulations and Field Experiments {{ ref\_intext\_clarke\_et\_al\_2023 }}**  Simulations show that:  - The TTE model tends to underestimate population density. In both walk ({{ ref\_intext\_loonam\_2019 }}) and random walk simulations ({{ ref\_intext\_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 ({{ ref\_intext\_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 ({{ ref\_intext\_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; {{ ref\_intext\_moeller\_et\_al\_2018 }}). Neither appeared to impact TTE estimates – indicating that the model applies well to actual populations, which often violate these assumptions ({{ ref\_intext\_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 ({{ ref\_intext\_loonam\_et\_al\_2021a }}). Density estimates could have been biased and misleadingly precise, however, because of non-random camera placement ({{ ref\_intext\_loonam\_et\_al\_2021a }}, {{ ref\_intext\_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*; {{ ref\_intext\_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*; {{ ref\_intext\_jensen\_et\_al\_2022 }}). | | | | | | |
| **Figures & Videos** | | | | | | |
| ```{figure} .//03\_images/03\_image\_files/clarke\_et\_al\_2023/clarke\_et\_al\_2023\_fig11\_clipped.png  :align: center  ```  **Figure 11.** Simple diagrams showing dispersed, clumped and Poisson-distributed animals (red dots) in space.  {{ ref\_intext\_clarke\_et\_al\_2023 }} | | |  | | | |
| **Analytical tools & resources** | | | | | | |
| **Name** | **Link** | | | **Reference** | | **Additional\_info** |
| spaceNtime: an R package for estimating abundance of unmarked animals using camera-trap photographs | <https://github.com/annam21/spaceNtime>  <https://link.springer.com/article/10.1007/s42991-021-00181-8> | | |  | | free and open-source R package designed to assist in the implementation of the STE and TTE models, along with the IS estimator  A diagram of a process flow  Description automatically generated  The spaceNtime workflow for count data. The user will go through five major steps for STE, TTE, and IS analyses. If the user has presence/absence (0 and 1) data instead of count data, the IS analysis is not appropriate, and the IS pathway should be removed from the flowchart |
|  |  | | |  | |  |
| **References**  {{ ref\_bib\_clark\_et\_al\_2003 }}  {{ ref\_bib\_clarke\_et\_al\_2023 }}  {{ ref\_intext\_jennelle\_et\_al\_2002 }}  {{ ref\_bib\_jensen\_et\_al\_2022 }}  {{ ref\_bib\_loonam\_et\_al\_2021a }}  {{ ref\_bib\_loonam\_et\_al\_2021b }}  ({{ ref\_bib\_lukacs\_2021 }}  {{ ref\_bib\_moeller\_et\_al\_2018 }}  {{ ref\_bib\_morin\_et\_al\_2022 }} | | | | | | |

**notes**

## (#i\_mod\_ste)=

# Space-to-event (STE)

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| **Space-to-event (STE) model ({{ ref\_intext\_moeller\_et\_al\_2018 }}):** A method used to estimate abundance or density that accounts for variable detection probability through the use of time-lapse images and is unaffected by animal movement rates (collapses sampling intervals to an instant in time, and thus estimates are unaffected by animal movement rates) ({{ ref\_intext\_moeller\_et\_al\_2018 }}). | | | | | | |
| **Overview - How the Model Works** | | | | | | |
| Advanced - How the Model Works {{ ref\_intext\_clarke\_et\_al\_2023 }} 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 ({{ ref\_intext\_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, {{ ref\_intext\_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.  A forest with mossy ground  Description automatically generated  ```{figure} .//03\_images/03\_image\_files/clarke\_et\_al\_2023/Clarke\_et\_al\_2023\_Fig12.png  :align: center  ```  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 ({{ ref\_intext\_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 ({{ ref\_intext\_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 m2, might look like: {NA, 40 m2, NA, NA, 1180 m2, NA, 800 m2}, where 40 m2 indicates that images from 2 cameras had to be drawn before observing an animal, 1180 m2 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 ({{ ref\_intext\_moeller\_et\_al\_2018 }}).  A black background with a white arrow  Description automatically generated  ```{figure} .//03\_images/03\_image\_files/clarke\_et\_al\_2023/Clarke\_et\_al\_2023\_Fig11\_clipped.png  :align: center  ```  **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.  As with the TTE, the average area of a camera viewshed is calculated using the equation:  A mathematical equation with numbers  Description automatically generated  ```{figure} .//03\_images/03\_image\_files/clarke\_et\_al\_2023\_eqn\_tte2\_ste1.png  :align: center  ```  where 𝑟 is detection distance and 𝜃 is the angle of the camera lens in degrees ({{ ref\_intext\_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 ({{ ref\_intext\_gilbert\_et\_al\_2021 }}, {{ ref\_intext\_moeller\_et\_al\_2018 }}). | | | | | | |
| **Simulations and Field Experiments {{ ref\_intext\_clarke\_et\_al\_2023 }}**  Random walk simulations show that the STE – unlike the TTE – is insensitive to movement speed ({{ ref\_intext\_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 ({{ ref\_intext\_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). STEderived 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 markrecapture and the random encounter model (REM; see *2.2.3 Random Encounter Model*; {{ ref\_intext\_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 ({{ ref\_intext\_loonam\_et\_al\_2021a }}). The STE may therefore still be an efficient alternative to DNA markrecapture. | | | | | | |
| **Assumptions** | | **Pros** | | | **Cons** | |
|  | |  | | |  | |
| **Figures & Videos** | | | | | | |
| A screenshot of a screen  Description automatically generated  ```{figure} ./03\_images/{{ ref\_intext\_moeller\_et\_al\_2018 }}\_Fig3.png  :align: center  ```  Conceptual diagram of the space to event (STE) model. The circular sectors represent three different cameras on two different occasions (a-b). On each occasion j = 1, 2,. . ., J, we randomly order the cameras i = 1, 2,. . ., M. If the first animal detection is in the nth camera, the observed STE S j is the sum of the areas of cameras 1, 2,. .. n. (a) On occasion j = 1, camera 1 contains at least one animal, so we record the space to first event S j=1 = a 1. (b) On occasion j = 2, cameras 2 and 3 both contain animals, but we use the first camera in the series. Therefore, we record the space to first event S j=1 = a 1 + a 2 . | | | |  | | |
| **Analytical tools & resources** | | | | | | |
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|  |  | |  | | |  |
| **References**  {{ ref\_intext\_clarke\_et\_al\_2023 }} | | | | | | |

**notes**

* should be neither attracted to nor repelled by the cameras, so sites should be unbaited and minimally disturbed

## (#i\_mod\_ste\_tte\_is)=

# STE/TTE/IS

**notes**

{{ ref\_intext\_moeller\_et\_al\_2018 }}

are distributed following a Poisson distribution at the camera level. For elk on a small spatial and temporal scale, this is a relatively realistic approximation of movement, but it may not apply to all species. It is worth noting that the REM and SC models make explicit assumptions about animal movement as well ({{ ref\_intext\_rowcliffe\_et\_al\_2008 }}, Royle\_et\_al\_2014). Further simulations would be useful in determining how robust these methods are to violations of this assumption, especially by social or

* {{ ref\_intext\_moeller\_et\_al\_2018 }} – TTE / STE / IS -- Animals should be neither attracted to nor repelled by the cameras, so sites should be unbaited and minimally disturbed.

## (#i\_mod\_is)=

# Instantaneous sampling (IS)

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| **Instantaneous sampling (IS) ({{ ref\_intext\_moeller\_et\_al\_2018 }}):** A method used to estimate abundance or density from time-lapse images from randomly deployed cameras; the number of unique individuals (the count) is needed ({{ ref\_intext\_moeller\_et\_al\_2018 }}). | | | | | |
| **Overview - How the Model Works** | | | | | |
| **Advanced - How the Model Works {{ ref\_intext\_clarke\_et\_al\_2023 }}**  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 ({{ ref\_intext\_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 ({{ ref\_intext\_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:    ```{figure} .//03\_images/03\_image\_files/clarke\_et\_al\_2023/Clarke\_et\_al\_2023\_eqn\_is1.png  :align: center  ```  where 𝐽 is the total number of sampling occasions, 𝑀 is the total number of camera stations, and 𝑛𝑚𝑗 is the count of animals in the viewshed and 𝑎𝑚𝑗 is the area of the viewshed at station 𝑚 on sampling occasion 𝑗 ({{ ref\_intext\_moeller\_et\_al\_2018 }}). | | | | | |
| **Assumptions** | | **Pros** | | **Cons** | |
|  | |  | |  | |
| **Simulations and Field Experiments {{ ref\_intext\_clarke\_et\_al\_2023 }}**  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 ({{ ref\_intext\_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 ({{ ref\_intext\_moeller\_et\_al\_2018 }}). | | | | | |
| **Figures & Videos** | | | | | |
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| **Analytical tools & resources** | | | | | |
| **Name** | **Link** | | **Reference** | | **Additional\_info** |
| jpe13913-sup-0002-appendixs2.mp4 | <<https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/1365-2664.13913>> Supporting Information | | ({{ ref\_intext\_palencia\_et\_al\_2021 }}) | | Video describing the estimatation of parameters to apply REM, REST, and DS |
| jpe13913-sup-0004-appendixs4.mp4 | <<https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/1365-2664.13913>> Supporting Information | | ({{ ref\_intext\_palencia\_et\_al\_2021 }}) | | Burst inconstistency record |
|  |  | |  | |  |
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| **References**  {{ ref\_intext\_clarke\_et\_al\_2023 }} | | | | | |

**notes**

# POST-DEMO 2

## (#i\_mod\_rai\_poisson)=\*\*\*

# Poisson model

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| info\_id |  | | | | | | |
| **Poisson regression:** A regression model for count data used when data are not overdispersed or zero-inflated (Lambert, 1992). [relative abundance indices] | | | | | | | |
| **Overview - How the Model Works** | | | | | | | |
| Advanced - How the Model | | | | | | | |
| **Assumptions** | | | **Pros** | | | **Cons** | |
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| **Figures & Videos** | | | | | | | |
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| **Analytical tools & resources** | | | | | | | |
| **Name** | | **Link** | | **Reference** | | | **Additional\_info** |
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| **References** | | | | | | | |

**notes**

## (#i\_mod\_rai\_nb)=\*

# Negative binomial (NB) model

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| **Negative binomial (NB) regression (Mullahy, 1986):** A regression model used for count data with overdispersion but without zero-inflation. [relative abundance indices] | | | | | | |
| **Overview - How the Model Works** | | | | | | |
| **Advanced - How the Model** | | | | | | |
| **Assumptions** | | **Pros** | | | **Cons** | |
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| **Figures & Videos** | | | | | | |
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| **Analytical tools & resources** | | | | | | |
| **Name** | **Link** | | **Reference** | | | **Additional\_info** |
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| **References** | | | | | | |

**notes**

## (#i\_mod\_rai\_zinb)=\*

# Zero-inflated negative binomial (ZINB)

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| **Zero-inflated negative binomial (ZINB) regression (McCullagh & Nelder, 1989):** A regression model used in the setting of excess zeros (zero-inflation) and overdispersion. This approach is a two-part model, where the zero-inflation is modelled separately from the counts and assumes that the count (abundance) is "conditional" on the zero-inflation model (occurrence) model. [relative abundance indices] | | | | | | |
| **Overview - How the Model Works** | | | | | | |
| **Advanced - How the Model** | | | | | | |
| **Assumptions** | | **Pros** | | | **Cons** | |
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| **Figures & Videos** | | | | | | |
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**notes**

## (#i\_mod\_rai\_zip)=\*

# Zero-inflated poisson (ZIP)

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| **Zero-inflated Poisson (ZIP) regression (Lambert, 1992**): A regression model for count data that both follows the Poisson distribution and contains excess zeros (Lambert, 1992). ZIP models are only appropriate for data for which the overdispersion is not solely due to zero-inflation. [relative abundance indices] | | | | | | |
| **Overview - How the Model Works** | | | | | | |
| **Advanced - How the Model**  “Zero-inflated Poisson models (hereafter ZIP; Lambert 1992) fit two linear models simultaneously to address the sources of zero-inflation (probability of a zero value; inversely, probability of occurrence) separately from zeros that belong to the count distribution (Lambert 1992; Blasco‐Moreno\_et\_al\_2019). The zero-inflation model-part is a logistic regression, and since counts are repeatedly measured over time, the binary response serves as a detection history (Dénes\_et\_al\_2015). Thus, the zero-inflation model-part can include predictors of “false” zeros (e.g., imperfect detection) and “true” zeros that relate to occurrence (Lambert 1992; Blasco-Moreno\_et\_al\_2019). Additionally, this model-part can also mitigate problematic variability from other “false” zeros (e.g., not present but generally occurs, or uses the feature, but not at that site). The second model-part is a Poisson model used to assess predictors of the counts (relative abundance given presence [Lambert 1992; Wenger and Freeman 2008]).” | | | | | | |
| **Assumptions** | | **Pros** | | | **Cons** | |
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| **Figures & Videos** | | | | | | |
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| **Analytical tools & resources** | | | | | | |
| Name | **Link** | | **Reference** | | | **Additional\_info** |
| glmmTMB: Generalized Linear Mixed Models using Template Model Builder | https://cran.r-project.org/web/packages/glmmTMB/index.html | |  | | |  |
| zicounts | https://github.com/cran/zicounts | |  | | |  |
| R package DHARMa (Hartig, 2019) | https://CRAN.R-project.org/package=DHARMa | | Hartig, F., 2019. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.2.2. https://CRAN.R-project.org/package=DHARMa | | | Can be used to assess goodness-of-fit of a mixed effect hurdle model via quantile–quantile (Q–Q) plots of standardized residuals  DHarma  we have made extensive simulations, which have shown that the various tests have certain advantages and disadvantages. The basic results are that:   * The most powerful and reliable test is option 3, but this costs a lot of time and is not available for all regression packages, as it requires that Pearson residuals are available * Option 2, the parametric Pearson-chi2 is fast if Pearson residuals are available, but based on a naive expectation of df (counts RE as 1 df) and the test statistic is thus biased towards underdispersion for mixed models. Similar to the df approximation, Bias increasing with the number of RE levels. When testing only for overdispersion (alternative = “greater”), this makes the test more conservative, but it also costs power. * The DHARMa default option 1 is fast, nearly unbiased (i.e. you can test under and overdispersion), and only slightly less powerful as test 3, PROVIDED that simulations are made conditional on the fitted REs. Note that the latter is not the DHARMa default, so you have to actively request conditional simulations, e.g. for lme4 by specifying re.form = NULL. Power compared to the parametric Pearson-chi2 test depends on the number of RE levels, it will be more powerful for typical number of RE levels. |
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**notes**

## (#i\_mod\_rai\_hurdle)=\*

# Hurdle model

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| **Overview - How the Model Works** | | | | | | |
| **Advanced - How the Model Works**   * Hurdle models differ from traditional linear models in that two linear models are fitted simultaneously to count data.---(Markle\_et\_al\_2020)   + Hurdle models are used to address overdispersion in count data by fitting two linear models that assess the sources of abundant zeros and positive counts, simultaneously (Mullahy, 1986)(McCullagh & Nelder 1989; Hinde & Deme´trio 1998; Poortema 1999).---(Martin, 2005) * “Hurdle models suggest a two-part process. The first part induces an event, and once the hurdle to the first event has been cleared, the second part determines the number of subsequent events.”---(Martin, 2005)   + “The first of these was a logistic linear model (can be used to model prevalence) and the second was a truncated Poisson or negative binomial linear model.” ---(Markle\_et\_al\_2020)     - “The first model is a logistic regression used to evaluate what factors influence whether a zero value occurs (i.e. for a given sample camera month, does a visit or not (Mullahy, 1986).”---(Martin, 2005)   + If a positive value does occur, the ‘hurdle’ is cleared, and those non-zero values are considered in the second linear model as a truncated Poisson to determine what factors influence the level of positive values {Mullahy, 1986 #900}.---(Martin, 2005) * The distribution of a hurdle model is best characterized by the zero-truncated “version of the parent distribution” {Mullahy, 1986 #900}(rather than positive values ).---(Mullahy, 1986) * Similar to most linear models, hurdle models have assumptions regarding independence of observations, error distributions, and linearity.---(Markle\_et\_al\_2020)   Model evaluation & fit   * You can evaluate autocorrelation in a hurdle model by evaluating residual plots of model fit via the R package pscl (Zeileis\_et\_al\_2008)---(Markle\_et\_al\_2020) * If autocorrelation is present, you might consider including random effects (mixed-effects hurdle model) (Molenberghs and Verbeke, 2005)---(Markle\_et\_al\_2020) * Goodness-of-fit of a mixed effect hurdle model can be assessed using rootograms (Kleiber and Zeileis, 2016) implemented in R package countreg (Zeileis\_et\_al\_2008), and quantile–quantile (Q–Q) plots of standardized residuals using R package DHARMa (Hartig).   Hurdle models vs Zero-inflated Poisson models (ZIP) regression models   * “Hurdle models are very similar to zero-inflated Poisson models (ZIP) regression models, except that in hurdle models, the distribution is dependant only on the truncated values (Mullahy, 1986), whereas, in a standard ZIP, the distribution of the positive values also relates to the probability of a zero outcome (Mullahy, 1986).” ---(Martin, 2005) * “Standard zero-inflated Poisson models are useful to differentiate between zeros that occur because of some other process or as a result of sampling error.” ---(Martin, 2005) * “Whereas hurdle models can more useful when only true sampling zeros are present and….In that case, the intersection of zero-values and non-zero values represent an inflection point between two processes.” ---(Martin, 2005) | | | | | | |
| **Assumptions** | | **Pros** | | | **Cons** | |
| Independence of observations, error distributions, and linearity (Markle\_et\_al\_2020) | |  | | |  | |
| **Figures & Videos** | | | | | | |
| Video: [Using Hurdle Models to Analyze Zero-Inflated Count Data](https://www.youtube.com/watch?v=CvM6j8hE8lE)  https://www.youtube.com/watch?v=CvM6j8hE8lE | | | | Video: [Hurdle models](https://www.youtube.com/watch?v=q2NRQBcihQY)  https://www.youtube.com/watch?v=q2NRQBcihQY | | |
|  | | | |  | | |
| **Analytical tools & resources** | | | | | | |
| Name | **Link** | | **Reference** | | | **Additional\_info** |
| R package “DHARMa” | <https://CRAN.R-project.org/package=DHARMa> | | Hartig, F., 2019. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.2.2. https://CRAN.R-project.org/package=DHARMa | | | Can be used to assess goodness-of-fit of a mixed effect hurdle model via quantile–quantile (Q–Q) plots of standardized residuals |
| R package “countreg” | <https://rdrr.io/rforge/countreg/>  <https://rdrr.io/rforge/countreg/f/inst/doc/countreg.pdf>  https://www.zeileis.org/papers/Kleiber+Zeileis-2016.pdf | | (Zeileis\_et\_al\_2008) | | | Can be used to assess goodness-of-fit of a mixed effect hurdle model via rootograms (Kleiber and Zeileis, 2016) |
| A guide to modeling outcomes that have lots of zeros with Bayesian hurdle lognormal and hurdle Gaussian regression models | https://www.andrewheiss.com/blog/2022/05/09/hurdle-lognormal-gaussian-brms/ | |  | | | but it cannot model correlation within individuals (sites) if they are sampled repeatedly (random effects) |
| R package “Pscl” |  | |  | | |  |
|  |  | |  | | |  |
|  |  | |  | | |  |
| **References**  (Blasco‐Moreno\_et\_al\_2019)  Hartig, F., 2019. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.2.2. [https://CRAN.R-project.org/package=DHARMa](https://cran.r-project.org/package=DHARMa)  (Heilbron, 1994)  (Kleiber & Zeileis, 2016)  (Markle\_et\_al\_2020)  (Martin\_et\_al\_2005)  (Mullahy, 1986)  (Welsh\_et\_al\_2000)  (Zeileis\_et\_al\_2008) | | | | | | |

**notes**

* **ECOL papers using hurdle refs:**The ecological literature has seen a recent upsurge of interest in techniques for dealing with excess zero values. Zero-inflated models have been applied in a range of ecological scenarios, including data sets with zero inflation caused by true zero (Welsh\_et\_al\_1996, 2000; Barry & Welsh 2002; Podlich\_et\_al\_2002; Kuhnert\_et\_al\_2005; Martin\_et\_al\_2005) and false-zero observations (Kery 2002; MacKenzie\_et\_al\_2002, 2003, 2004; Tyre\_et\_al\_2003; Wintle\_et\_al\_2004).
* …. As such, hurdle models often perform better than standard ZIP models when the ….{Martin, 2005 #913} and should be used when… {Lambert, 1992 #919}{Welsh, 2000 #920}{Martin, 2005 #913}